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WINNERS AND LOSERS IN REFORESTATION EFFORTS IN THE LOWER RIO GRANDE  
VALLEY OF TEXAS, AND THE PREDICTIVE POWER OF XYLEM ANATOMY ON  
LONG-TERM GROWTH AND SURVIVAL

A Thesis

by

CLIFTON F. ALBRECHT

Submitted to the Graduate College of  
the University of Texas Rio Grande Valley  
in partial fulfillment of the requirements for the degree of  
MASTER OF SCIENCE

May 2021

Major Subject: Biology



WINNERS AND LOSERS IN REFORESTATION EFFORTS IN THE LOWER RIO GRANDE  
VALLEY OF TEXAS, AND THE PREDICTIVE POWER OF XYLEM ANATOMY ON  
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May 2021



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## ABSTRACT

Albrecht, Clifton F., Winners and losers in reforestation efforts in the lower rio grande valley of texas, and the predictive power of xylem anatomy on long-term growth and survival. Master of Science (MS), May 2021, 89 pages, 7 Tables, 12 Figures, 136 references.

Reforestation has been ongoing in the Lower Rio Grande Valley of Texas annually since the 1980s. However, there has been little subsequent study of the change and development of those forests as they mature. This thesis consists of two studies: (1) surveys of a chronosequence of restored forests undertaken to assess long-term development therein, and (2) quantification of xylem anatomical traits of a subset of species present at these reforestation sites and comparison of those traits with species growth and survival metrics at a variety of time scales post-planting to assess predictive power. A reduction in species diversity and abundance was observed and a suite of species which predictably persist on the landscape was identified. Several highly competitive exotic grasses were seen to increase post-planting and to suppress regeneration of woody species. The suite of xylem anatomical traits show no predictive power on growth and survival post-planting.



## DEDICATION

This thesis is dedicated to the tough, beautiful flora of the Rio Grande Valley and to the people who love it. May these acacias perfume the spring air and the nightjars cry their strange cries for centuries hence.



## ACKNOWLEDGEMENTS

I express my sincere gratitude to everybody with whom I had the chance to work over the course of the studies reported here. Both projects required a great deal of time from many people, and the fact that we carried out not one, but two studies of this scale is a testament to their skill and dedication. Thanks to Krys Salazar and Zarek Contreras, who braved rattlesnakes, August heat and January chill, ticks, and thorns to bring the field research reported here to completion within two years. It was a pleasure to be out with y'all. My gratitude also to Kayla DeLeon, Maryam Khalil, Daniela Garcia, Jonnah Garza, and David Garza for their participation in the xylem anatomical study reported here. Thanks to Mylen Arias and Faeqa Mohsin for being wonderful colleagues and friends. Finally, thanks to Dr. Bradley Christoffersen, Dr. Engil Pereira, and Dr. Andrew McDonald for support, feedback, and guidance throughout this entire process.



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## CHAPTER I

### INTRODUCTION

Reforestation of the Lower Rio Grande Valley of Texas has been carried out annually since the early 1980s and, as of this publication, over 5 million seedlings have been planted across a total of at least 6475 ha in Cameron, Willacy, Hidalgo, and Starr Counties (Ewing and Best 2004, K. Wahl-Villareal personal communication). Despite the scale and duration of these efforts very little long-term monitoring of reforested sites has been carried out, and there consequently remain major open questions about forest regeneration and the overall effectiveness of the reforestation program. Unquantified observational evidence suggests both a long-term decline in species diversity and strong suppression of natural regeneration by several species of highly competitive invasive grasses, but these observations have not undergone rigorous testing before this point. Formal assessments of restored forests in this area may inform improvements in species selection and planting methods chosen by those directly managing restoration efforts, leading to increases in the effectiveness and/or efficiency of the project as it continues into the future. Furthermore, information on differential growth, survival, and recruitment rates of regionally native species in the context of reforestation may inform similar work in areas globally where a climate and species pool like those of south Texas coincide.

The staggered nature of reforested plots' development times in this region creates a situation conducive to the use of a chronosequence. Chronosequence studies, sometimes called

“space-for-time” studies, rely on a method in which surveys are made at sites which are identical in terms of initial state and environmental conditions and differ only in the duration for which they have been developing (Foster and Tilman 2000). If vegetation of all sites develops along the same trajectory, then the future state of a site which has been developing for a given amount of time can be predicted by the current state of a site which has been developing for a relatively longer period. This type of study has been applied successfully multiple times in tropical wet forests, but examples exist for ecosystems worldwide (Aide et al. 2000, Chazdon et al. 2010, Denslow & Guzman 2000, DeWalt et al. 2003, Druckenbrod et al. 2017, Feldpausch et al. 2007, Lebrija-Trejos et al. 2010, Letcher & Chazdon 2009, Letcher et al. 2012, Maza-Villalobos et al. 2011, Zanini et al. 2014). Chronosequence surveys are a powerful tool which allows a single research team to quickly estimate change over many years, but interpretation of results rest on two critical underlying assumptions (Lebrija-Trejos et al. 2010). The first of these is that initial conditions at all sites were identical. Producing strong support for this assumption may be difficult or impossible when no documentation of initial conditions exists, but it may be treated as provisionally true when environmental conditions and disturbance regimes are identical or nearly so across sites. The second of these assumptions is that, if initial conditions were identical across the studied sites, subsequent development at each followed a similar trajectory of compositional and structural change. As with the first assumption this can be difficult to prove conclusively. The extent to which it can be treated as provisionally true can be estimated by follow-up surveys of each studied site at some lapse of time after the initial surveys, at which time the agreement between predicted and observed site status can be assessed.

The purely descriptive nature of surveys is complemented and deepened by information on the mechanistic underpinnings of observed trends and patterns. The identification of these

mechanisms at the physiological level is a central goal of the field of plant ecophysiology (Lambers, Chapin, and Pons 2008). Successful identification of one or a suite of such underlying traits promises both explanatory and predictive power at a variety of spatial and temporal scales, although the wide variety of traits which comprise a species' overall survival strategy, as well as the idiosyncratic nature of their arrangement at the species level, make doing so a difficult task (Poorter et al. 2008, Yang et al. 2018). Plant ecophysiological traits are many but variation in each can be mapped theoretically as occurring across a spectrum from, at one extreme, allowing for rapid use of abundant resources and, at the other, allowing for persistence under conditions of resource scarcity (Reich 2014). Xylem anatomical traits are no exception to this theory and may be found to have explanatory power on inter-species variation in growth and mortality as observed in surveys (Cosme et al. 2017). Both the ability of xylem to convey water and its susceptibility to dysfunction under conditions of water stress scale at an exponential rate with size so, all else being equal, larger vessels are more appropriate to wetter sites where survival is determined primarily by competitive ability and smaller vessels are more suitable for sites where water availability is periodically or chronically limiting and competition is proportionally lower. It has been proposed that traits co-vary and that a species' overall strategy for survival and reproduction can therefore also be conceptualized in terms of this spectrum, although this likely best describes trait correlation patterns at the ecosystem scale and shouldn't be applied uncritically to any single species (Reich 2014). Strategies which exemplify the rapid resource-use extreme of this spectrum are those of agricultural weeds and pioneers of sunny disturbed floodplains, while those which exemplify the other extreme are slow-growing conifers of cold, dry mountains and inhabitants of exceptionally dark forest understories (Grime 1977).

Any study which reports the explanatory power of only a single trait must be treated as incomplete, albeit informative.

Two studies are reported in this thesis. The first of these is a chronosequence of vegetation surveys carried out in reforested plots at the Sal del Rey and Teniente tracts of the Lower Rio Grande Valley Wildlife Refuge in northern Hidalgo Co. and adjacent western Willacy Co., Texas. This series of surveys was undertaken to quantify the relative survival, growth, and recruitment rates of mostly woody plant species planted in an initial reforestation effort at multiple durations post-planting, as well as the change with time of forest structure, aboveground woody biomass, and areal coverage in native versus non-native herbaceous species. Results of these surveys will inform future restoration efforts in this region and serve as a dataset against which ecophysiological information can be compared. The second study reported here is an evaluation of the predictive power of xylem anatomy on growth and mortality of 11 species of woody plants at 3 months, 12 months, and 23 years post-planting at reforestation sites at Sal del Rey. 3- and 12-month growth and mortality data is that reported from monthly seedling surveys carried out between the winters of 2018 and 2019 (Mohsin et al. 2021), and the 23 year data is that reported in this thesis. Four xylem anatomical traits were considered: areal density of vessels, mean vessel size, mean hydraulically weighted diameter, and cross-sectional fraction of a stem devoted to xylem lumen. The comparison of multiple survey and xylem anatomical datasets generated from work principally carried out at a single locality represent an unusually detailed study of so small an area.

## CHAPTER II

### WINNERS AND LOSERS IN REFORESTATION EFFORTS

#### **Introduction**

Semi-arid regions are estimated to cover 15.3% of the Earth's land surface and represent a significant fraction of the overall 41.5% percent of the Earth's land surface which experiences a dryland climate (aridity index [AI] of between 0.0 and 0.65) (Bastin et al. 2017). The vegetation of semi-arid areas globally varies along a continuum from grassland to closed forest, with fraction of areal coverage in tree canopy roughly increasing with precipitation (Bastin et al. 2017). As of 2015, 24.7% (559 Mha) of semi-arid areas worldwide were observed to have a minimum of 10% tree canopy cover, 12% (276 Mha) to have a minimum of 40% tree canopy cover, and 11.2% (254 Mha) to be fully covered by tree canopies (Bastin et al. 2017). Semi-arid areas are being increasingly targeted for reforestation in order to address severe degradation, biological invasion, and loss of resource provisioning to society and wildlife (Marshall et al. 2012, Adkins et al. 2014, Song et al. 2018). While the potential for carbon sequestration in dryland forests is lower than that of many other biomes, it plays an important role in the global carbon cycle by virtue of its vast extent (Erb et al. 2018; Bastin et al. 2017). The region of focus in this work is classified as experiencing a semi-arid climate.

The Lower Rio Grande Valley (LRGV) of south Texas is host to a biologically diverse set of communities (Leslie 2016). Plant species richness at small spatial scales (km<sup>2</sup>) is comparable

with the broader southern United States, but unusually sharp gradients in both precipitation and hydro-edaphic conditions across the region cause rapid species turnover and consequently give rise to high beta diversity in both flora and fauna (Flores 2019; Kartesz 2015; Whittaker et al. 2001; Perez et al. 2021). In fact, recent work suggests that the vegetation of the region consists of at least eight overlapping but essentially distinct communities, each developing in areas where edaphic and climatic conditions coincide in a particular way (Flores 2019). Numbers of bird and Lepidopteran species are among the highest in the continental United States (Jenkins et al. 2015; Stanford 1993). Many species found in the region have very limited distributions within the United States and are more widespread in Mexico and Central America (Saghatelian 2017; Kartesz 2015). Sadly, 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). Those patches that do remain are generally small and isolated from each other, preventing exchange of genetic information and re-colonization should local extinction of any animal or plant species found therein occur (Reed 2004). Biodiversity and habitat quality would be expected to increase with time on unmanaged, abandoned agricultural land under natural conditions, but the presence of a guild of highly competitive non-native grasses at many sites across the region is suspected to have altered secondary successional trajectories, leading to a serious simplification of diversity and physical structure of the vegetation thereon.

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 U.S. Fish and Wildlife Service (FWS) began to reforest plots of retired agricultural land in the LRGV to increase forest area and inter-patch connectivity (Judd et al.

2002; Vora 1992; Ewing and Best 2004). Between 1982 and 2020 an average of ~170 ha were reforested per year, totaling at least 6475 ha as of this publication, and over 5 million seedlings have been planted during that time (K. Wahl-Villareal, personal communication). Solely woody species and dicotyledonous forbs have historically been used in reforestation in this area, although it's not clear that some sites on which restoration projects have been carried out were not in fact grasslands before widespread alteration of vegetation and disturbance regimes (Johnston 1963). Despite the scale and expense of this project, post-planting assessments of seedling survival, species recruitment, and forest development are lacking and the studies which have been carried out have focused solely on seedling growth and survival and for a maximum of two years post-planting (Mohsin et al. 2021; Alexander et al. 2016, Arias et al. *in review*). Annual mortality rates of seedlings within their first one to two years post-planting growth can be high in this context, even when outplanted after germination and early development in a nursery. Overall mortality in a study of 3600 seedlings carried out at Sal del Rey between November 2018 and October 2019 was observed to be 21%, although rates varied from 8-69% by species, and mortality of seedlings subject to similar conditions at the Laguna Atascosa National Wildlife Refuge were approximately 15% percent after two years (Mohsin et al. 2021; Alexander et al. 2016). Chronic drought and extreme summer heat pose significant challenges to seedling survival in the LRGV, especially in the context of oldfield restoration where established woody nurse plants are absent and soil structure and organic content may be impaired. Populations of whitetail deer (*Odocoileus virginianus*) and exotic nilgai (*Boselaphus tragocamelus*) and wild pigs (*Sus scrofa*) exert a significant effect on planted seedlings at reforestation sites (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 and Clay 2010). 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 (MacDougall and Turkington 2005, Tix 2000, Marshall et al. 2012). Strong depression of biodiversity by buffelgrass (*Cenchrus ciliaris*) 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 be expected to revert to savannah or grassland as mature trees begin to die without a sufficient density of replacement individuals in the subcanopy. In sum, decadal trends in growth, survival, and recruitment remain key unknowns within the context of LRGV reforestation.

Chronosequences are a powerful tool for estimating vegetation dynamics (growth, mortality, recruitment) over decadal to millennial time scales, by substituting space for time (Walker et al. 2010). They have been successfully used to chart changes in vegetation characteristics at a variety of temporal scales (Lichter 1998, Lebrija-Trejos et al. 2010). Furthermore, directional change in ecosystem functioning and soil characteristics have been identified (Huggett 1998, Stoy et al. 2006). Care must be taken when using the chronosequence approach, as interpretation of results rests on the assumptions that initial conditions at all sites were identical and that subsequent development at each followed a similar trajectory of compositional and structural change. While both are difficult to prove conclusively, proximity of sites and similar land use histories (e.g., common agricultural practices), or sufficient within-age replication can mitigate potential differences. Repeat surveys of plots can be used to test these assumptions (e.g., Lebrija-Trejos et al. 2010). The presence of many reforestations carried out at

intervals on clustered sites with highly similar soils and initial conditions, varying principally in age, lends itself to study in the chronosequence approach. 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 (see Ewing and Best 2004 for an early version of this approach). 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 the combined chronosequence-planting approach to address several questions associated with vegetation dynamics and the trajectory of reforested communities. 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 vs. 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 vs. recruitment.* As plots age, are communities evolving towards 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 vs. 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 presence of woody canopy cover, impact seedling recruitment?

## **Methods**

### **Geographical Context of Study Site**

Two tracts of the Lower Rio Grande Valley National Wildlife Refuge (hereafter “the Refuge”), Sal del Rey and Teniente, were selected for this study because they share similar soil types and a history of reforestation dating back to 1987. Sal del Rey is the site of ongoing reforestation, and results of a 1-year intensive study on species survival and growth from 2018-2019 are reported in Mohsin et al. (2021) and included in this study.

### **Chronosequence**

The Refuge is an extensive, multi-tract wildlife refuge administered by the U.S. Fish and Wildlife Service which spans the four southernmost counties in Texas (Willacy, Cameron, Hidalgo, and Starr) and preserves some acreage of nearly every vegetation type occurring therein (Leslie 2016). Surveys in addition to Mohsin et al. (2021) were made of six plots, four at the Sal del Rey tract of the Refuge and two at the nearby Teniente tract (Fig. 1 and Supplemental Table S1), resulting in a plot age span of 1 - 33 years (Table 1). Sites were chosen so as to share edaphic conditions to as large a degree as possible (Table 1) and were planted with a shared complement of species in initial reforestation efforts. Records of planting species composition were not found for Teniente (Supplemental Table S2).

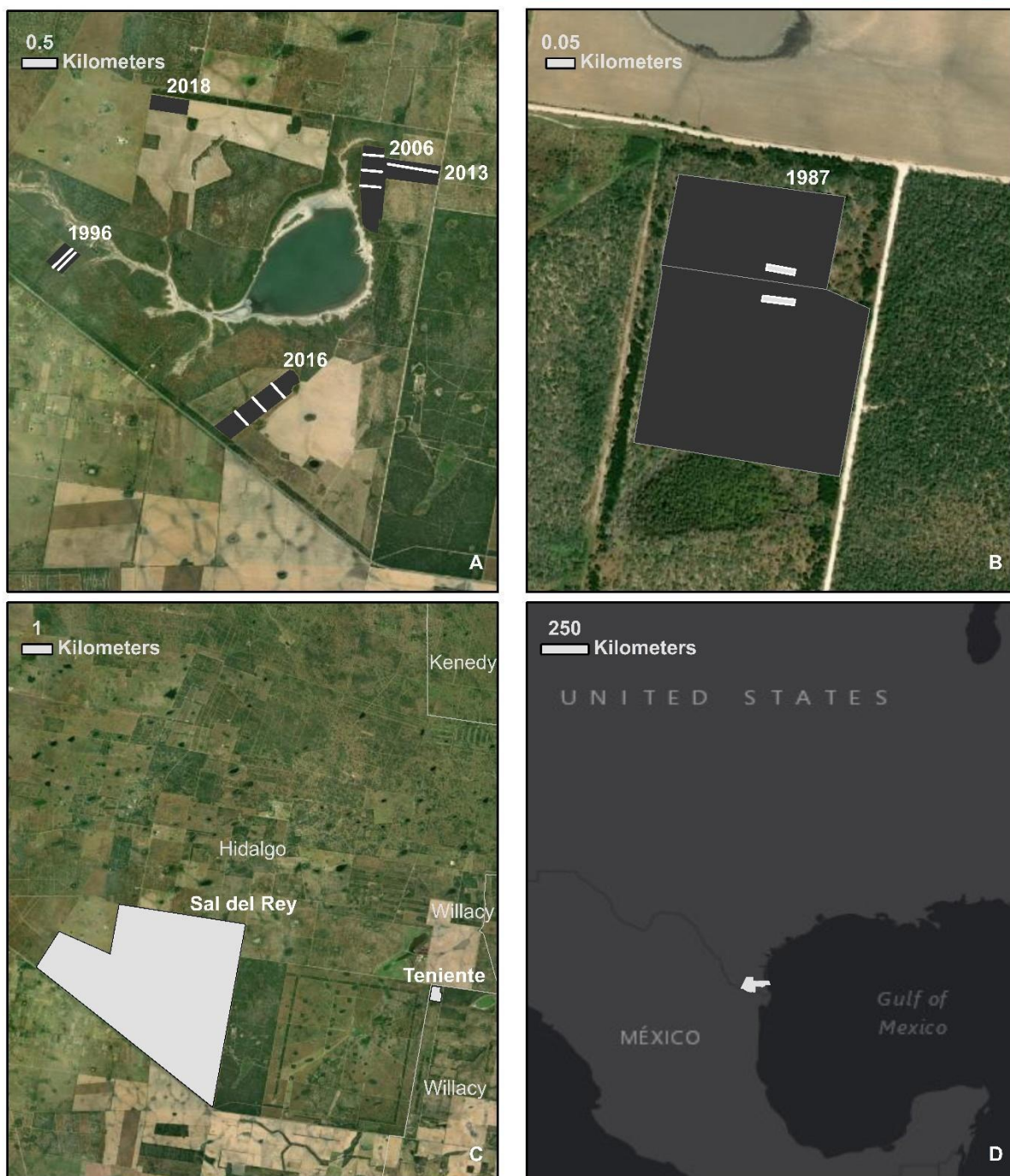


Figure 1. Maps of study sites.

A: Location of plots and transects on the Sal del Rey tract. Dark gray polygons represent reforestation plots and light gray polygons represent survey transects

B: Location of plots and transects on the Teniente tract. Symbology is the same as that in A.

C: Location of tracts relative to each other and parts of Hidalgo, Willacy, and Kenedy Cos., Texas.

D: Location of Hidalgo and Willacy Counties relative to the United States, Mexico, and the Gulf of Mexico.

Service Layer Credits: Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

**Table 2.1.** 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 disked rows.

Tract	USFWS Plot Code	Planting & Survey Information								Soil Types Represented			
		Planting Year	Survey Year	Plot Age (yrs)	Planting Method	Area Planted (ha)	Area Sampled (ha)	% Plot Sampled	Source for survey data	Fine Sandy Loam (%)	Sandy Clay Loam (%)	Clay Loam (%)	Sandy Loam (%)
Sal del Rey	6a	2018	2019	1	Seedlings	1.21	1.21	100	Mohsin et al. (2021)	87.2	0	0	12.8
Sal del Rey	10fg	2016	2019	3	Seedlings	18.25	0.78	4.3	This study	99	0	1	0
Sal del Rey	11d	2013	2019	6	Seedlings	18.53	0.64	3.5	This study	81	16	3	0
Sal del Rey	SR80	2006	2020	14	Seedlings	33.40	0.77	2.3	This study	100	0	0	0
Sal del Rey	SR52	1996	2019	23	Seedlings	9.59	0.68	7.1	This study	100	0	0	0
Teniente	Rudman02	1987	2020	33	Seedlings*	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	76.8	22.2	0	0

\* Failed planting (near 100% mortality) according to USFWS records.

## Geology & Soils of Study Site

This publication follows the geographic naming conventions of Leslie (2016), who defines the LRGV as the contiguous area of Cameron, Willacy, Hidalgo, and Starr Counties, and the Rio Grande delta as specifically those areas underlain by exposed Rio Grande alluvial sediment. This paper adds to the latter definition the detail that alluvial sediment deposited by the Rio Grande river in the LRGV constitutes unnamed Holocene deposits of the historic river floodplain and the Beaumont and Lissie formations, which represents Pleistocene deltaic deposits (Ewing and Gonzalez 2016). The Rio Grande is believed to have integrated into the Gulf of Mexico as recently as ~800 ka, in the middle Pleistocene, before which time it terminated in a series of internally drained basins in west Texas, New Mexico, and southern Colorado (Galloway et al. 2011, Repasch et al. 2017, Connell et al. 2005). All sites included in this study are situated on the older Goliad Formation, which has been variously assigned to the Pliocene and Miocene, indicating that they cannot be included in the delta of the Rio Grande river as it currently exists in even its broadest definition (Baskin and Hulbert 2008). Results from these sites may nonetheless be informative of dynamics at sites underlain by younger sediment, although less so on sites with soils predominantly of clay or deep sand.

Both tracts contain atypically xeric areas by the standards of the Refuge but are representative of conditions in much of north-central Hidalgo County, northeast Starr county, western Willacy County, and northwestern Cameron County (approximately the Bordas Cuesta physiographic zone of Flores 2019). Although a variety of soil types underlay both tracts, plots are in areas of predominantly mildly alkaline sandy loam soil without a near-surface water-restrictive layer (Table 1) (Soil Survey Staff 2019). All sites included in this study experience a semi-arid climate, defined here as a ratio of precipitation to potential

evapotranspiration (Aridity Index, AI) of 0.2 to 0.5 (Sorensen 2009). The site receives an average of 583 mm (22.95 inches) of rainfall per year (Hollister et al. 2010). Average annual temperature is 23.8 C (74.84 F), with a cool winter and an extremely hot summer during which temperatures above 37.8 C (100 F) are commonplace (Hollister et al. 2010).

## **Regional Baseline**

Each of the communities identified by Flores (2019) can be found at one of eight representative study sites, of which Cactus Flats is the closest to Sal del Rey and Teniente. Surveys carried out at Cactus Flats showed a vegetation of low shrub- and tree-forming species, frequently armed with thorns. Common species within surveyed areas were Texas ebony (*Ebenopsis ebano*) and snake eyes (*Phaulothamnus spinescens*), the former constituting a significant part of the canopy and the latter the understory. These two species accounted for over half of all observed coverage in vegetation at any canopy stratum, although significant coverage was also contributed in mid- and understories by colima (*Zanthoxylum fagara*), granjeno (*Celtis pallida*), coma (*Sideroxylon celastrinum*), guayacán (*Guaiacum angustifolium*), and blue boneset (*Tamaulipa azurea*). Only 3 species, Texas ebony, coma, and honey mesquite (*Prosopis glandulosa*) attained heights greater than 4 meters. Honey mesquite was encountered only infrequently but contributed over half of the observed canopy coverage greater than 5 meters above ground level in the 0.1 ha plot where it was encountered, although it was not encountered in an adjacent plot of the same area. Notably, the vegetation at this site is spatially heterogenous. Cactus Flats is situated roughly 15 km to the south of La Sal del Rey and Teniente and is underlain by similar soils to those which underlie the survey sites of focus in this paper (Soil Survey Staff). While this site is known to have escaped historic conversion into farmland and has not hosted cattle since at least the 1950s, it remains unknown whether forests of this composition

and structure were widespread or restricted before early-historic land conversion and fire suppression.

## **Reforestation History**

Reforestation has been ongoing at Sal del Rey since 1993 and at Teniente since 1986. Individual site histories vary but, in general, sites were private farmland until either acquisition of the tract in question by FWS, or after acquisition until reforestation (Ewing and Best 2006). In no case was established forest present on the reforested plots, and pre-planting disking served to remove any volunteer trees and forbs so that bare soil was exposed during planting. Pre-planting disking was, in all cases, done on rows of a constant bearing across the entirety of the plot such that all of the resulting furrows are parallel within a given plot. These rows are visible at ground level and on satellite imagery as linear pits and mounds for some years post-planting, and can be identified in satellite imagery as unnaturally straight lines of trees after longer durations. All Sal del Rey plots included in this study were planted using the same technique – nursery-raised seedlings of 32 to 37 tree species were planted directly into furrows left from previous disking. Excepting the 2018 planting, in no case were seedlings fertilized, irrigated, or provided with any protection from vertebrate or invertebrate herbivores. Documents detailing the species compositions and planting rates of all reforestations carried out at this and other tracts have been maintained by the regional branch of the U.S. Fish and Wildlife Service. Access to these documents allowed a comparison to be made between species composition and number density at the time of planting versus those at the time of surveys. No information on planting composition or density was maintained for Teniente, however, so comparisons were not possible at that site.

## Field Assessments

Surveys were conducted using transects, these linear “belts” including all area to five meters on either side of a central midline (Fig. S2). Methodology varied between mature tree surveys and seedling surveys. All mature trees, defined here as any with a basal diameter of five or more centimeters, which was rooted partially or wholly in the transect area were measured. Seedlings, defined here as having a basal diameter of less than five centimeters, were included only if they were rooted within a 1 m<sup>2</sup> seedling quadrat, of which two were positioned on the transect midline at intervals of five meters for the entirety of each transect’s length (Fig. S2). The height and basal diameter of each stem encountered was recorded, as was the tree species identity and position within the transect. Each stem of multi-stem trees and shrubs were measured separately but were later aggregated for biomass and other calculated metrics. Transects were laid at a bearing as nearly perpendicular as possible to that of the rows in which trees were initially planted by FWS (Supplemental Table S1 and Figure S2). The area surveyed per plot varied, but in no case was the aggregate area of all transects less than 0.64 ha or greater than 0.77 ha (Table 1). Estimates of aboveground biomass (AGB) were made using allometric equations for which basal diameter and height were the only required variables (Navar et al. 2004).

## Biomass Estimation

The aboveground biomass of individual trees was estimated using allometric equations. These equations were developed by destructively harvesting and weighing a sample of naturally-occurring trees, and then deriving equations whereby the measured basal diameter and height of all harvested trees most closely predicted observed mass (Navar et al. 2004). However,

the biomass of some species is only estimable using broadly applicable equations developed for forests of similar physiognomy. Species for which biomass was estimated using species-specific equations include *Prosopis glandulosa*, *Ebenopsis ebano*, *Havardia pallens*, *Zanthoxylum fagara*, *Celtis pallida*, *Vachellia rigidula*, *Vachellia farnesiana*, *Senegalia berlandieri*, *Condalia hookeri*, *Diospyros texana*, *Forestiera angustifolia*, following equations from Navar et al. (2004), and Rojas-Garcia et al. (2014). Species without species-specific equations but which share similar tree-like architecture to others of Tamaulipan thornscrub were estimated using a “global tree” equation were *Cercidium macrum*, *Parkinsonia aculeata*, *Vachellia schaffneri* (Navar et al. 2004):  $AGB_{global} = 0.026884 + 0.001191*diam.basal^2*height + 0.044529*diam.basal - 0.01516*height + 1.025041 + 0.023663*diam.basal^2*height - 0.17071*height - 0.09615*log(height) - 0.43154 + 0.011037*diam.basal^2*height + 0.113602*diam.basal + 0.307809*log(diam.basal)$ , where AGB denotes aboveground biomass (kg \* individual<sup>-1</sup>), diam.basal denotes the basal diameter of a tree (centimeters), and height denotes the height of a tree’s highest point (meters). Biomass of all remaining species was estimated using the “global shrub” equation of Navar et al. (2004):  $AGB_{shrub} = (-0.05266) + ((0.000052)*height) + ((0.092582)*(log(diam.basal^2*height))) + (0.109003) + ((0.014021)*((diam.basal^2*height) - ((1.62531)*height) + ((0.89543)*(log(diam.basal^2*height)))) + (0.3558) + ((0.010336)*(diam.basal^2*height)) - ((0.51147)*diam.basal) + ((1.5063)*(log(diam.basal)))$ , where terms and units are the same as above. The full R code for all equations used in this study, complete with corrections made (where errors existed in the original equations of Navar et al. (2004) or Rojas-Garcia et al. (2014)) is given in the Supplemental Code S1.

## Functional Trait Classification

The relationships between several plant functional traits and growth and mortality were evaluated. A literature search was conducted to classify species as in one of several levels of each of these trait spectra (nitrogen fixation, rooting depth, and habit of mature individuals). Traits were considered as non-binary and occurring on a spectrum for two distinct reasons. In the case of 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 definitely to fix nitrogen. Unassessed species in families from which nitrogen fixation is not known are treated as non-fixing. In terms of rooting depth and habit, a binary classification oversimplifies the array of possible root and stem architectures. Traits were collapsed into simple binaries for analysis, but are reported here as spectra for other uses. These traits are catalogued in Table 2, and their predictive power on growth and mortality is shown graphically in Fig. 6.

**Table 2.2.** Species functional traits as determined from the literature (leaf habit, N-fixing ability, root depth, and stature) and personal observations (photosynthetic stem). *Leaf habit codes*: U: unknown; D-C: cold deciduous; D-D: drought deciduous; D-CD: cold and drought deciduous; E: evergreen; FE: facultative evergreen (dying back in cold temperatures). *N-fixing codes*: U-U = unknown-unlikely (based on family affiliation); U-P = unknown-possible (based on family/subfamily affiliation with known N-fixer); U-L = unknown-likely (based on genus affiliation with known N-fixer); N = No; Y = yes. *Root depth codes*: blank: unknown; S:

shallow; I: intermediate; D: deep. References corresponding to superscripts: 1. Bogusz et al. 1990; 2. Correll and Johnson 1970; 3. Cross and Wiedmann 1985; 4. Felker and Clark 1981; 5. Francis 2004; 6. Gibbens and Lenz 2001; 7. Grow Florida Edibles (2013); 8. Gucker 2005; 9. Kahle et al. 2020; 10. Lady Bird Johnson Wildflower Center (n.d.); 11. Liu et al. 2013; 14. Nokes 2001; 15. Richardson and King 2011; 16. Tedersoo et al. 2018; 17. USDA-NRCS (2021); 18. Van Dersal 1938.

Species	Family	Leaf Habit	Photosynthe tic Stem	N-fixing	Root Depth	Stature
<i>Adelia vaseyi</i>	Euphorbiaceae	U	No	U-U		Shrub <sup>12, 17</sup>
<i>Aloysia gratissima</i>	Verbenaceae	D-C <sup>11</sup>	No	U-U	S <sup>11</sup>	Shrub <sup>9</sup>
<i>Amyris texana</i>	Rutaceae	E	No	U-U		Shrub <sup>9</sup>
<i>Bernardia myricifolia</i>	Euphorbiaceae	D-C <sup>11</sup>	No	U-U		Shrub <sup>10</sup>
<i>Capsicum annuum</i>	Solanaceae	FE <sup>12</sup>	No	U-U	S	Shrub <sup>2</sup>
<i>Castela erecta</i>	Simaroubaceae	E	No	U-U		Shrub <sup>2</sup>
<i>Celtis ehrenbergiana</i>	Cannabaceae	FE	No	N <sup>1,11</sup>	I <sup>11</sup>	Shrub <sup>2</sup>
<i>Cercidium macrum</i>	Fabaceae	D-CD <sup>12</sup>	Yes	U-U <sup>4</sup>		Tree <sup>2</sup>
<i>Chromolaena odorata</i>	Asteraceae	FE	No	U-U	S	Subshrub <sup>2</sup>
<i>Colubrina texensis</i>	Rhamnaceae	D-C <sup>11</sup>	No	N <sup>11</sup>	D <sup>11</sup>	Shrub <sup>11</sup>
<i>Condalia hookeri</i>	Rhamnaceae	FE <sup>11</sup>	No	N <sup>11</sup>	I <sup>11</sup>	Variable <sup>10</sup>

<i>Cordia boissieri</i>	Boraginaceae	D-D <sup>12</sup>	No	U-U		Tree <sup>2</sup>
<i>Coursetia axillaris</i>	Fabaceae	D-CD <sup>12</sup>	No	U-L <sup>14</sup>		Shrub <sup>2</sup>
<i>Croton cortesianus</i>	Euphorbiaceae	FE <sup>13</sup>	No	U-U		Shrub <sup>2</sup>
<i>Diospyros texana</i>	Ebenaceae	FE <sup>11</sup>	No	U-U <sup>11</sup>	I <sup>11</sup>	Tree <sup>2</sup>
<i>Ebenopsis ebano</i>	Fabaceae	E	No	Y <sup>15,16</sup>		Tree <sup>2</sup>
<i>Eysenhardtia texana</i>	Fabaceae	D-C <sup>11</sup>	No	Y <sup>11</sup>		Shrub <sup>10</sup>
<i>Forestiera angustifolia</i>	Oleaceae	E <sup>11</sup>	No	U-U <sup>11</sup>		Shrub <sup>2</sup>
<i>Guaiacum angustifolium</i>	Zygophyllaceae	E <sup>12</sup>	No	U-P <sup>16</sup>	D <sup>9</sup>	Tree <sup>2</sup>
<i>Havardia pallens</i>	Fabaceae	FE	No	Y <sup>16</sup>		Tree <sup>2</sup>
<i>Koeberlinia spinosa</i>	Koeberliniaceae	LL <sup>13</sup>	Yes	U-U	D <sup>6</sup>	Shrub <sup>2</sup>
<i>Lantana urticoides</i>	Verbenaceae	D-C <sup>9</sup>	No	N <sup>16</sup>	S	Shrub <sup>2</sup>
<i>Leucophyllum frutescens</i>	Scrophulariaceae	FE <sup>9</sup>	No	N <sup>16</sup>		Shrub <sup>2</sup>
<i>Lycium berlandieri</i>	Solanaceae	D-D <sup>9</sup>	No	N <sup>16</sup>	D <sup>6</sup>	Shrub <sup>2</sup>
<i>Malpighia glabra</i>	Malpighiaceae	FE <sup>12</sup>	No	N <sup>16</sup>	S <sup>7</sup>	Shrub <sup>2</sup>
<i>Parkinsonia aculeata</i>	Fabaceae	D-C <sup>11</sup>	Yes	N <sup>11</sup>	S <sup>11</sup>	Tree <sup>2</sup>
<i>Phaulothamnus spinescens</i>	Achatocarpaceae	D-C <sup>2</sup>	No	N <sup>16</sup>		Shrub <sup>2</sup>
<i>Prosopis glandulosa</i>	Fabaceae	D-C <sup>11</sup>	No	Y <sup>11</sup>	D <sup>11</sup>	Variable <sup>2</sup>
<i>Randia rhagocarpa</i>	Rubiaceae	FE	No	N <sup>16</sup>		Shrub <sup>2</sup>

<i>Rhamnus humboldtiana</i>	Rhamnaceae	E <sup>11</sup>	No	N <sup>11</sup>		Shrub <sup>2</sup>
<i>Sapindus saponaria</i> var. <i>drummondii</i>	Sapindaceae	D-C <sup>12</sup>	No	N <sup>16</sup>		Tree <sup>2</sup>
<i>Schaefferia cuneifolia</i>	Celastraceae	E <sup>11</sup>	No	N <sup>11</sup>	I <sup>11</sup>	Shrub <sup>2</sup>
<i>Senegalia berlandieri</i>	Fabaceae	D-D	No	Y <sup>16</sup>	D <sup>18</sup>	Shrub <sup>2</sup>
<i>Senegalia greggii</i>	Fabaceae	D-C <sup>5</sup>	No	N <sup>11</sup>	D <sup>8</sup>	Tree <sup>2</sup>
<i>Sideroxylon celastrinum</i>	Sapotaceae	E <sup>9</sup>	No	N <sup>16</sup>		Tree <sup>2</sup>
<i>Trixis inula</i>	Asteraceae	U	No	N <sup>16</sup>		Shrub <sup>2</sup>
<i>Vachellia farnesiana</i>	Fabaceae	D-C <sup>11</sup>	No	Y <sup>11</sup>	D <sup>11</sup>	Tree <sup>2</sup>
<i>Vachellia rigidula</i>	Fabaceae	D-C <sup>11</sup>	No	Y <sup>11</sup>	I <sup>11, 3</sup>	Shrub <sup>2</sup>
<i>Vachellia schaffneri</i>	Fabaceae	D-C	No	Y <sup>16</sup>		Shrub <sup>2</sup>
<i>Vigueria stenoloba</i>	Asteraceae	E <sup>12</sup>	No	N <sup>16</sup>		Shrub <sup>2</sup>
<i>Yucca treculeana</i>	Asparagaceae	E	No	N <sup>16</sup>		Tree <sup>2</sup>
<i>Zanthoxylum fagara</i>	Rutaceae	E <sup>11</sup>	No	N <sup>11</sup>	S <sup>11</sup>	Shrub <sup>2</sup>
<i>Ziziphus obtusifolia</i>	Rhamnaceae	D-D <sup>11</sup>	Yes	N <sup>11</sup>	I <sup>11</sup>	Shrub <sup>2</sup>

### Distinguishing planted vs. recruited individuals

Estimation of species-specific recruitment rate, and comparisons between recruited and planted individuals of a species, required discrimination of planted from naturally-occurring

individuals. This task was eased considerably by the planting methodology used by FWS, in which trees are planted in rows of known bearings separated by approximately constant distance intervals. These rows are frequently visible at ground level as unnaturally straight, regular rows of trees, and any individual obviously in a row was recorded as having been planted in an initial reforestation. Any individual obviously not in a row was recorded as natural regeneration. In many cases, however, no patterning of trees into rows was evident and visual discrimination was not possible. In these cases, the position of all rows intersecting a transect was estimated by determining the row spacing which best described obvious row-transect intersections. If a tree that was not visibly in a row was positioned in such a way as to match an estimated row, and if it was of comparable size to conspecifics about which there was no question, it was recorded as being planted. Species-specific germination rates were not assessed, as no estimation of seedling mortality was possible at any site of greater than one year in age.

## Statistical Methods

The species-specific survival of all species surveyed in the plots was determined based on the ratio of the number density of surveyed individuals which we determined were planted (as described above) to that of the planting density for that species, and modeled the change in survival with time using an exponential decay function (Eq. 1):

$$survival_{species\ i} = \frac{NDensitySurveyedInRow_{species\ i}}{NDensityPlanted_{species\ i}} = e^{\lambda_i t} \quad (1)$$

$NDensitySurveyedInRow_{species\ i}$  denotes the modeled number density (indiv\*ha<sup>-1</sup>) of species *i* at time of surveys, and  $NDensityPlanted_{species\ i}$  denotes the known number density of species *i* at planting.  $Survival_{species\ i}$  denotes survival of species *i* at time *t*, and is equal to the

number of individuals encountered per area at time  $t$  as a fraction of number of individuals per area at  $t=0$ .  $\lambda$  denotes the per-capita mortality rate of species  $i$  in units of number of deaths\*number of individuals<sup>-1</sup>\*year<sup>-1</sup>. A linear mixed effects model (Bates et al. 2004) was applied, where survival was log-transformed and time was not. Species identity was used as a random slope effect, time as the main effect, and the regression line was forced through the origin (Sheil and May 1996).

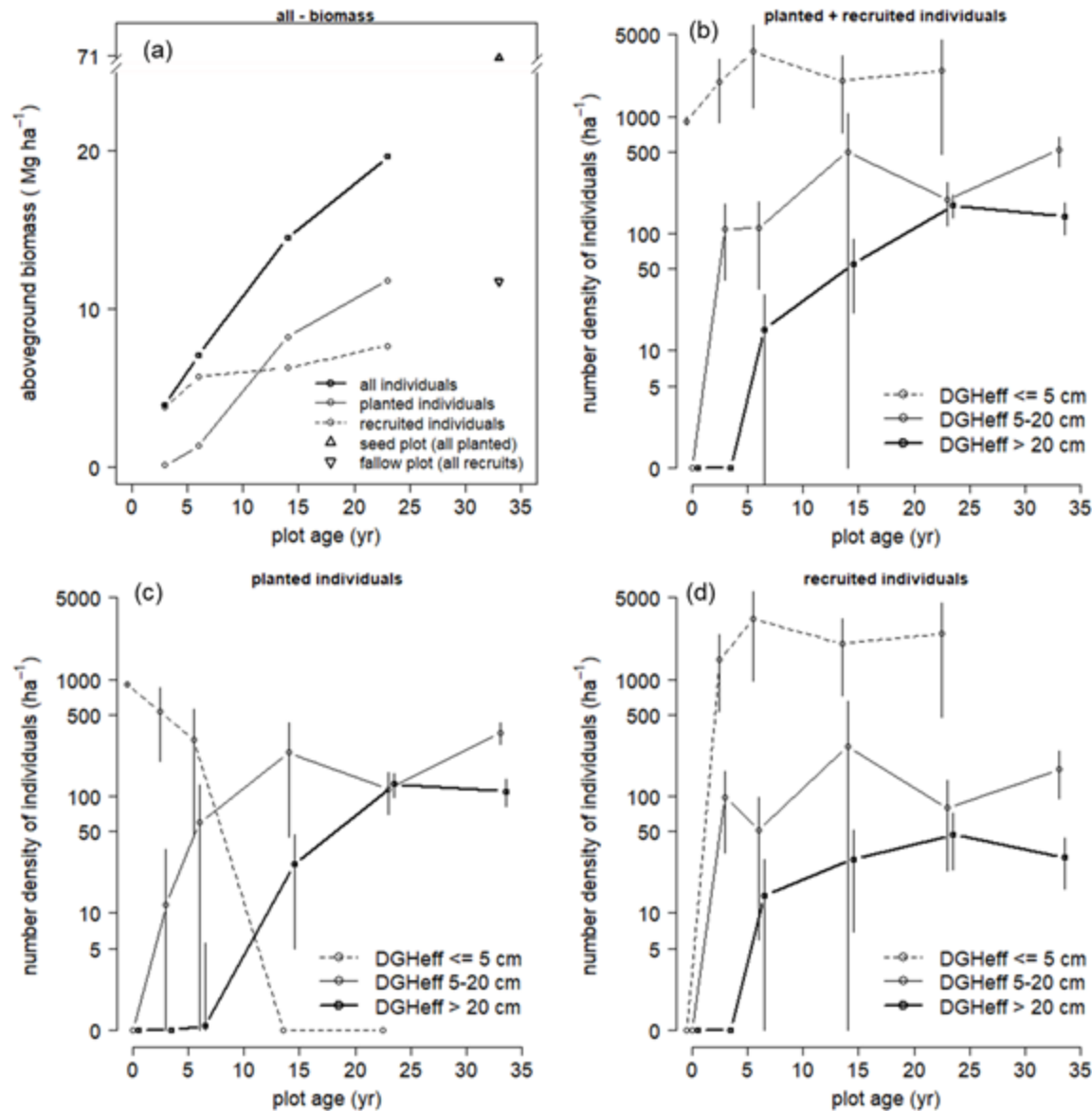
Individual-level biomass of all species surveyed was determined by applying a linear regression to log-transformed observed biomasses. The value of this regression line at a given time is here considered as the modeled biomass of an individual member of that species at that time.

$$\text{Aboveground Biomass}_{\text{species } i} = GR_{AGB,i} t^{\tau}$$

Aboveground Biomass<sub>species  $i$</sub>  denotes estimated above ground biomass of species  $i$ , in units of kilograms per individual.  $GR_{AGB,i}$  is the aboveground growth rate of species  $i$  in units of kilograms\*year<sup>-1</sup>. Time in years is shown by  $t$ .  $\tau$  is a unitless constant scaling exponent. The power function given above directly follows from the allometric equations of Enquist, Brown, and West (Enquist et al. 1998). A linear mixed effect model (Bates et al. 2004) was applied to estimated biomass results of the surveys, where estimated biomass was log-transformed and time was not.

## Results

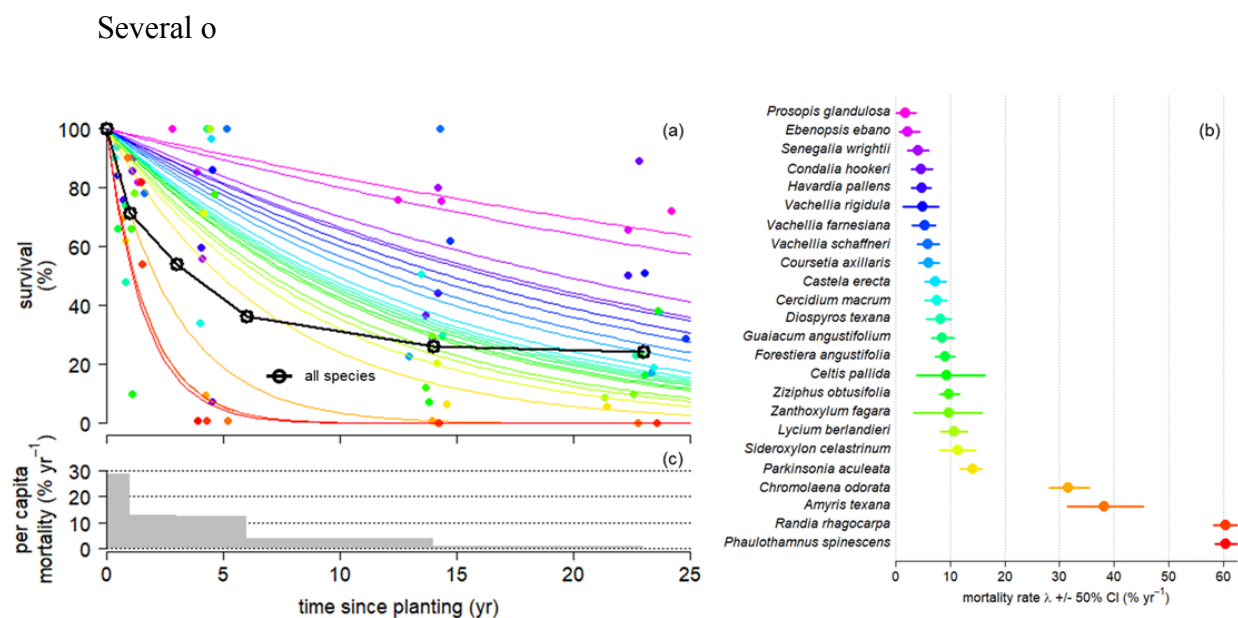
Aggregate biomass  $\text{Mg ha}^{-1}$  of plots was observed to increase with time and was not observed to stabilize at 23 years post-planting (Fig. 2a). Points denoting biomass at 33 years post-planting are included for reference but are not connected by lines to points denoting biomass of younger plots because the initial characteristics of both sites were non-comparable with those of younger sites. The site exhibiting  $\sim 71 \text{ Mg ha}^{-1}$  was planted by direct broadcast of seeds of a low-diversity planting mixture, and the other is believed to have suffered nearly complete mortality and is here treated as indicative of regeneration on an unplanted fallow field. The number density (individuals per hectare) of all trees in the middle and large size classes (those with aggregate basal diameters of between 5-20 and  $>20$  cm, respectively) increased with time, although the rate of increase itself decreased and may have reached a plateau as of the time of surveys (Fig. 2b). Number density of trees in the smallest size class (trees with an aggregate basal diameter of  $<5$  cm) stayed stable at a high value, although the size class was composed entirely of recruited individuals by no later than 15 years post-planting (Fig. 2b). Number density of planted individuals in the smallest size class predictably fell to zero rapidly with time, with loss of individuals in this case is attributable both to mortality and to growth beyond 5cm basal diameter and subsequent inclusion into the middle and upper size classes (Fig. 2c). Number density of planted individuals in both the middle and largest size classes increased at a decreasing rate with time (Fig. 2c). Recruited individuals in the smallest size class rapidly increased to a high, but steady, number density (Fig. 2d). Number density of recruits in the middle and largest size classes increased to a steady value by five years post-planting and did not appreciably increase or decrease in the subsequent years (Fig. 2d).



**Figure 2.** Chronosequence of (a) aboveground biomass and (b)-(d) number density, standardized to a planting density of 1000 individuals per hectare (see Methods). 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 diameter at ground height (DGHeff) size class. The 33-year aged point is represented by 2 field plots, a direct seeded plot of a single species (*E. ebano*) and a 'fallow' plot (a failed planting of unknown species mix with near-100% mortality). Panel a) shows both plots separately, while b) presents the mean of these two plots, c) presents only the direct seeded plot, and d) only the fallow plot.

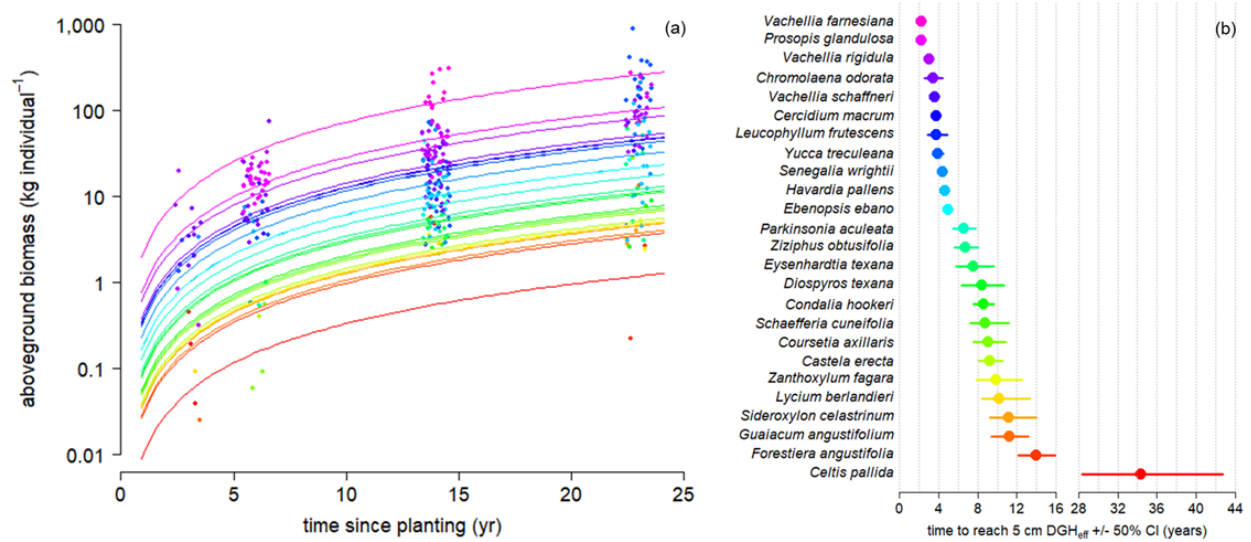
Wide variation in mortality rates of planted individuals was observed between species over the course of the chronosequence study. Mortality rates of all species were high initially and slowed over time, reflecting high initial mortality of seedlings due to some combination of

transplant shock, environmental stress, and early herbivory (Fig. 3a and Fig. 3b). Subsequent decreased mortality reflects higher survival of those individuals which survived the seedling stage. Honey mesquite and Texas ebony suffered the lowest mortality rates, with greater than 60% survival 23 years post-planting. Observed mortality rates decrease from this maximum, with many species suffering complete or near-complete mortality by 23 years post-planting. At the community level, mortality was observed to decrease with time, with a peak immediately after an initial planting and subsequently increasing survival with time (Fig. 3c).



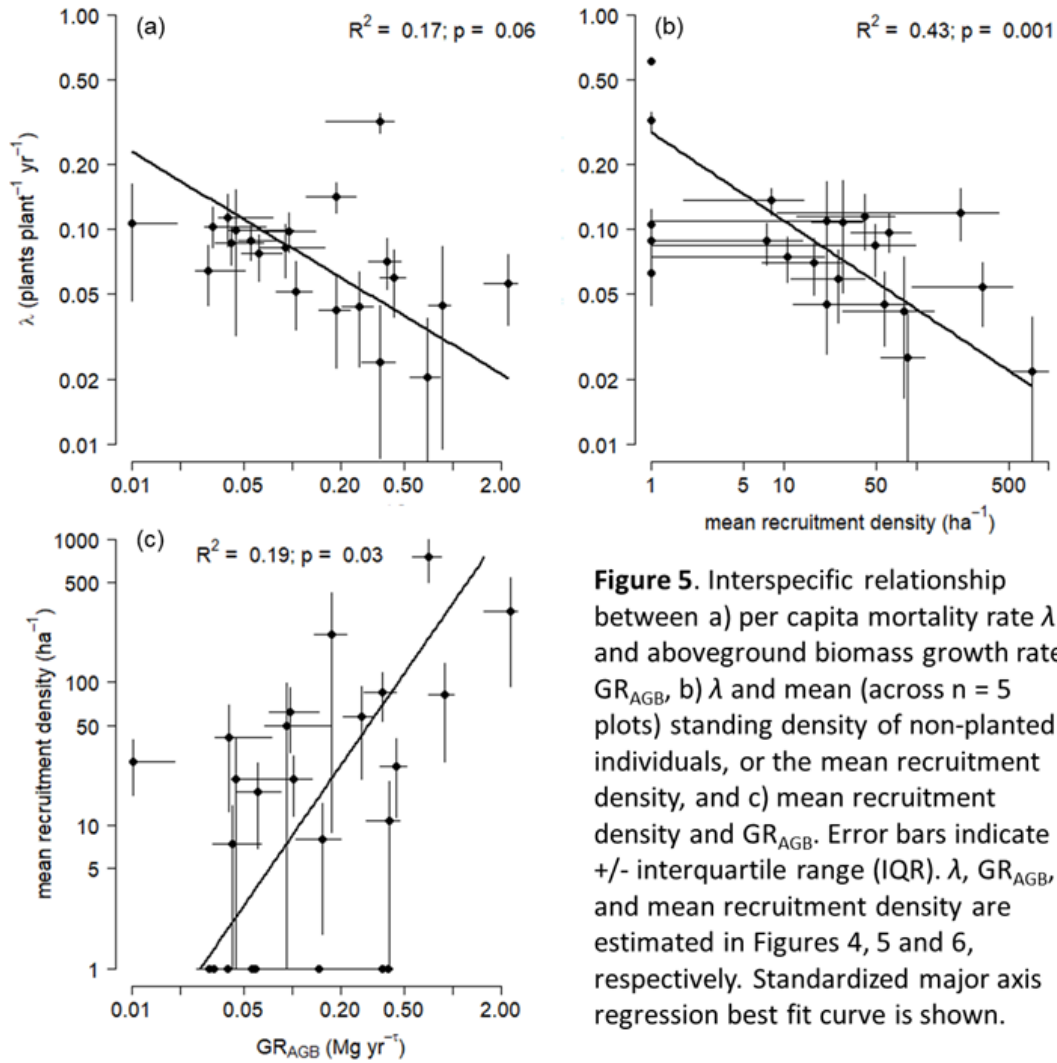
**Figure 3.** Community and species-specific survival trajectories and associated mortality rates as determined from a chronosequence spanning 1-23 years since planting. (a) Species are ordered and colored cool to warm in terms of increasing per capita mortality rate  $\lambda$  (% yr<sup>-1</sup>), shown in (b). (c) Inferred community-level per capita mortality rate  $m$  (% yr<sup>-1</sup>) in between successive plot ages.

Orders of magnitude in the rate of accumulation of aboveground biomass at the individual scale was observed between species (Fig. 4a).



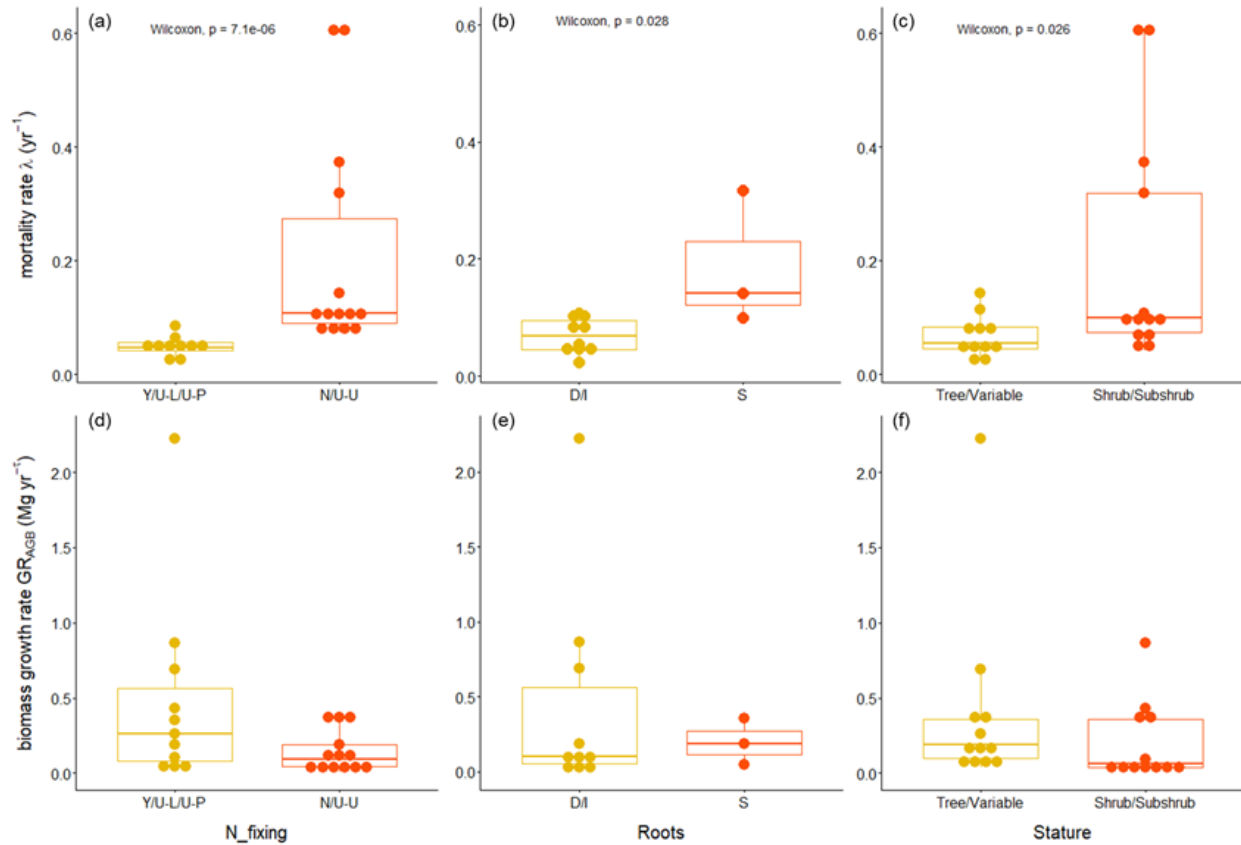
**Figure 4.** a) Biomass growth trajectories for planted individuals encountered in at least one plot, fitted to the function  $AGB_i \sim GR_{AGB,i} t^\tau$ , where  $GR_{AGB}$  is the species-specific biomass growth rate and scaling exponent  $\tau$  is a constant. b) Species are ordered top to bottom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

A significant negative correlation was found between a species' mortality rate and mean recruitment density (Fig 5b). A significant positive correlation was observed between a species' recruitment density and its biomass growth rate (Fig 5c). A non-significant negative correlation between species-specific biomass growth rate and mortality rate was observed (Fig. 5a).



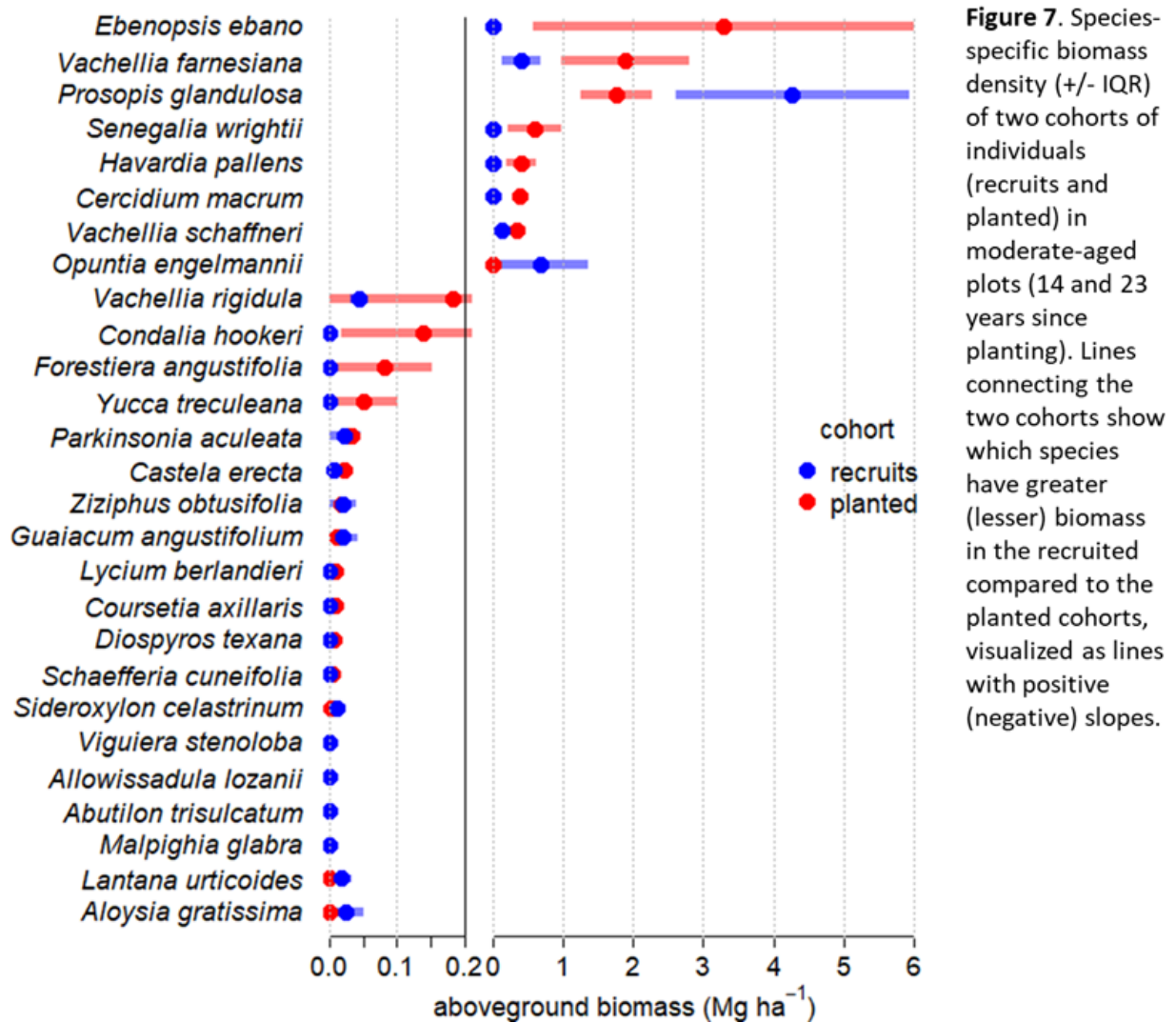
**Figure 5.** Interspecific relationship between a) per capita mortality rate  $\lambda$  and aboveground biomass growth rate  $GR_{AGB}$ , b)  $\lambda$  and mean (across  $n = 5$  plots) standing density of non-planted individuals, or the mean recruitment density, and c) mean recruitment density and  $GR_{AGB}$ . Error bars indicate  $\pm$  interquartile range (IQR).  $\lambda$ ,  $GR_{AGB}$ , and mean recruitment density are estimated in Figures 4, 5 and 6, respectively. Standardized major axis regression best fit curve is shown.

Growth and mortality were compared with a series of qualitative variables to test for predictive power (Fig. 6). Mortality was observed to be higher in species which do not fix nitrogen (versus those which do), which have shallow roots (versus those which have roots of intermediate or great depth), and which attain tree stature (versus those which are shrubs or subshrubs). No significant differences were observed in aboveground biomass growth rate of species which differed in these three predictor variables.

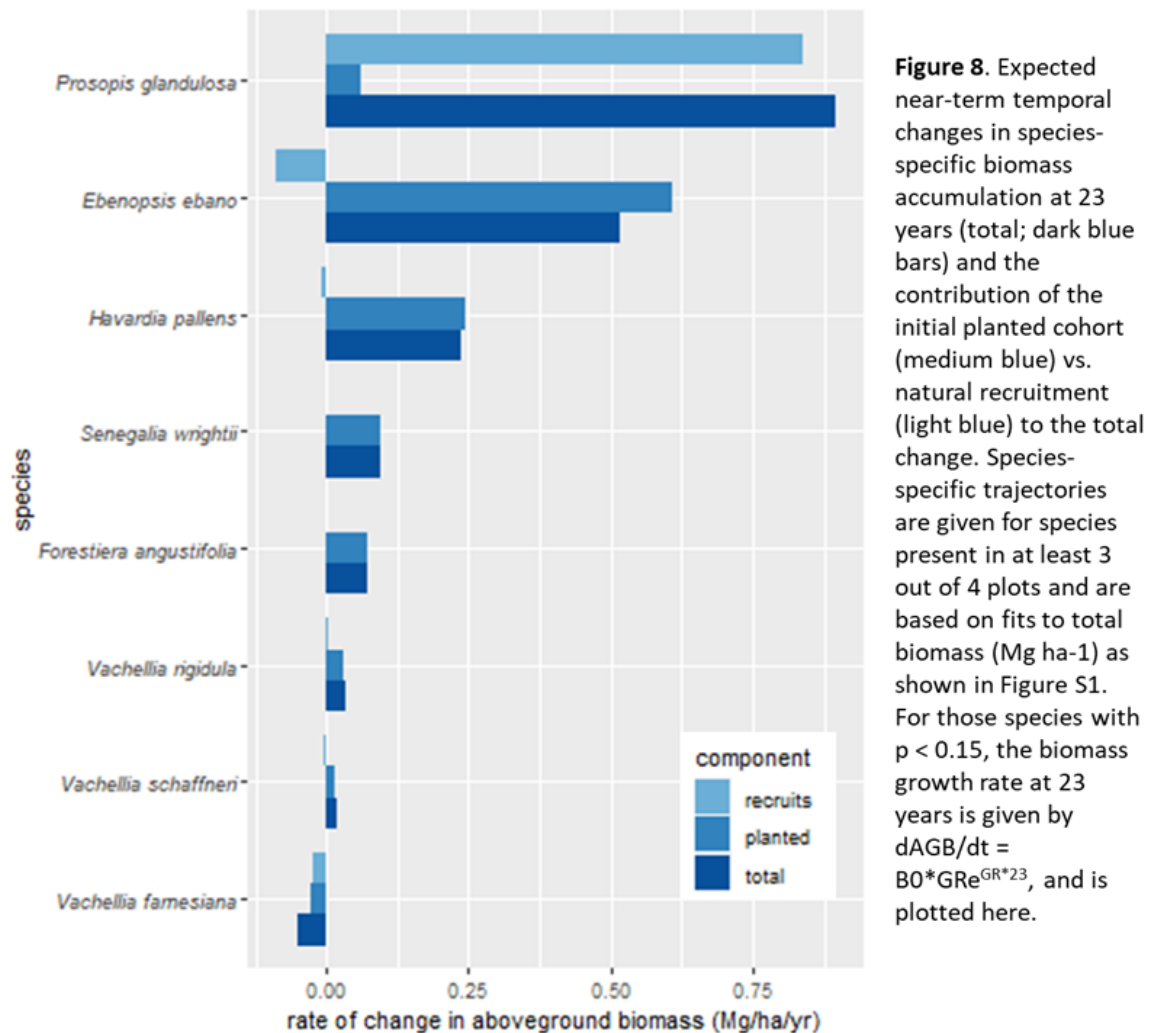


**Figure 6.** Boxplots of species mortality rate (a – c) and biomass growth rate (d – f) as given by three functional characteristics: a), d) nitrogen fixing ability (Y = yes, U-L = unknown but likely based on genus or family affiliation, U-P = unknown but possible based on a family or subfamily with 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  $\alpha = 0.05$  level.

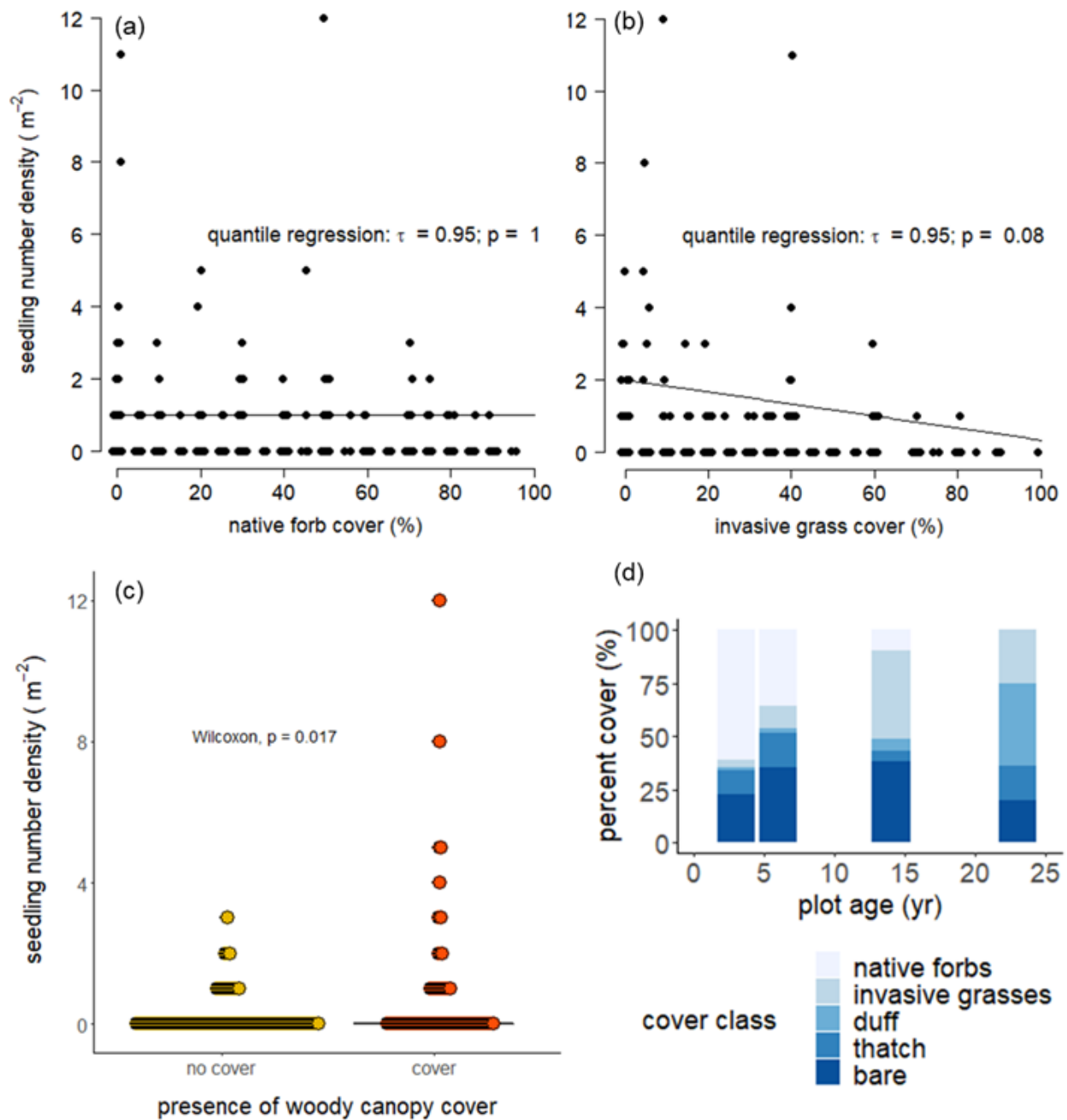
A consistent trend towards dominance of the woody component of the flora at reforestation sites by a handful of leguminous trees was observed, where Texas ebony, huisache, and honey mesquite contributed an overwhelming portion of total biomass on an areal basis, the remainder contributed by 24 woody and suffrutescent species. (Fig. 7). However, the origin of the trees contributing this biomass varies, with biomass of Texas ebony and huisache contributed primarily by trees which had been included in the original reforestation, and that of mesquite contributed primarily by volunteer trees. Many species which were planted on the landscape persist at low areal density of biomass, this contributed by a handful of individuals.



Near-future biomass accumulation rate estimates were derived from species' 23-year biomass accumulation rate (Fig. 8).



Species-level trends in biomass accumulation suggest that rates of near-future accumulation of biomass density on the landscape will vary widely (Fig. 8). Most species for which estimation was possible are expected to increase in total biomass density, although *Vachellia farnesiana* is expected to decline in the near future. Of note here are the different relative contributions to a species' total expected biomass accumulation rate of planted versus recruited individuals.



**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 ( $\tau = 0.95$ ).

Seedling number density is relatively stable at a range of coverages in native forbs, but decreases when associated with higher coverages of invasive grasses at the 1 m<sup>2</sup> scale (Fig. 9 and b). In quadrats with less than 10% cover in invasive grasses seedling number density is significantly higher under canopy coverage than in full sun (Fig. 9c). Over time, the herbaceous component became dominated by a handful of invasive exotic grasses (primarily *Cenchrus ciliaris*, but also *Megathyrsus maximus*, *Melinis repens*, *Dichanthium annulatum*, and *Cynodon dactylon*)

## Discussion

Here we show that even as reforested areas steadily accumulate biomass over ~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 that volunteer individuals are primarily of a limited subset of those species which survive in the initial planted cohort (Supplemental Table 3). Additionally, a shift in understory vegetation from native forbs and graminoids to non-native grasses was observed, suggesting a trend towards increasingly suppressed recruitment of native woody species. 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. While specific recommendations for planting methodology are beyond the scope of this publication, several recent works are rich sources of information directly useful to land managers in this region (Mohsin et al. 2021, Dick et al. 2016, Alexander et al. 2016).

**Biomass accumulation is expected to continue even as woody plant abundance stabilizes**

Although the number density of mature trees at these sites stabilizes with time (Fig. 2b), surviving trees are continuing to grow and accumulation of biomass per hectare at the landscape level continues (Fig. 2a). Comparisons can be made with similar forests of this and other regions. A series of forests similar to that of the LRGV in northeastern Mexico were estimated to contain  $60.31 \pm 12.24 \text{ Mg ha}^{-1}$  (Navar et al. 2002). This value represents a weighted average of sites across the state of Nuevo Leon, which range from 59.83 to 83.37  $\text{Mg ha}^{-1}$  and, importantly, represents the sum of an estimated aboveground biomass of 30.75  $\text{Mg ha}^{-1}$  and estimated root biomass of  $23.56 \pm 4.25 \text{ Mg ha}^{-1}$ . The highest aboveground biomass recorded at any site included in this study was that of the northern 1987 planting, where a value 70.87  $\text{Mg ha}^{-1}$  was estimated (Fig. 2a). However, this site may not represent high-quality habitat when considered from a conservation standpoint, due to a lack of species diversity and palatable ground-level vegetation. A site at which reforestation is believed to have failed accrued 11.66  $\text{Mg ha}^{-1}$  over the same period which is, interestingly, substantially less than younger sites at which initial reforestation did not fail entirely.

### **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 per capita mortality rates of the planted cohort changed over time (Fig. 3c). Knowing the timescale over which mortality remains elevated above background levels has important implications for management, especially when restoration interventions are available to reduce such mortality (Mohsin et al. 2021, Padilla et al. 2011). Long term forest dynamics plots subject to repeat surveys are nonexistent within our region and are generally rare within dry forests (Moonlight et al. 2020). 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 7-15 years in the chronosequence here.

### **Species survival scales with growth rate, ability to fix nitrogen, and a deep rooting habit**

Identification of one or a suite of traits which predict growth and survival metrics of woody species is a central goal of plant ecophysiologicalists (Lavorel and Garnier 2002, Aguirre-Gutiérrez et al. 2019). Identification of such traits is not possible without data from on-the-ground survey efforts, and the results of this study clearly demonstrate temporal trends in species composition, biomass accumulation, and forest structure for which mechanistic explanations can be sought. A species' ability to fix atmospheric nitrogen was found to be a strong predictor of survival post-planting and subsequent recruitment at these farmed oldfield sites (Fig. 6a). This may indicate that soil nitrogen content limits growth of species seen to suffer relatively higher mortality rates, and that inclusion of nitrogen-fixing plants may be increased in future restorations. Additionally, species reported in the literature to develop deep root systems at maturity survive at a higher rate than do those which develop root systems of intermediate or shallow depth.

Interestingly, species which exhibit relatively biomass high growth rates also survived post-planting and recruited at relatively high rates (Fig. 5). 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. A possible avenue of study is suggested by a marginally-insignificant positive correlation between species survival and biomass accumulation (Fig 5a) and a significant relationship between species mean recruitment rate and aboveground rate of biomass accumulation (Fig. 5c). Possible explanations for this

correlation can be placed into either of two categories: those for which a high growth rate is itself the underlying cause of survival and those for which high growth and survival rates are both underlain by an unknown explanatory factor. Rapid growth of above- or below-ground organs may allow a species to escape competition for light or water with invading forbs and grasses early in life. Similarly, rapid height increase may allow survival for the simple reason that the pool of relevant herbivores decreases as height increases.

### **Caveats to interpretation of results**

Interpretation of the results of this study is limited in that mortality or growth-rate depression of any individual tree cannot be definitively linked with a stressor known to be important at the site, such as browsing, transplant shock, or drought. In some cases, the presence of visible browsing damage on surviving individuals of a species inconclusively implicates herbivory as a partial or whole cause of decline in that species' number density since planting. Large mammalian herbivores such as white-tailed deer (*Odocoileus virginianus*), wild pigs (*Sus scrofa*) and nilgai (*Boselaphus tragocamelus*) are present on the site and are likely to exert significant pressure on vegetation. Recent work suggests that seedling mortality due to herbivory is an obstacle for reforestation at Sal del Rey, as evidenced by an elevated mortality rate of unprotected versus protected seedlings during one year of regular surveys following a November 2018 planting (Mohsin et al. 2021). However, this claim must be treated cautiously because seedling shelters alter microsite conditions and may influence survivorship primarily in that way rather than by offering physical protection. A second possible causative agent of decline is transplant shock in the days and weeks immediately after the initial planting event. High mortality during this period was observed during the 2018-19 surveys and is assumed to have been a factor in species' number density declines in all historic reforestations, but a definitive

proof of that is not possible (Mohsin et al. 2021). The final stressor which may influence survival and growth rates are this region's regular periods of extreme heat and water limitation. Summer weather conditions are severe, with a combination of extremely high temperatures and periods of little to no rainfall, although a summer peak in seedling mortality is neither confirmed nor denied by the data reported in Mohsin et al. (2021). Precipitation is lower in winter than in the summer in the LRGV and, though cooler, temperatures still routinely exceed 25 C and drought stress may be considerable. Seedlings, relative to mature individuals of any given species, are poorly equipped to survive these conditions because they have shallow or otherwise poorly developed root systems and minimal amounts of stored carbohydrates and water for periods during which stomatal closure is necessary (Vallejo et al. 2012, Sevanto et al. 2014). The relative importance of these three possible stressors to observed declines in number density or growth of planted individuals can be investigated using both ecological and ecophysiological tools.

### **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. Some species included in these reforestations such as *E. ebano* and *V. rigidula*, survive and accumulate biomass at a high rate, but only very rarely produce offspring which survive beyond the seedling stage (Fig. 7). These species, as well as any others which reproduce at a sub-replacement rate, may begin a rapid decrease in number density and biomass per hectare as individuals begin to senesce without enough replacements to maintain a stable number density on the landscape. A comparison of seedling maturation rate and the mortality rate of mature, healthy trees is not possible in this case, as little information on these species' lifespans exists. A concerning trend

was observed in the composition of herbaceous vegetation across all surveyed sites at Sal del Rey, in which highly competitive exotic grasses increased in abundance on the landscape over time to the exclusion of an initial cover of native forbs. Herbaceous cover during the first growing season after plowing at a Sal del Rey study site was dominated by *Verbesina encelioides*, *Croton capitatus*, *Urochloa texana*, and lower densities of assorted other native forbs and graminoids (Mohsin et al. 2021, Arias et al. *in review*). At this time, scattered bunches of *C. ciliaris* and *M. maximus* were present but did not contribute appreciably to overall cover (C. Albrecht, personal observation). From this initial high coverage in native herbaceous vegetation and negligible cover invasive grasses, the areal fraction of land covered in native forbs and graminoids consistently decreased with age in the four chronosequence plots, replaced principally by invasive grasses or their accumulating thatch (Fig 9d). A strong negative correlation was observed between the number density of seedlings within seedling survey quadrats and fractional coverage of that quadrat in invasive grass (Fig 9b). This is consistent with the observation that the recruit biomass of every species of tree except honey mesquite is stable or decreasing with time (Fig. 7), suggesting that a relatively high early tree recruitment rate has slowed or stopped in concert with areal increases in invasive grass.

Under natural conditions and at large spatial scales, a ‘shifting mosaic’ of seral stages affords habitat for species which cannot survive in climax vegetation and which persist on the landscape by migrating between sites which are recovering from disturbance (Wu and Loucks 1995, Huston 1979). Studies of second-growth forest developing on abandoned agricultural and timber land have shown that biodiversity and biomass can rapidly reach values comparable to nearby old-growth forest, although the dominant species may be partially or wholly different than those of the old-growth (Letcher and Chazdon 2009). Under ideal conditions, the dissimilar

floras at Sal del Rey and Cactus Flats could be viewed through the lens of this shifting mosaic theory, with the latter supporting slow-growing climax species and the former supporting an established forest of pioneers sheltering an understory of species more abundant at later-seral sites. However, for this mosaic to be sustainable over long periods of time succession at a given site must proceed unimpeded. At Sal del Rey, an observed negative correlation between recruitment and ground-level coverage in invasive grasses, as well as a generally low rate of recruits in all but a handful of species, suggest that succession is obstructed by some combination of competitive exclusion of seedlings by invasive grasses and low number densities of reproductively mature trees. Although the current vegetation of reforested sites at Sal del Rey is likely highly dissimilar to what would have been encountered in pre- and early-historic times, it is nonetheless indicative of development as it occurs on degraded agricultural land which has experienced invasion by competitive, non-native species. Secondary forests which experience these conditions are widespread and increasing in extent worldwide, so information on their development is valuable even though their degraded state is undesirable from a biodiversity standpoint (Padilla et al. 2009, Reynolds et al. 2007, Marshall et al. 2012).

### **Implications for management**

While technical recommendations are beyond the scope of this paper, the data reported here identifies clear avenues of research relevant to increasing the effectiveness of reforestation in the LRGV and similar regions. All data reported here are best contextualized by recent studies of seedling mortality and growth under the conditions of reforestation in the LRGV (Mohsin et al. 2021, Arias et al. *in review*, Dick et al. 2016). Two major challenges to reforestation are seen: an initial, rapid decline in species diversity post-planting (Fig. 3a and 3c) 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 (Fig. 2d, Fig. 9).

Mortality of seedlings in the first several years post-planting is nonrandom with regard to species, and identification of the species-specific cause(s) of death may inform modifications to planting methodology which reduce the impact thereof (Mohsin et al. 2021). Seedlings are subject to very harsh conditions - long periods of water stress may occur at any time of year, summer temperatures routinely exceed 37 C, oldfield soils may be unstructured and/or nutrient-poor, and insolation rate is very high except where volunteer forbs and grasses provide shade. However, little attention was historically paid to these species' seedling habitat requirements, leaving open the possibility that survival of some species at the seedling stage may be increased relative to historic levels by providing them with conditions to which they're adapted. This suggests two possible modifications to planting methodology. First, temporally staggered plantings at a site may be warranted, where an initial cohort of species observed to perform well when faced with the stressors above are planted initially and followed some years later by species adapted at the seedling stage to the relatively lower temperature and insolation under established canopy (Padilla et al. 2009). Secondly, steps may be taken at a single, initial planting to provide each species conditions conducive to survival at the seedling stage. Research exploring this possibility has been carried out but, but many questions remain (Mohsin et al. 2021, Arias et al. *in review*, Dick et al. 2016) This also suggests the need 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). Significant differences were found between myriad functional traits of species which did and did not typically benefit from facultative interactions in the arid southwestern United States (Butterfield

and 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. A preliminary assessment inconclusively supported the hypothesis that species adapted to shade performed poorly on the landscape at the decadal scale relative to those which are adapted to high insolation (Fig. 10). A species' position along a scale of increasing ratio of biomass accumulation in tubes to not in tubes is treated as a rough metric of the light environment to which seedlings are best adapted. Tubes offer shade and reduce ambient temperature. A statistically significant positive correlation was observed between this ratio and a species' per-capita mortality rate at 23 years, implying that long-term mortality on the landscape scales with a species' degree of shade adaptation as quantified in this way.

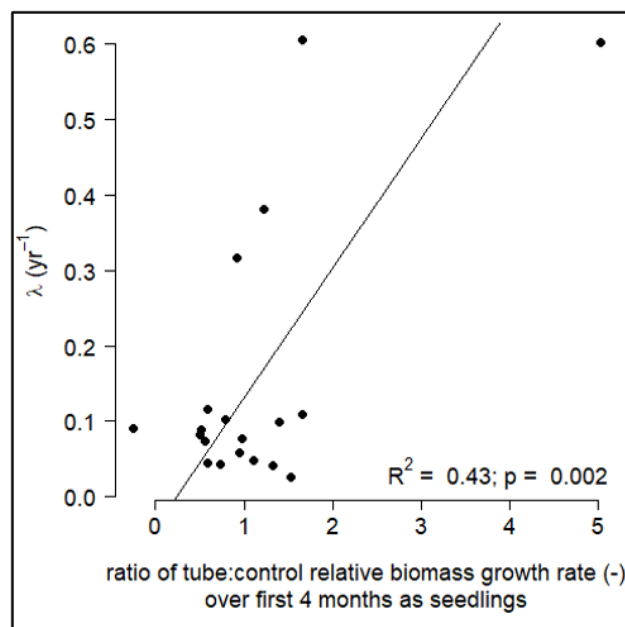


Figure 10. Ratio of tube:control relative biomass growth rates at 4 months post-planting.

Invasion of restored forests by competitive, non-native grasses is strongly associated with a depression in recruitment rate of woody species. This suggests that a sustainable recruitment rate of woody species may not be possible on sites at which herbaceous vegetation is dominated by these grasses, and that a reversion of current forest vegetation to savannah or grassland is possible at the temporal scale of mature trees' natural lifespans. The goal of regional reforestation to create sustainable, rather than temporary, habitat for wildlife is challenged at least as strongly by this possible future as it is by observed early declines in biodiversity at planted sites, and there exists the immediate need for research concerning the prevention and removal of dense populations of these grass species. One avenue of possible research is suggested by observations that these grasses do not establish in primary forests in this area, even where conditions are apparently appropriate (R. Flores, personal communication). The causes of this pattern are unknown, but will certainly inform management if ascertained. The clearest explanation for maintained dominance of a given site by primary forest is that competition is asymmetric and dominated by established individuals (Fukami et al. 2016). However, a second possibility that should not be discounted out of hand is that these invasive grasses are adapted at the juvenile stage to conditions of soil disturbance, and their absence in primary forest and dominance in reforested sites follows primarily from differences in soil conditions, with physiognomy of woody vegetation somewhat incidental and a correlate of time since disturbance. Research should be conducted concerning prevention of invasion by grasses and eradication thereof on sites at which they have achieved a high population density. Furthermore, the roles of established, dense woody vegetation and pre-planting soil disturbances in contributing to invasability of a site, as well as the nature of competition between primary forest, invasive grasses, and seedlings should be elucidated.

A focus on restoration of woody and suffrutescent species in the LRGV, while worthwhile, is limited insofar as the region may have been a mosaic of grasslands, savannahs, and closed forest before widespread land conversion and degradation (Johnston 1963). Evidence suggests that mechanisms believed to underlie global-scale encroachment of woody species into grasslands are operating in south Texas (Van Auken 2000, Fensholt et al. 2012, Archer 1989), although exact quantification of pre-historic percentages of the region in various habitat types is impossible due to the fluid nature of such a mosaic and a simple lack of records. A shift in focus to restoration of portions of natural areas to a state of dominance in native grasses and forbs may increase habitat heterogeneity in restored areas and the value of those areas to wildlife (Erdős et al. 2018), although many questions remain about species selection and long-term development of these sites. What were the extents of grassland and savanna in the LRGV during its late pre-history (Archer et al. 1989)? What is the species composition of a desirable herbaceous community in this region? Directional change in grassland ecosystems is documented, although replacement of one guild by another is not borne on by identical factors as is the replacement of canopy-forming tree guilds (Collins and Adams 1983, Pickett et al. 1987). Finally, to what extent can established grassland resist invasion both by invasive grasses and native woody vegetation? Grasslands dominated by established perennial bunchgrasses have been observed to resist invasion by invasive grasses and woody species, although grasslands near Alice, Texas, were observed to undergo slow invasion by pioneer *P. glandulosa* nucleating a slowly-growing copse of trees (Blumenthal et al. 2005, Porensky et al. 2014, Archer et al. 1989).

## **Conclusion**

Surveys of a chronosequence of sites allowed for the detection of trends in the development of planted forests and some ability to predict near-future changes. Mortality of planted trees stabilized at a low rate after 7-15 years, but competition between invasive grasses and naturally regenerating seedlings is expected to increase and may hamper replacement of mature trees. We observed a large decline in tree species diversity with time, such that diversity at the longest time scale measured was a small portion of that at the time of an initial planting. Natural regeneration was limited to a small number of species, themselves a subset of those species observed to survive at relatively high rates on the landscape when planted as seedlings. This work was undertaken to identify methodological shortcomings of reforestation as practiced historically in the LRGV, and to identify topics conducive to study by ecological and ecophysiological tools. More broadly, this work contributes to the growing body of literature concerning reforestation in semi-arid climates under conditions of soil degradation and biological invasion.

## Supplemental Information

**Supplemental Table S2.1** Geographic characteristics of each transect included in this survey.

The “Begin Lat/Lon” corresponds with x=0 on a given transect, and the “End Lat/Lon” corresponds with the end of that transect. The bearing is the compass direction of “End Lat/Lon” from “Begin Lat/Lon.” Length is the overall length of that transect.

USFWS Plot Code	Transec t	Begin Lat/Lon	End Lat/Lon	Bearing (degrees)	Length (m)
10fg	a	26.52074 -98.05957	26.522547 -98.061223	320	260
10fg	b	26.51901 -98.06199	26.520769 -98.063639	320	270
10fg	c	26.51730 -98.06425	26.519001 -98.065843	320	250
11d	a	26.54928 -98.04019	26.55033 -98.04648	280	640
SR80	a	26.55133 -98.04706	26.551520 -98.049576	274	250
SR80	b	26.54934 -98.04724	26.549579 -98.049815	274	260
SR80	c	26.54738 -98.04743	26.547602 -98.049962	274	260
SR52	a	26.53911 -98.08604	26.53692 -98.08824	222	330
SR52	b	26.53959 -98.08647	26.53723 -98.08894	222	350
Rudman02	a	26.533937 -97.982181	26.534001 -97.982692	280	50
Rudman30	a	26.534412 -97.982178	26.534495, -97.982623	280	50

**Supplemental Table S2.2.** Species planting densities (number planted ha<sup>-1</sup>), with total number of individuals planted in parentheses, across the five Sal del Rey plots where planting information was known.

Species	Years since planting (year planted)				
	1 (2018)	3 (2016)	6 (2013)	14 (2006)	23 (1996)
<i>Abutilon trisulcatum</i>	0 (0)	0 (0)	0 (0)	3 (108)	0 (0)
<i>Adelia vaseyi</i>	0 (0)	10 (289)	16 (294)	2 (65)	0 (0)
<i>Allowissadula lozanii</i>	0 (0)	0 (0)	0 (0)	3 (93)	0 (0)
<i>Aloysia gratissima</i>	0 (0)	10 (289)	16 (294)	12 (398)	24 (241)
<i>Amyris texana</i>	41 (50)	30 (866)	45 (833)	0 (0)	0 (0)
<i>Baccharis neglecta</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Bernardia myricifolia</i>	0 (0)	10 (289)	0 (0)	0 (0)	0 (0)
<i>Capsicum annum</i>	0 (0)	0 (0)	0 (0)	14 (461)	14 (142)
<i>Castela erecta</i>	41 (50)	59 (1733)	89 (1649)	22 (733)	13 (128)
<i>Celtis laevigata</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Celtis pallida</i>	41 (50)	49 (1444)	119 (2205)	21 (701)	34 (347)
<i>Cercidium macrum</i>	41 (50)	7 (202)	11 (196)	31 (1039)	23 (234)
<i>Chromolaena odorata</i>	41 (50)	7 (202)	8 (147)	35 (1158)	0 (0)
<i>Citharexylum berlandieri</i>	41 (50)	0 (0)	0 (0)	0 (0)	0 (0)

<i>Colubrina texensis</i>	41 (50)	5 (144)	8 (147)	8 (269)	12 (117)
<i>Condalia hookeri</i>	41 (50)	49 (1444)	74 (1374)	13 (449)	17 (175)
<i>Cordia boissieri</i>	0 (0)	5 (144)	8 (147)	11 (374)	10 (102)
<i>Coursetia axillaris</i>	0 (0)	0 (0)	3 (49)	12 (387)	8 (79)
<i>Croton cortesianus</i>	0 (0)	4 (115)	0 (0)	0 (0)	0 (0)
<i>Cylindropuntia leptocaulis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Diospyros texana</i>	41 (50)	49 (1444)	74 (1374)	13 (439)	9 (91)
<i>Ebenopsis ebano</i>	41 (50)	20 (578)	56 (1040)	40 (1336)	36 (363)
<i>Ehretia anacua</i>	0 (0)	0 (0)	0 (0)	16 (519)	0 (0)
<i>Eysenhardtia texana</i>	0 (0)	8 (231)	12 (220)	5 (166)	4 (36)
<i>Forestiera angustifolia</i>	41 (50)	59 (1733)	159 (2940)	11 (360)	13 (127)
<i>Guaiacum angustifolium</i>	41 (50)	59 (1733)	89 (1649)	18 (596)	12 (117)
<i>Havardia pallens</i>	41 (50)	40 (1155)	59 (1099)	27 (893)	17 (177)
<i>Koeberlinia spinosa</i>	0 (0)	10 (289)	16 (294)	0 (0)	0 (0)
<i>Lantana urticoides</i>	0 (0)	10 (289)	11 (196)	2 (83)	0 (0)
<i>Leucophyllum frutescens</i>	0 (0)	20 (578)	5 (98)	1 (18)	2 (17)
<i>Lycium berlandieri</i>	0 (0)	20 (578)	30 (550)	10 (341)	17 (171)
<i>Malpighia glabra</i>	0 (0)	7 (202)	11 (196)	0 (0)	3 (32)
<i>Opuntia engelmannii</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

<i>Parkinsonia aculeata</i>	0 (0)	0 (0)	0 (0)	39 (1304)	25 (255)
<i>Phaulothamnus spinescens</i>	41 (50)	40 (1155)	59 (1099)	7 (241)	13 (135)
<i>Prosopis glandulosa</i>	0 (0)	6 (173)	9 (165)	40 (1333)	35 (350)
<i>Randia rhagocarpa</i>	41 (50)	30 (866)	45 (833)	4 (132)	4 (37)
<i>Rhamnus humboldtiana</i>	40 (49)	59 (1733)	29 (539)	6 (208)	18 (178)
<i>Sapindus saponaria</i> var. <i>drummondii</i>	0 (0)	0 (0)	9 (160)	0 (0)	0 (0)
<i>Schaefferia cuneifolia</i>	0 (0)	30 (866)	0 (0)	0 (0)	8 (76)
<i>Senegalia berlandieri</i>	41 (50)	49 (1444)	74 (1374)	28 (937)	30 (302)
<i>Senegalia wrightii</i>	40 (49)	0 (0)	21 (392)	58 (1922)	25 (251)
<i>Sideroxylon celastrinum</i>	41 (50)	30 (866)	45 (833)	6 (214)	18 (187)
<i>Trixis inula</i>	0 (0)	10 (289)	0 (0)	0 (0)	0 (0)
<i>Vachellia farnesiana</i>	0 (0)	0 (0)	0 (0)	28 (921)	15 (156)
<i>Vachellia rigidula</i>	41 (50)	30 (866)	45 (833)	13 (439)	0 (0)
<i>Vachellia schaffneri</i>	41 (50)	30 (866)	45 (833)	9 (314)	26 (262)
<i>Viguiera stenoloba</i>	41 (50)	10 (289)	16 (294)	2 (72)	0 (0)
<i>Yucca treculeana</i>	0 (0)	40 (1155)	40 (735)	125 (4161)	9 (96)
<i>Zanthoxylum fagara</i>	41 (50)	40 (1155)	5 (98)	0 (0)	3 (29)
<i>Ziziphus obtusifolia</i>	41 (50)	41 (1184)	86 (1589)	13 (444)	15 (149)

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**Supplemental Table S2.3.** Number density (number ha<sup>-1</sup>) of individuals surveyed (number recorded in parentheses) in each of seven plots at Sal del Rey and Teniente tracts. ‘P’ and ‘R’ refer to surveyed individuals determined to be of the original planted cohort vs. volunteer recruits, respectively. The two plots at Teniente, 33DS and 33F, are direct seeded and fallow (failed transplantation) plots, respectively. Individuals in 33DS and 33F were inferred to be entirely planted and recruited, respectively. Surveys in the 2018 plot were done exclusively on planted seedlings and thus recruitment estimates are unavailable. Entries are color coded as follows: gray cells: not planted and not recorded; yellow cells: not planted but recorded; red cells: planted but not recorded; blue cells: planted and recorded. Planting information was not available for 33DS and 33F, and thus are not shaded.

Species	Years since planting (year planted)											
	1 (2018)		3 (2016)		6 (2013)		14 (2006)		23 (1996)		33DS (1987)	33F (1987)
	P	P	R	P	R	P	R	P	R	P	R	
<i>Abutilon trisulcatum</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
<i>Adelia vaseyi</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
<i>Allowissadula lozanii</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
<i>Aloysia gratissima</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	479 (15)	0 (0)	0 (0)	0 (0)	0 (0)	

<i>Amyris texana</i>	34 (41)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Baccharis neglecta</i>	0 (0)	0 (0)	0 (0)	0 (0)	12 (8)	0 (0)	128 (4)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Bernardia myricifolia</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Capsicum annuum</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Castela erecta</i>	20 (24)	0 (0)	0 (0)	0 (0)	0 (0)	7 (5)	32 (1)	3 (2)	49 (1)	0 (0)	0 (0)
<i>Celtis laevigata</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Celtis pallida</i>	30 (37)	142 (3)	0 (0)	55 (1)	55 (1)	0 (0)	32 (1)	0 (0)	49 (1)	0 (0)	0 (0)
<i>Cercidium macrum</i>	37 (45)	0 (0)	0 (0)	6 (4)	0 (0)	16 (12)	0 (0)	4 (3)	49 (1)	0 (0)	0 (0)
<i>Chromolaena odorata</i>	29 (35)	0 (0)	0 (0)	2 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Citharexylum berlandieri</i>	38 (46)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Colubrina texensis</i>	29 (35)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	32 (1)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Condalia hookeri</i>	35 (42)	0 (0)	0 (0)	109 (2)	0 (0)	4 (3)	32 (1)	9 (6)	49 (1)	0 (0)	20 (1)
<i>Cordia boissieri</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Coursetia axillaris</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (2)	0 (0)	3 (2)	0 (0)	0 (0)	0 (0)

<i>Croton cortesianus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Cylindropuntia leptocaulis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	32 (1)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Diospyros texana</i>	27 (33)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	243 (5)	0 (0)	0 (0)
<i>Ebenopsis ebano</i>	34 (41)	49 (2)	0 (0)	6 (4)	164 (3)	30 (23)	32 (1)	24 (16)	147 (4)	920 (46)	80 (4)
<i>Ehretia anacua</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Eysenhardtia texana</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Forestiera angustifolia</i>	27 (33)	0 (0)	0 (0)	164 (3)	0 (0)	1 (1)	0 (0)	3 (2)	0 (0)	0 (0)	0 (0)
<i>Guaiacum angustifolium</i>	4 (5)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	32 (1)	4 (3)	0 (0)	0 (0)	0 (0)
<i>Havardia pallens</i>	31 (38)	1 (1)	0 (0)	59 (4)	55 (1)	12 (9)	32 (1)	9 (6)	196 (5)	0 (0)	0 (0)
<i>Koeberlinia spinosa</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Lantana urticoides</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	33 (2)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Leucophyllum frutescens</i>	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Lycium berlandieri</i>	0 (0)	47 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)
<i>Malpighia glabra</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

<i>Opuntia engelmannii</i>	0 (0)	0 (0)	0 (0)	0 (0)	55 (1)	0 (0)	214 (116)	0 (0)	0 (0)	0 (0)	20 (1)
<i>Parkinsonia aculeata</i>	0 (0)	0 (0)	0 (0)	0 (0)	3 (2)	3 (2)	32 (1)	1 (1)	0 (0)	0 (0)	0 (0)
<i>Phaulothamnus spinescens</i>	22 (27)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Prosopis glandulosa</i>	0 (0)	96 (3)	1267 (53)	6 (4)	1375 (31)	30 (23)	668 (112)	25 (17)	252 (75)	0 (0)	160 (8)
<i>Randia rhagocarpa</i>	37 (45)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Rhamnus humboldtiana</i>	26 (32)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	64 (2)	0 (0)	49 (1)	0 (0)	20 (1)
<i>Sapindus saponaria</i> var. <i>drummondii</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Schaefferia cuneifolia</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (2)	0 (0)	0 (0)	0 (0)
<i>Senegalia berlandieri</i>	35 (42)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	64 (2)	0 (0)	49 (1)	0 (0)	0 (0)
<i>Senegalia wrightii</i>	35 (42)	0 (0)	0 (0)	2 (1)	0 (0)	21 (16)	32 (1)	22 (15)	1019 (21)	0 (0)	0 (0)
<i>Sideroxylon celastrinum</i>	26 (31)	47 (1)	0 (0)	0 (0)	55 (1)	1 (1)	0 (0)	0 (0)	146 (3)	0 (0)	0 (0)
<i>Trixis inula</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

<i>Vachellia farnesiana</i>	0 (0)	0 (0)	205 (51)	0 (0)	1188 (47)	17 (13)	9 (7)	4 (3)	150 (6)	0 (0)	20 (1)
<i>Vachellia rigidula</i>	37 (45)	0 (0)	0 (0)	44 (28)	273 (5)	11 (8)	128 (4)	0 (0)	3 (2)	0 (0)	0 (0)
<i>Vachellia schaffneri</i>	32 (39)	149 (8)	47 (1)	17 (11)	0 (0)	16 (12)	72 (8)	4 (3)	6 (4)	0 (0)	0 (0)
<i>Viguiera stenoloba</i>	7 (9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Yucca treculeana</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	8 (6)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Zanthoxylum fagara</i>	39 (47)	0 (0)	0 (0)	55 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	80 (4)
<i>Ziziphus obtusifolia</i>	32 (39)	0 (0)	47 (1)	0 (0)	109 (2)	4 (3)	0 (0)	1 (1)	149 (5)	0 (0)	0 (0)

Supplemental Code S1: 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-Garcia et al. (2014).

```
### Allometric biomass equations from Rojas-Garcia et al. 2014, Navar et al.
(2004), and Navar et al. (2001)
```

```
## UNITS
```

```
## Returns individual aboveground biomass in units of (kg)
```

```
# note (CA): Rojas Garcia uses D0.0 to mean basal diameter and height to mean
height. heightis code uses diam.basal = basal diameter and height = height.
```

```
require(hutils) ## For vectorized Switch() function (BC)
```

```
wrap_AGB <- function(gen.spp, diam.basal, height){
```

```
  Switch(gen.spp,
```

```
    Prosopis.glandulosa = pro.gla_AGB(diam.basal,height),
```

```
    Ebenopsis.ebano     = ebe.eba_AGB(diam.basal,height),
```

```
    #Ebenopsis.ebano     = global_AGB(diam.basal,height),
```

```
    Havardia.pallens    = hav.pal_AGB(diam.basal,height),
```

```
    Zanthoxylum.fagara = zan.fag_AGB(diam.basal,height),
```

```
    Celtis.pallida       = cel.ehr_AGB(diam.basal,height),
```

```
    Celtis.ehrenbergiana = cel.ehr_AGB(diam.basal,height),
```

```

Vachellia.rigidula      = vac.rig_AGB(diam.basal,height),

Vachellia.farnesiana    = vac.far_AGB(diam.basal,height),

Senegalia.berlandieri   = sen.ber_AGB(diam.basal,height),

Condalia.hookeri        = con.hoo_AGB(diam.basal,height),

Diospyros.texana        = dio.tex_AGB(diam.basal,height),

Forestiera.angustifolia = for.ang_AGB(diam.basal,height),

## Other shrubs from Table 1 of Navar et al. (2004)

Amyris.texana           = oth.shr_AGB(diam.basal,height),

Senegalia.greggii       = oth.shr_AGB(diam.basal,height),

Senegalia.wrightii      = oth.shr_AGB(diam.basal,height),

Citharexylum.berlandieri= oth.shr_AGB(diam.basal,height),

Rhamnus.humboldtiana    = oth.shr_AGB(diam.basal,height), # Synonym
Karwinskia humboldtiana

Leucophyllum.frutescens = oth.shr_AGB(diam.basal,height),

Ziziphus.obtusifolia    = oth.shr_AGB(diam.basal,height),

## Other trees use the global AGB equation of Navar et al. (2004)

Celtis.laevigata        = global_AGB(diam.basal,height),

Cercidium.macrum        = global_AGB(diam.basal,height), # synonym =
Parkinsonia texana (Texas paloverde)

Cordia.boissieri        = global_AGB(diam.basal,height),

```

```

    Ehretia.anacua          = global_AGB(diam.basal,height),

    Fraxinus.berlandieriana = global_AGB(diam.basal,height),

    Leucaena.pulverulenta   = global_AGB(diam.basal,height), # tepehuaje

    Parkinsonia.aculeata    = global_AGB(diam.basal,height), # retama

    Vachellia.schaffneri    = global_AGB(diam.basal,height),

    Sabal.mexicana          = pre.mon_AGB(height), # As suggested by USDA
FS Urban Tree Database and Allometric Equations

    #Baccharis.neglecta     = bac.con_AGB(height), # equation doesn't make
sense (see below)

    DEFAULT                 = oth.shr_AGB(diam.basal,height)

)

}

# Table 1 of Frangi & Lugo (1985) Ecological Monographs (BC)

pre.mon_AGB <- function(height){

    8.4*height - 10.2

}

# Table 2 of Navar et al. (2004)

global_AGB <- function(diam.basal,height){

```

```

0.026884+0.001191*diam.basal^2*height+

0.044529*diam.basal-0.01516*height+

1.025041+0.023663*diam.basal^2*height-

0.17071*height-0.09615*log(height)-

0.43154+0.011037*diam.basal^2*height+

0.113602*diam.basal+0.307809*log(diam.basal)

}

#CHECKED GOOD (CA); CHECKS GOOD (BC)

# sp <- Prosopis.glandulosa; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila,Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Prosopis.glandulosa

pro.gla_AGB <- function(diam.basal,height){

    (0.15545)+(0.110531*diam.basal)+

    (0.000797*(diam.basal^2*height))+

    (4.2362)+

    (3.2482*diam.basal)-

    (11.6949*(log(diam.basal)))+

    (-2.04254)+

    (0.387649*diam.basal)+

```

```

(0.5166*height)

}

#CHECKED GOOD (CA); DISCREPANCY BETWEEN NAVAR ET AL 2004 and ROJAS-GARCIA,
(missing - sign; went with the original NAVAR EQN (BC)

# sp <- Ebenopsis.ebano; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Pithecellobium.ebano

ebe.eba_AGB <- function(diam.basal,height){

    (-0.9523)+(0.002317*(diam.basal^2*height))+

    (-1.28375)+

    (0.027484*(diam.basal^2*height))+

    (-3.08371)+ (0.025196*(diam.basal^2*height))

}

#CHECKED GOOD (CA); CHECKS GOOD (BC)

# sp <- Havardia.pallens; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
***Pithecellobium.pallens

hav.pal_AGB <- function(diam.basal,height){

    (-0.00523)+(0.000689*(diam.basal^2*height))+

```

```

(0.8018*( log(diam.basal) ))+

(0.332213)+(0.017196*(diam.basal^2*height))-

(0.94861*diam.basal)+(3.388551*( log(diam.basal) ))+

(-0.58367)+(0.004255*(diam.basal^2*height))+

(0.393071*diam.basal)

}

#CHECKED GOOD (CA); CHECKS GOOD (BC)

# sp <- Zanthoxylum.fagara; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Zanthoxylum.fagara

zan.fag_AGB <- function(diam.basal,height){

(-0.58283)+(0.000668*(diam.basal^2*height))-

(0.29147*( log(height) ))+(3.288)+

(1.1233*diam.basal)+(0.84592*( log(height) ))+

(1.08316)+(0.005911*(diam.basal^2*height))-

(0.11339*height)

}

```

```

#CHECKED GOOD (CA); CHECKS GOOD (BC)

# sp <- Celtis.ehrenbergiana; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila; ref <- Navar 2004; habit <- shrub; syn <- Celtis.pallida

cel.ehr_AGB <- function(diam.basal,height){

    ((-0.02387)+(0.071082*diam.basal))+

    ((0.822031)-

    (0.3336*diam.basal)+(0.027934*(diam.basal^2*height)))+

    ((-0.97513)+(0.622086*diam.basal)))

}

# CHECK AGAINST NAVAR 2004 - SECTION "D0.0*D0.0^2" SEEMS QUESTIONABLE (CA)

# THE log(D0.0*D0.0^2*TH) portion WAS incorrect. FIXED (BC)

# sp <- Vachellia.rigidula; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Acacia.rigidula

vac.rig_AGB <- function(diam.basal,height){

    ((0.2984)-(0.3663*height)+(0.8857*( log(height) )))+

    (0.001589*(diam.basal^2*height)))+

    ((1.7299)- (1.7568*height)+(0.02176*(diam.basal^2*height)))+

```

```

      (1.1115*(    log(diam.basal^2*height)    ))+

      ((0.5772)+ (0.011244*(diam.basal^2*height))))

}

# CHECKS GOOD (CA); CHECKS GOOD (BC)

# sp <- Vachellia.farnesiana; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shurb; syn <-
Acacia.farnesiana

vac.far_AGB <- function(diam.basal,height){

      ((1.1856)+(0.7046*diam.basal)-(2.9935*(log(diam.basal))))+

      ((18.48)+(13.01*diam.basal)-(53.9*(    log(diam.basal)    )))+

      ((-4.4576)+(1.4946*diam.basal)))

}

# CHECKS GOOD (CA); CHECKS GOOD (BC)

# sp <- Senegalia.berlandieri; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Acacia.berlandieri

sen.ber_AGB <- function(diam.basal,height){

```

```

((0.006009)+(0.241108*height)+(0.000847*(diam.basal^2*height))-(0.47883*(
log(height)    )))+

      ((1.946)+(0.01667*(diam.basal^2* height)))+

      ((-0.8765)+(0.541821*diam.basal))

}

# CHECKS GOOD (CA); CHECKS GOOD (BC)

# sp <- Other.shrubs; pub <- Rojas-Garcia 2014; unit <- kg; state <- Coahuila,
Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <- Other.shrubs

oth.shr_AGB <- function(diam.basal,height){

      (-0.05266)+((0.000052)*height)+

      ((0.092582)*(    log(diam.basal^2*height)    ))+

      #(0.109003)+ ((0.014021)*(    log(diam.basal^2*height)    ))-
## Rojas-Garcia 2014 transcription error (Looks WRONG)

      (0.109003)+ ((0.014021)*(          (diam.basal^2*height)    ))-
## As originally reported in Navar 2004 (Looks CORRECT)

      ((1.62531)*height)+ ((0.89543)*(    log(diam.basal^2*height)
))+

      (0.3558)+ ((0.010336)*(diam.basal^2*height)))-

      ((0.51147)*diam.basal)+ ((1.5063)*(    log(diam.basal)    ))

```

```

}

#CHECKS GOOD (CA); CHECKS GOOD (BC)

# sp <- Condalia.hookeri; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Condalia.hookeri

con.hoo_AGB <- function(diam.basal,height){

      ((-0.49169)+(0.119894*diam.basal))+

      ((-1.34514)-(0.57648*diam.basal)+(0.036956*(diam.basal^2*height))-

      (0.07861*( log(diam.basal^2*height) ))+

      ((-2.28529)+

      (6.281245*height)+(0.004902*(diam.basal^2*height))-

      (14.8795*( log(height) ))))

}

# CHECKS GOOD (CA); FIXED 2 signs from minus to plus (BC)

# sp <- Diospyros.texana; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Diospyros.texana

dio.tex_AGB <- function(diam.basal,height){

```

```

      ((-0.4384)+(0.12124*(    log(diam.basal^2*height)    ))+

      (0.072176*height)))+(3.32259)+

      (0.010964*(diam.basal^2*height)))+(0.937974)+

      (0.0126*(diam.basal^2*height))))))

}

#CHECKS GOOD (CA); CHECKS GOOD (BC)

# sp <- Forestiera.angustifolia; pub <- Rojas-Garcia 2014; unit <- kg; state <-
Coahuila, Nuevo.Leon,Tamaulipas; ref <- Navar 2004; habit <- shrub; syn <-
Forestiera.angustifolia

for.ang_AGB <- function(diam.basal,height){

      ((-0.062164)+(0.011566*(diam.basal^2*height))+

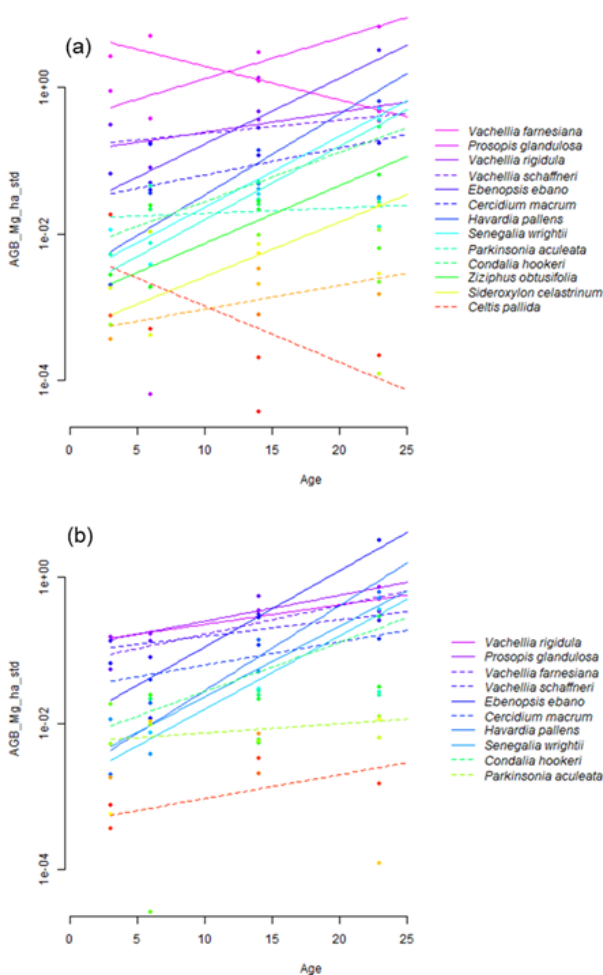
      (0.05652*(    log(diam.basal^2*height)    ))+

      ((-0.088)+(0.115089*(diam.basal^2*height))))+

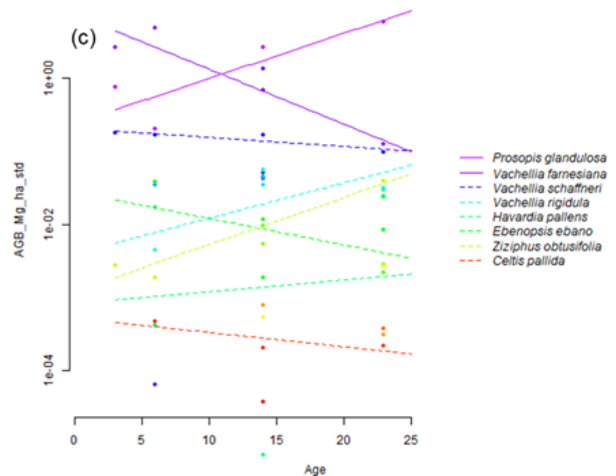
      ((-0.08742)+ (0.014452*(diam.basal^2*height))))

}

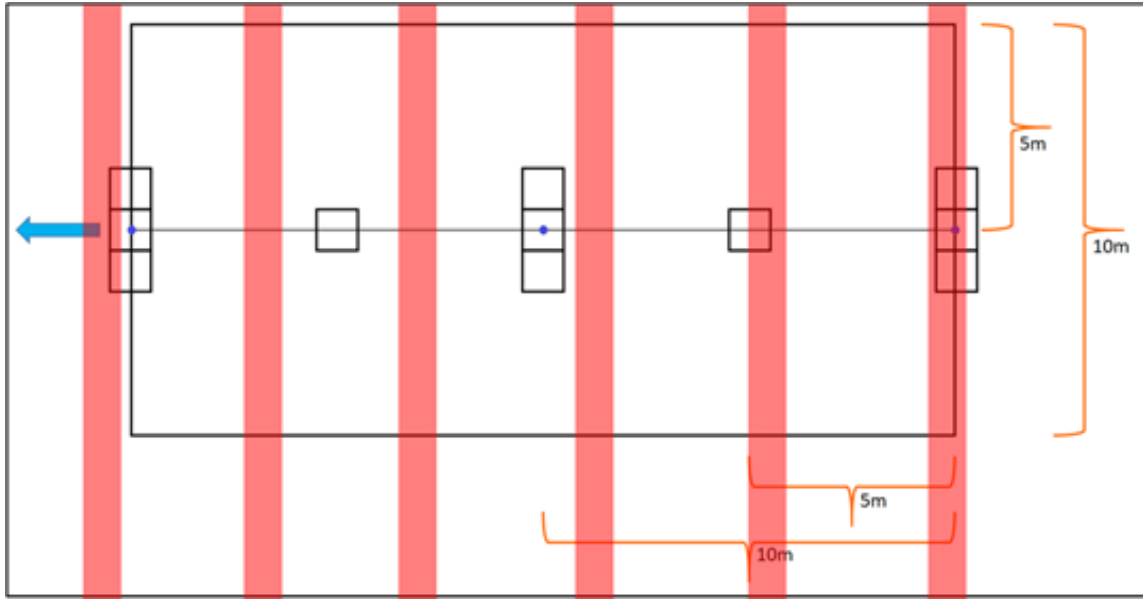
```



**Figure S1.** Species-specific temporal trends of area-based standardized aboveground biomass ( $\text{Mg ha}^{-1}$ ) of all (a), planted (b), and recruited (c) individuals. Both the total and planted AGB are standardized to a common species-specific planting density, based on the mean planting density of each species across the 4 plots. Recruitment biomass is estimated by in-field determination of species planted in vs. out of rows (see Methods). Curves were fit based on 4 different plots spanning 3 – 23 years in age (time since planting), following the equation  $\text{AGB} = B_0 e^{\text{GR} \cdot t}$ , where  $B_0$  ( $\text{Mg ha}^{-1}$ ) and  $\text{GR}$  ( $\text{yr}^{-1}$ ) are the species-specific biomass constant and accumulation rate, respectively. Species with a regression p-value  $< 0.15$  are plotted with solid lines; otherwise regression lines are dashed. Species not occurring in at least 3 out of 4 plots have no regression line. For those species with  $p < 0.15$ , the biomass growth rate at 23 years is given by  $d\text{AGB}/dt = B_0 \cdot \text{GR} e^{\text{GR} \cdot 23}$ , and is plotted in Figure 08 of the main text.



**Figure S1.** Species-specific temporal trends of area-based standardized aboveground biomass



**Figure S2.** Scale diagram of 20 m of transect. Blue dots represent midline markers, and the rightmost blue dot represents  $x=0$ , or the beginning of the transect. The transect continues to the left, as shown by the arrow. Black boxes represent seedling survey effort, and the grey line represents the midline. Orange bars marked 5m and 10m are for scale. Red fields perpendicular the midline represent tree rows, although rows vary in distance apart by site so this figure should be treated as illustrative but not exact in terms of row positions.

## CHAPTER III

### XYLEM ANATOMY PREDICTIVE POWER ON GROWTH AND SURVIVAL

#### **Introduction**

Plant physiological ecology is the sub-discipline of ecology which “seeks to describe the physiological mechanisms that underlie ecological observations” of the geographic distributions, life cycles, and ecological interactions of plants (Lambers, Chapin, and Thijs 2008). In this context, a trait is defined as “any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization” (Violle *et al.* 2007). Particular attention has been given to plant traits which influence plant performance (growth, survival, and fitness) under different light, water, and temperature conditions as well as the responses of ecosystems to these traits (Violle *et al.* 2007, Lavorel and Garnier 2002, McGill *et al.* 2006). A central goal of this field is to provide explanations for observations of plants’ responses to and interactions with their environment. Another goal is to predict changes in ecological relationships, such as shifts in geographic ranges and changes in ecosystem-level function, under novel environmental conditions based on an understanding of plants’ traits (Lavorel and Garnier 2002).

The existence of plant survival strategies follows from the need of individuals to avoid or tolerate stress while maximizing utilization of those resources which are available (Harper 1967). The most impactful stressors that an individual plant faces will be different depending on its

ecological context – plants in fertile, undisturbed sites may be in the most danger from the shade of neighbors’ leaves while plants in sites that are critically hot, cold, toxic, or infertile may suffer the most from the abiotic aspects of their environment but experience little to no competition from neighbors (Harper 1967). Tradeoffs exist between adaptation to different points along gradients of many critical resources because the architecture, vasculature, and photosynthetic investment that makes full use of a given amount of a resource may be superfluous at lower levels of that resource or insufficient at higher levels (Gleason *et al.* 2016, Onoda *et al.* 2017, Boardman 1977). It follows from this that many root, wood, and leaf traits exist on a spectrum that is variously described as “fast to slow” or “resource-acquisitive to resource-conservative,” which describes the ability of a given trait to contribute to an overall survival strategy of either outcompeting neighbors for resources under conditions conducive to growth or of enduring conditions inimical to growth and thereby largely avoiding competition. The existence of a trade-off spectrum to which traits are constrained, as well as hypothesized multi-trait coordination across this spectrum, leads to a hypothesized and experimentally supported theory of a spectrum of survival strategies, each developed by plants subject to different combinations of disturbance and stress (Grime 1977, Wright 2004, Reich 2014).

Xylem anatomy can be viewed through the lens of the spectrum noted above (Zanne *et al.* 2010; Pratt *et al.* 2007). Water flows through xylem as an uninterrupted column from plants’ roots to leaves, powered by the tension on the column generated by evaporation at the leaf-atmosphere interface (Brown 2013). When that water column is placed under tension by rapid transpiration, low soil water potential, or both, gas pockets known as emboli can form. These emboli disrupt the continuity of the water column and render that segment of the plant’s circulatory system unusable (Sperry and Tyree 1988). A tradeoff is theorized to exist between the

maximum rate of water flow through a given xylem vessel and the susceptibility of water in that vessel to loss of continuity due to embolism (Tyree et al. 1994). The maximum rate of water movement through an idealized vessel varies to the fourth power of that vessel's radius, so an apparently minor difference between two species' mean vessel size can translate into a relatively very large difference in the maximum rate of water transport between them. However, the susceptibility of a given vessel to embolism under conditions of water stress increases with diameter. A tradeoff also exists between investing cross-sectional area in vessel lumen or non-conductive parenchyma and/or fibers. Non-conductive wood surrounding vessels influences whole-stem mechanical strength and affects a species' ability to endure water stress by both preventing physical vessel collapse under tension and by contributing area for water and carbohydrate storage (Borchert 1994; Pratt and Jacobsen 2017).

Perennial plant species with woody aboveground tissues rely on myriad root, shoot, and leaf traits to survive periods of water stress. While a species' overall strategy is multifaceted and cannot be understood without study of multiple traits, useful information can nonetheless be derived from a study of a single trait abstracted from its context. Xylem anatomical and broader stem cross-sectional characteristics represent a constellation of such traits and are the focus of this study. We set out to ask a single question:

1. What are the predictive powers of four xylem anatomical metrics on growth and mortality of seedlings at 3 months, 12 months, and 23 years post-planting?

## Methods

11 tree- and shrub-forming species native to Hidalgo County, Texas, were chosen for inclusion in this study (Table 2). The chosen species are a subset of 24 included in a 2018 reforestation and subject to 12 months of post-planting surveys (Mohsin et al. 2021). Seedlings included in Mohsin et al. (2021) were categorized as having been planted without any assisting technology (“control”), within 0.8 meter tall plastic shelter tubes (“tubes”), and within encircling, buried cardboard troughs designed to provide supplemental irrigation during the initial seedling establishment phase (“cocoons”). Of the 24 species included in that survey effort, species included in this study suffered mortality at rates spanning the full range observed in specifically tube-enclosed seedlings at that study site and are, as such, considered to be a representative sample thereof. The initial decision to restrict species included here to tube-enclosed individuals present in the 2018 planting was made so as to minimize the impact of mammalian herbivory on growth and survival data, leaving species’ responses to environmental conditions the primary underlying factor. Growth and mortality response data were subsequently expanded to include data at 23 years post-planting (that reported in chapter 2 of this thesis), and that from 1, 3 and 12 months post-planting for controls, tubes, and cocoons as reported in Mohsin et al. (2021) (Table 1, Table 3).

All mature individuals from which stems were collected were rooted on or immediately adjacent to the Sal del Rey tract of the Refuge. Stems were collected from unshaded sections of boughs on the south side of individual trees, then immediately placed into plastic bags with damp napkins and transported ~27 km south to the UT Rio Grande Valley campus for later sectioning, photographing, and analysis. Stems which were not used immediately were kept damp and under refrigeration until use. At least one mature, field grown individual of all species included in this

study were recorded on iNaturalist in lieu of physical voucher collections. Sectioned seedlings were grown in a nursery managed by the US Fish and Wildlife Service near Alamo, Texas and were kept irrigated and under grow lights until sectioning. Seedlings did not experience periods of extended water stress before sectioning.

Sectioning was done with a sledge microtome (GSL1, Birmensdorf, Switzerland; Gartner et al. 2014) and sections varied in thickness from 20 to 50  $\mu\text{m}$ . Photography was done under a model OM36 Omano compound microscope at 40X (mature) and 100X (seedling) magnification and 2048 x 1536 pixels resolution. Images were captured using a high-speed model MU503B Microscope Central camera (Xihu District, Hangzhou). All final cross-sectional images were constructed by stitching together multiple individual images, so all final cross-sectional images were of dimensions larger than individual photographs as captured by the camera. Analysis of resultant photographs was carried out in imageJ image analysis software by a method adapted from that published on PrometheusWiki (Jansen and Choat 2021).

Pairwise comparisons were made between 4 anatomical “predictor” variables as measured in both seedling and mature individuals, and 18 survey-based “response” variables (Table S1). Comparisons were linear regressions, and returned p-values of  $>0.05$  were discounted as non-significant (R Core Team 2021; Wickham H 2016)

## Results

Of 72 pairwise comparisons between 4 anatomical predictor variables and 18 response variables, none were observed to be statistically significant at  $\alpha = 0.05$ . Means of all assessed variables are reported in Table 3.1.

**Table 3.1.** Species- and age class-specific means of all xylem anatomical traits quantified.

	Species	Number of Individuals Studied	Number of AOIs studied	Mean Vessel Area $\pm$ SE	Mean Number Density $\pm$ SE	Mean Vessel Fraction in Lumen $\pm$ SE	Mean Hydraulically Weighted Diameter $\pm$ SE
Mature	<i>Celtis pallida</i>	3	11	0.00151 $\pm$ 0.00045	45 $\pm$ 13	0.0639 $\pm$ 0.019	0.057 $\pm$ 0.01
	<i>Condalia hookeri</i>	3	10	0.0004 $\pm$ 0.00012	84 $\pm$ 26	0.0345 $\pm$ 0.01	0.027 $\pm$ 0.01
	<i>Diospyros texana</i>	3	11	0.0005 $\pm$ 0.00015	57 $\pm$ 17	0.0291 $\pm$ 0.008	0.027 $\pm$ 0.01
	<i>Ebenopsis ebano</i>	3	12	0.00098 $\pm$ 0.00028	59 $\pm$ 16	0.0571 $\pm$ 0.016	0.039 $\pm$ 0.01
	<i>Guaiacum angustifolium</i>	3	12	0.00082 $\pm$ 0.00023	63 $\pm$ 18	0.0529 $\pm$ 0.015	0.035 $\pm$ 0.01
	<i>Havardia pallens</i>	2	7	0.00147 $\pm$ 0.00055	54 $\pm$ 20	0.0763 $\pm$ 0.028	0.049 $\pm$ 0.02
	<i>Rhamnus humboldtiana</i>	3	12	0.00079 $\pm$ 0.00022	132 $\pm$ 38	0.1045 $\pm$ 0.03	0.041 $\pm$ 0.01
	<i>Senegalia berlandieri</i>	3	12	0.00119 $\pm$ 0.00034	39 $\pm$ 11	0.0466 $\pm$ 0.013	0.046 $\pm$ 0.01
	<i>Sideroxylon celastrina</i>	3	12	0.00048 $\pm$ 0.00013	60 $\pm$ 17	0.0298 $\pm$ 0.008	0.027 $\pm$ 0.01
	<i>Vachellia schaffneri</i>	3	12	0.00139 $\pm$ 0.00039	35 $\pm$ 10	0.0465 $\pm$ 0.013	0.048 $\pm$ 0.01
	<i>Zanthoxylum fagara</i>	2	8	0.00055 $\pm$ 0.00019	72 $\pm$ 25	0.0397 $\pm$ 0.014	0.03 $\pm$ 0.01
Seedlings	<i>Celtis pallida</i>	2	6	0.00018 $\pm$ 0.00007	26 $\pm$ 10	0.0048 $\pm$ 0.001	0.016 $\pm$ 0.01
	<i>Condalia hookeri</i>	2	6	0.00017 $\pm$ 0.00006	66 $\pm$ 26	0.0109 $\pm$ 0.004	0.015 $\pm$ 0.01
	<i>Diospyros texana</i>	2	8	0.00032 $\pm$ 0.00011	28 $\pm$ 9.9	0.008 $\pm$ 0.002	0.021 $\pm$ 0.01
	<i>Ebenopsis ebano</i>	2	8	0.00018 $\pm$ 0.00006	30 $\pm$ 10	0.0052 $\pm$ 0.001	0.015 $\pm$ 0.01
	<i>Guaiacum angustifolium</i>	2	7	0.00018 $\pm$ 0.00006	40 $\pm$ 15	0.0078 $\pm$ 0.002	0.016 $\pm$ 0.01
	<i>Havardia pallens</i>	2	7	0.00021 $\pm$ 0.00007	30 $\pm$ 11	0.0062 $\pm$ 0.002	0.017 $\pm$ 0.01
	<i>Rhamnus humboldtiana</i>	2	7	0.0002 $\pm$ 0.00007	96 $\pm$ 36	0.0191 $\pm$ 0.007	0.016 $\pm$ 0.01
	<i>Senegalia berlandieri</i>	2	8	0.0003 $\pm$ 0.0001	52 $\pm$ 18	0.0157 $\pm$ 0.005	0.021 $\pm$ 0.01
	<i>Vachellia schaffneri</i>	2	7	0.00016 $\pm$ 0.00006	55 $\pm$ 20	0.0089 $\pm$ 0.003	0.015 $\pm$ 0.01
	<i>Zanthoxylum fagara</i>	2	7	0.0002 $\pm$ 0.00007	89 $\pm$ 33	0.0181 $\pm$ 0.006	0.017 $\pm$ 0.01

## Discussion

The broad inability of this suite of xylem anatomical traits to predict growth and mortality is not unexpected, given that myriad root, shoot, and leaf traits compose any species' overall strategy for utilizing resources and responding to stress. Although these results offer little insight into the mechanistic underpinnings of observed growth and survival rates in this context, it does serve to eliminate these traits from consideration as those which may exert an overwhelming effect on growth or mortality rates at any life stage. Hydraulic failure has been implicated as a primary cause of mortality in multiple studies of tree drought response, but susceptibility to failure is known to be influenced by xylem traits which were not quantified in this work (Choat et al. 2008, Allen et al. 2010, Rowland et al. 2015, Barigah et al. 2013). Study of two of these traits, pit architecture and non-conductive wood hydraulic capacitance, may yield data complementary to the analyses reported here (Jansen et al. 2004, Meinzer et al. 2009).

Due to the presence of a lower bound in resolving power of the microscope and camera used in this study, some misidentification of lumen-like structures may have occurred. To reduce the impact of possible misidentifications, all lumen-like structures with an area below  $.0001 \text{ mm}^2$  were excluded from calculations of species-level means and subsequent analysis. Structures larger than this threshold which were identified as xylem lumen by the image analysis software were manually removed if clearly misidentified. Some xylem particles may be below this threshold in area, and their exclusion would artificially inflate the species-specific calculated mean vessel size. Some regions of translucent wood or fiber lumens may have exceeded the  $.0001 \text{ mm}^2$  threshold and, if not recognized as such and manually excluded, may have artificially lowered calculated vessel mean area. This is primarily of concern when interpreting species mean vessel area, hydraulically weighted diameter, and number density (vessels  $\times \text{mm}^{-2}$  cross

sectional area of stem). Because any possible misidentifications or accidental exclusions will have been made of lumen-like structures at the extreme minimum of areas observed, species cross-sectional fraction in xylem and mean calculated maximum conductance will be generally unaffected.

Although minimally informative in this context, the data underlying the analyses presented here may be useful when studied through any of a variety of other lenses. Large scale summary statistics of the data given here may be informative of community-level responses to climatic and edaphic conditions at Sal del Rey. All of the xylem traits considered here vary widely across woody plants globally, and the range of values presented here may be found to differ significantly from that of sites which experience significantly different environmental conditions (Kattge et al. 2011, Patiño et al. 2009, Sobrado 2011). If so, means or ranges of the traits reported here may be seen to correlate with changes in environmental conditions when making comparisons across larger spatial scales or at sites differing more widely in edaphic conditions.

Comparisons between these traits and any of the other myriad traits which affect a species' growth and survival can be used to support or oppose hypothesized inter-trait coordination across a unifying spectrum. Coordination is hypothesized to develop because any system of energetic allocation which produces interacting organs capable of processing a given resource at different rates will necessarily yield some combination of organs which produce at a rate too high for others to process, and organs which can not process the full amount provided to them by an adjacent one (Reich 2014). The most efficient way of allocating energy to the creation and maintenance of organs, then, is to coordinate the capacity of these organs to process

a given resource. Xylem characteristics as observed may coordinate with quantifiable root or leaf traits.

## Supplemental Information

**Table S3.1.** Response variables employed in this study.

Response Variable Description	Variable Code	Units
Aboveground biomass growth rate (chronseq.)	chron_AGB0	Megagrams C per year per individual
Per-capita mortality rate (chronseq.)	chron_lambda	Deaths per individual per year
First-survey control mortality (seedlings)	cn01_mortality_Control	Number of deaths * number planted <sup>-1</sup>
First-survey cocoon mortality (seedlings)	cn01_mortality_Cocoon	Number of deaths * number planted <sup>-1</sup>
First-survey tube mortality (seedlings)	cn01_mortality_Tube	Number of deaths * number planted <sup>-1</sup>
First survey difference between control and cocoon mortality (seedlings)	cn01_mortality_Control-mortality_Cocoon	Number of deaths * number planted <sup>-1</sup>
Second census control relative growth rate (seedlings)	cn03_rgr_Control	Cm * cm-1 * year <sup>-1</sup>
Second census cocoon relative growth rate (seedlings)	cn03_rgr_Cocoon	Cm * cm-1 * year <sup>-1</sup>
Second census cocoon v. control relative growth rate (seedlings)	cn03_cocoon_relative_increase ((cn03_rgr_Cocoon-cn03_rgr_Control)/cn03_rgr_Control)	Cm * cm-1 * year <sup>-1</sup>
Second census tube relative growth rate (seedlings)	cn03_rgr_Tube	Cm * cm-1 * year <sup>-1</sup>
1-year census control relative growth rate (seedlings)	cn12_rgr_Control	Cm * cm-1 * year <sup>-1</sup>
1-year census cocoon relative growth rate (seedlings)	cn12_rgr_Cocoon	Cm * cm-1 * year <sup>-1</sup>
1-year census cocoon v. control relative growth rate (seedlings)	cn12_cocoon_relative_increase ((cn12_rgr_Cocoon-cn12_rgr_Control)/cn12_rgr_Control)	Cm * cm-1 * year <sup>-1</sup>
1-year census tube relative growth rate (seedlings)	cn12_rgr_Tube	Cm * cm-1 * year <sup>-1</sup>
1-year census control mortality (seedlings)	cn12_mortality_Control	Number of deaths * number planted <sup>-1</sup>
1-year census cocoon mortality (seedlings)	cn12_mortality_Cocoon	Number of deaths * number planted <sup>-1</sup>
1-year census tube mortality (seedlings)	cn12_mortality_Tube	Number of deaths * number planted <sup>-1</sup>
1-year census difference between cocoon and control mortality (seedlings)	cn12_mortality_Control-mortality_Cocoon	Number of deaths * number planted <sup>-1</sup>

## CHAPTER IV

### CONCLUSIONS

Three main results are reported here:

1. Species diversity declines rapidly post-planting in regional reforestations as practiced historically.
2. Invasion of the developing forest understory by a guild of highly competitive exotic grasses is associated with significant depression in the recruitment rate of woody species.
3. None of a constellation of xylem anatomical traits visible at the mm<sup>2</sup> scale correlate significantly with any measure of growth and mortality of native species at a range of time scales under the conditions of oldfield replanting.

Results reported here are of immediate applicability to regional reforestation, and land managers may respond to the results reported here in any of a number of ways. The observed rapid decline in species diversity suggests either that species which may be expected to disappear from the landscape should be excluded from future plantings, or that modifications to planting methodology which promote relatively more vulnerable species should be researched and employed. Three qualitative traits, the ability to fix nitrogen, a tree habit of mature individuals, and the development of deep roots, were observed to correlate with post-planting survival and may inform inclusion of novel species in future efforts here and elsewhere. Generally poor responses to field conditions of species included in reforestation efforts historically suggests an

opportunity to consider alternative modes of restoration, namely a greater focus on the establishment of native grasses and forbs (Haddad et al. 2020, Buisson et al. 2020). Increased inclusion of graminoids and other herbaceous vegetation in restoration efforts may influence the invasability and habitat quality of sites at decadal time scales (Blumenthal et al. 2005, Porensky et al. 2014).

Although invasive grasses do not apparently exert lethal competitive pressure on mature trees, these grasses were found to be associated with a suppression in seedling number density and are strongly suspected of exerting lethal competitive pressure on that life stage of woody plants. The rate of seedling establishment at the landscape scale is expected to decrease in concert with the observed increase in population density of these grass species. A worst-case scenario is that regeneration is suppressed to such a degree as to cause reversion to grassland or savannah as established trees begin to senescence. A more likely scenario is that forests suffer long-term declines in species diversity and physical complexity as only one or a handful of species successfully regenerate in a matrix of grasses. This represents a serious threat to the long-term sustainability of restored forests and brings research on and implementation of methods of non-native grass control to the forefront of regional restoration efforts.

The two studies reported here represent, among other things, a coherent overall picture of how to carry out a plant ecophysiological study. To reiterate, the central goal of plant ecophysiology is to elucidate the underlying physiological basis for patterns observed in the natural world. First, we carried out large-scale surveys of tree growth and survivorship across a chronosequence of planted forests and quantified clear patterns of change in composition and structure of the forest with time. Then, we quantified traits which are known to relate to susceptibility of a species to one of the primary stressors in the LRGV, hot droughts, and

assessed the predictive power of those traits on plant growth and survival. Several broad, qualitative functional classifications did show predictive power on survival. Although we did not successfully correlate any studied xylem anatomical trait with growth or mortality of native species under field conditions, the sequence in which we carried out these two studies is nonetheless informative and the search for factors underlying the survey results reported here will be continued.

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