

University of Texas Rio Grande Valley

ScholarWorks @ UTRGV

Theses and Dissertations

8-2020

Optimizing Species Selection for Forest Restoration in the Lower Rio Grande Valley

Faeqa Mohsin

The University of Texas Rio Grande Valley

Follow this and additional works at: <https://scholarworks.utrgv.edu/etd>



Part of the [Biology Commons](#), [Forest Sciences Commons](#), and the [Plant Sciences Commons](#)

Recommended Citation

Mohsin, Faeqa, "Optimizing Species Selection for Forest Restoration in the Lower Rio Grande Valley" (2020). *Theses and Dissertations*. 722.

<https://scholarworks.utrgv.edu/etd/722>

This Thesis is brought to you for free and open access by ScholarWorks @ UTRGV. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of ScholarWorks @ UTRGV. For more information, please contact justin.white@utrgv.edu, william.flores01@utrgv.edu.

OPTIMIZING SPECIES SELECTION FOR FOREST RESTORATION IN THE LOWER RIO
GRANDE VALLEY

A Thesis

by

FAEQA MOHSIN

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

August 2020

Major Subject: Biology

OPTIMIZING SPECIES SELECTION FOR FOREST RESTORATION IN THE LOWER RIO
GRANDE VALLEY

A Thesis
by
FAEQA MOHSIN

COMMITTEE MEMBERS

Dr. Bradley Christoffersen
Chair of Committee

Dr. Rupesh Kariyat
Committee Member

Dr. Alejandro Fierro Cabo
Committee Member

August 2020

Copyright 2020 Faeqa Mohsin
All Rights Reserved

ABSTRACT

Mohsin, Faeqa, Optimizing Species Selection for Forest Restoration in the Lower Rio Grande Valley. Master of Science (MS), August, 2020, 75 pp., 7 tables, 36 figures, references, 104 titles.

Over the past four decades, the Lower Rio Grande Valley has been reforested with over 3.3 million native thornscrub plants in old agricultural land. However, assessments of LRGV forest restoration efforts are scarce, and to address the knowledge gap, we examined species-specific responses to restoration interventions aimed at minimizing seedling mortality during critical the seedling stage, when high mortality occurs due to the interactive effects of abiotic stress, compromised soil nutrient status and herbivory. We evaluated seedling mortality and growth in 24 native species in response to seedling shelters & mycorrhiza-biostimulants admixture. We also quantified 15 plant functional traits including, wood density and root mass fraction to determine the potential of these plant traits to serve as predictors of native plant mortality in restoration. We found that only physical shelters reduced overall mortality and greater wood density, root mass fraction and lower root tips, stem height were associated with lower seedling mortality. These results contribute to an integrative understanding of native plant physiology and extend the scope of this work to aid in the selection of species and interventions in forest restoration.

DEDICATION

I would like to dedicate this thesis to my lifelong academic mentors, my beloved parents. My late father, Md. Mohsin Chowdhury's untethered passion for knowledge inspired me to seek the same in my adulthood. My mother, Hamida Parveen Akhtar, taught me how to have the courage of my convictions and break barriers as a woman in academia, and life in general. Even with both of your starkly different personalities, you have shown me how easy cooperation becomes when you are driven by passion for your work and compassion for the people around you. A final word of gratitude to my elder brother, Ahnaf Mohsin, for adding some healthy kin competition earlier in life and for giving me the reality check we both needed as a result of being raised by big-hearted, idealistic parents.

ACKNOWLEDGMENTS

I would like to express my deepest appreciation to Dr. Bradley Christoffersen, my thesis committee chair, for his time, patience, commitment, and mentorship during the research process. I am also grateful to my committee members Dr. Rupesh Kariyat and Dr. Alejandro Fierro Cabo for their insight and guidance over the last 2 years. My tenure as a graduate student would not have been the same without Dr. Alexis Racelis. I am grateful for his incredible kindness and generosity as an academic and non-academic mentor over the past year.

This project was done in collaboration with US Fish & Wildlife Services in Alamo, Texas, and Land Life Company in Amsterdam, Netherlands. Thanks to everyone at USFWS and LLC, especially Kimberly Wahl-Villareal and Willemijn Stoffels, for always helping me and teaching me everything you all possibly could about LRGV's restoration program. I would also like to express my gratitude to my amazing colleagues, Mylen Arias and Clifton Albrecht, for introducing me to Mexican and Texan food & culture, among many other things. This project would not have been possible without the contributions of the wonderful undergraduate and graduate students in the field & lab. Thank you so much John Cortinas, Reyna Chavez, Kayla Deleon, Noe Rodriguez, Megan Hanks, Julissa Roman, Stephany Mendez, Marco Garza, Roxann Lerma, Jonnah Garz, Julio Cerroblanco, Nicolas Ramos, Gilberto Aguillon, Ricardo Almaguer, & Krys Salazar. A final word of gratitude to Sudipa Bhattacharyya, Senjuti Yesmin, Stephanie Kasper, Joy Youwakim, & Matthew Kutugata for their constant positive reinforcements that fueled me throughout. You all have made this a wonderfully worthwhile experience!

TABLE OF CONTENTS

	Page
ABSTRACT	iii
DEDICATION	iv
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	vi
LIST OF TABLES	viii
LIST OF FIGURES	ix
CHAPTER I. INTRODUCTION	1
Forest Restoration in the Lower Rio Grande Valley.....	1
Unraveling the Mechanisms of Successful Seedling Establishment.....	2
Plant Traits and Seedling Survival	4
CHAPTER II. SPECIES-SPECIFIC RESPONSES TO FOREST RESTORATION	
INTERVENTIONS IN A TAMAULIPAN THORN FOREST.....	6
Abstract	6
Introduction	8
Methods	12
Results	17
Discussion	20

CHAPTER III. CAN PLANT FUNCTIONAL TRAITS PREDICT SPECIES' SUITABILITY
FOR FOREST RESTORATION? A CASE STUDY FROM SEMI-ARID SOUTH

TEXAS.....	40
Abstract	40
Introduction	41
Methods	44
Results	48
Discussion	50
CHAPTER IV. CONCLUSION	64
REFERENCES	67
BIOGRAPHICAL SKETCH	75

LIST OF TABLES

	Page
Table 2.1 Species Family Data	25
Table 3.1 Mean values of species' mortality percentages in different shelter types	54
Table 3.2 Pearson's correlation matrix showing intra-specific and interspecific correlation of laboratory quantified plant traits	55
Table 3.3 Pearson's correlation matrix showing interspecific correlation between mean trait values in 24 species	56
Table 3.4: Mean root structural and functional traits.....	61
Table 3.5: Mean stem structural and functional traits	62
Table 3.6: Mean leaf structural and functional traits	63

LIST OF FIGURES

	Page
Figure 2.1 Plot Layout.....	26
Figure 2.2 Mortality and height of live individuals shelter treatment	27
Figure 2.3a Time series of mortality rate	28
Figure 2.3b Relative height growth rate of all live individuals	28
Figure 2.3c Relative height growth rate of all live individuals not affected by mammalian damage	28
Figure 2.4a Mean height of 24 species across shelter type: tube	29
Figure 2.4b Mean height of 24 species across three shelter types: cocoon.....	30
Figure 2.4c Mean height of 24 species across three shelter types: control	31
Figure 2.4d Mean height of 24 species across three shelter types: all shelter types	32
Figure 2.5a Mortality of 24 species across shelter type: tube	33
Figure 2.5b Mortality of 24 species across three shelter types: cocoon.....	34
Figure 2.5c Mortality of 24 species across three shelter types: control	35
Figure 2.5d Mortality of 24 species across three shelter types: all shelter types	36
Figure 2.6a Treatment comparison of species-specific height: cocoon vs control.....	37
Figure 2.6b Treatment comparison of species-specific height: tube vs control.....	37
Figure 2.6c Treatment comparison of species-specific height: tube vs cocoon.....	37
Figure 2.6d Treatment comparison of species-specific mortality: cocoon vs control.....	38
Figure 2.6e Treatment comparison of species-specific mortality: tube vs control.....	38

Figure 2.6f Treatment comparison of species-specific mortality: tube vs cocoon.....	38
Figure 2.7a Interspecific relationship between mortality and relative height growth rate of all live individuals at 2 months post-planting.....	39
Figure 2.7b Interspecific relationship between mortality and relative height growth rate of all live individuals at 12 months post-planting.....	39
Figure 3.1a Bivariate relationships between seedling mortality in cocoon shelters and root branching intensity.....	57
Figure 3.1b Bivariate relationships between seedling mortality in cocoon shelters and stem wood density.....	57
Figure 3.2a The actual vs predicted plot of cocoon shelter mortality in multiple regression model: stem height, stem wood density & stem height*stem wood density.....	58
Figure 3.2b The leverage plot of cocoon shelter mortality in multiple regression model: stem height.....	58
Figure 3.2c The leverage plot of cocoon shelter mortality in multiple regression model: stem wood density.....	58
Figure 3.2d The leverage plot of cocoon shelter mortality in multiple regression model: stem height*stem wood density	58
Figure 3.3a The actual vs predicted plot of cocoon shelter mortality in multiple regression model: stem wood density & root tips.....	59
Figure 3.3b The leverage plot of cocoon shelter mortality in multiple regression model: stem wood density.....	59
Figure 3.3c The leverage plot of cocoon shelter mortality in multiple regression model: root tips.....	59
Figure 3.4a The actual vs predicted plot of cocoon shelter mortality in multiple regression model: root tip, root mass fraction & root tips*root mass fraction.....	60
Figure 3.4b The leverage plot of cocoon shelter mortality in multiple regression model: root mass fraction.....	60
Figure 3.4c The leverage plot of cocoon shelter mortality in multiple regression model: root tips.....	60
Figure 3.4d The leverage plot of cocoon shelter mortality in multiple regression model: root mass fraction*root tips.....	60

Figure 4.1 Species with lowest mortality overall.....	66
Figure 4.2 Species with highest mortality overall.....	66

CHAPTER I

INTRODUCTION

Forest Restoration in the Lower Rio Grande Valley

The Lower Rio Grande Valley (LRGV), located in the southernmost tip of the United States and northeastern Mexico, is a deltaic plain sloping away from the Rio Grande river, resulting in a combination of climate and edaphic factors that give rise to a highly biodiverse ecosystem composed of multiple unique biotic communities of immense ecological significance (Jahrsdoerfer and Leslie 1988). These biotic communities are supported by a range of different habitats including riparian woodlands, floodplains, woodland potholes and basins, and Tamaulipan thorn forests which is unique to the Rio Grande Valley and northeastern Mexico with its characteristic dense and thorny vegetation (Leslie 2016; Shindle and Tewes 1998). These habitats support a host of flora and fauna comprising approximately 1,200 plant, 700 vertebrate, and 300 butterfly species, including 17 federally listed endangered and threatened species (USFWS 2014b). Apart from functioning as a wildlife corridor for many species and a crossroad for bird migration for many of the 520 documented bird species in the region, these unique habitats also serve as a transition point between tropical and temperate regions (Mathis and Matisoff 2004).

The LRGV is semi-arid with infrequent frosts resulting in long growing seasons and has a unique climate which can be defined as neither temperate nor tropical. However, the Köppen-Geiger climate classification describes the area as hot semi-arid (Kottek et al., 2006). Mean annual precipitation ranges between 96.93 to 46.91 centimeters going from the Gulf of Mexico coast inland to Rio Grande City, and most of the rainfall is received in September – October (National Weather Service 2014, Norwine & John 2007).

Agriculture and urbanization have removed over 95% of the original vegetation of the Lower Rio Grande Valley including 99% of the native brush in riparian areas (Jahrsdoerfer and Leslie, 1988). In historically degraded lands such as the LRGV, ecological restoration provides the opportunity to reintroduce and re-establish communities of native biota, which can promote soil conservation and mitigate biodiversity loss, forest clearance, and other emerging environmental challenges. Since 1958, facilitated succession through direct seeding or transplanting of native species has been the primary means of habitat restoration, primarily on abandoned pasture or agricultural land (Judd 2002).

Unraveling the Mechanisms of Successful Seedling Establishment

A critical period determining the success of forest restoration is the seedling stage where high mortality due to the interactive effects of abiotic stress, mammalian herbivory, and increased competition from invasives and agricultural weeds leading to soil nutrient depletion, constrains native plant density until they reach reproductive maturity. Although adult plants can survive abiotic stress due to plasticity in growth traits, and physiological and morphological adaptations, seedlings introduced through planting are extremely sensitive to abiotic stressors such as drought since their root systems are not yet well established (Vallejo et al. 2012).

Moreover, the increasing coincidence of anomalously high temperatures with droughts under climate change can further exacerbate seedling mortality (Breshears et al. 2005).

Studies have shown that one of the key predictors of seedling mortality in semiarid restoration sites is soil water content, which is exacerbated by transplanting-induced water stress (Vora 1992; Struve 2009). Transplant shock, which is a condition of impaired functionality in plants due to distress, is one of the primary challenges of native plant restoration, which accounts for the initial pulse of post-planting mortality (Struve 2009). Several restoration practices have been developed to regulate soil moisture and facilitate the survival of seedlings transplanted for restoration, including various types of artificial tree shelters (Vallejo et al. 2012) or belowground reservoirs for holding slow-release water. Shelters and reservoirs can modify the physical environment of planted seedlings, reduce transpiration and herbivory, promote shoot growth, and improve overall plant performance (Bellot et al. 2002; Vallejo et al. 2012). However, shelters and reservoirs may have certain drawbacks. For example, promoting shoot growth may lead to reduced root-to-shoot ratio, which diminishes plants' ability to withstand subsequent drought stress. Moreover, increasing shoot growth can lead to the formation of leggy stems from insufficient support to deal with wind damage when shelters are removed (Vallejo et al. 2012). Hence, shifting abiotic conditions in these shelters coupled with the structural and physiological differences among species suggests species will respond to shelters differently.

To promote growth, microbial activity, and nutrient assimilation in plants, which in turn affects its ability to withstand environmental stress, plants are often supplied with biostimulants. These biostimulants are microorganisms or substances or a combination of both applied to plants to stimulate growth, increase abiotic stress tolerance and nutrition efficiency (du Jardin 2015). They comprise mixtures of plant hormones, manures, and mycorrhiza which have shown to

mediate the effects of plant stress, particularly water stress. The mycorrhizae, which are symbiotic fungi that facilitate nutrient and water uptake in seedlings, have the potential to reduce mortality resulting from relatively low water content available to reforested plants in arid environments. Hence, pellets containing a mixture of beneficial biostimulants when supplied to the roots have the potential to help plants withstand abiotic stress (Struve 2009).

Plant Traits and Seedling Survival

Plant traits associated with plant-water relations and drought resistance may be key predictors of seedling survival in arid environments. Adaptive traits for drought may be morphological, physiological, or a combination of both. Morphological traits include wide-spreading, deep, and highly branched roots, which is reflected through the increase in root mass fraction, and specific root length (*SRL*) (Kramer & Boyer 1995). Leaf mass per area (*LMA*), the ratio of leaf dry mass to fresh area, is an indicator of the degree of structural investment in leaf tissue and is higher in species that live on nutrient-poor, dry soil since it may increase resistance to wilting in dry conditions (Wright, Westoby and Reich 2002; Bartlett, Scoffoni and Sack 2012). Wood specific gravity (*WSG*), the ratio of stem dry mass to fresh volume, is associated with the prevention of xylem implosion caused by negative pressure, and thus drought tolerance (Hacke et al. 2001).

Plant functional traits, which are defined as the morpho-physio-phenological characteristics of plants that impact plant performance, have been used to understand interspecific variation in species performance (Werden, et al. 2018; Violle et al. 2007). While certain traits, such as water-use efficiency, photosynthetic parameters, wood density have been found to predict survival at different ontogenetic stages of plants, easily measurable traits other

than leaf dry mass content, are not always good predictors of survival (Werden, et al. 2018). Werden et al. showed that wood density was a key predictor of survival during the first wet season and transplant shock. However, after the first dry season, only, photosynthetic and water use traits were predictive of survival. Hence, it is important to select functional traits that covered a broad range of processes and that are specifically good predictors of survival in thornscrub species.

To investigate species-specific responses to restoration interventions and elucidate the relationship between plant functional traits and plant performance, we conducted a two-tiered study. In the first part, we quantified time-specific mortality and growth of 24 species of restored native plants post-transplantation for 1 year in response to two different restoration intervention components aimed at preventing herbivory and water stress. Then we quantified the root, stem, and leaf functional traits of a subsample of seedlings of the 24 species used in restoration plantings through destructive measurements in the laboratory. The goal was to link species-specific mortalities to restoration interventions and plant functional traits for understanding which underlying physiological processes lead to greater tolerance to the primary environmental stressors for determining the fate of reforested plants.

CHAPTER II

SPECIES-SPECIFIC RESPONSES TO RESTORATION INTERVENTIONS IN A TAMAULIPAN THORN FOREST

Abstract

Globally, unmitigated environmental degradation has created an urgency to restore native forests. In the Lower Rio Grande Valley, native thornscrub forest restoration in semi-arid regions has been ongoing for the past 4 decades and involves either direct seeding or transplanting native species in old croplands. A critical period determining the success of forest restoration is the seedling stage when high mortality constrains resultant native plant density until they reach reproductive maturity. Restoration interventions (RIs), defined as the modification of physical and environmental factors that impede ecosystem recovery, have been shown to facilitate native plant restoration outcomes in the LRGV. Since species-specific response to restoration interventions aimed at minimizing seedling mortality post-planting is key for quantifying benefits of RIs and optimizing species selection, to this end, we evaluated the survival and growth rate of 3600 native seedlings belonging to 24 species on a bi-monthly basis in response to RIs incorporating a combination of physical seedling shelters, slow-release moisture, and a mycorrhiza-biostimulant admixture in a semi-factorial design for one year since planting. We found that while seedling shelters successfully decreased mortality and increased growth, species-specific responses were

more varied since only 4 species had reduced mortality due to shelter use and 20 species had increased growth due to shelter use. These results indicate that while well-designed interventions tailored to offset the key environmental stressors increase survival during this one year, the role of these interventions in facilitating survival is not that straightforward, potentially due to the varying role that plant traits play in determining the growth-survival tradeoff across the 24 different species. This is further corroborated by the large species differences in survival ranging from 31% to 92%. Hence, we can conclude that forest restoration strategies should increasingly focus on the selection of appropriate species and investments in other costly restoration interventions require ecological prudence. These results contribute to an integrative understanding of how the physiology of native plants translates into performance at the critical seedling stage for informing future restoration efforts.

Introduction

Human activities have led to a substantial decline in natural habitat through altering almost half of the Earth's surface (Vitousek, Mooney, Lubchenco & Melillo, 1997). Semi-arid regions, which currently account for 17.7% of the Earth's land surface area, were historically comprised in large part by forests, and play important roles in climate regulation (Rotenberg and Yakir, 2010, Schimel 2010). Such areas have undergone some of the most intense land-use changes due to urban and agricultural expansion precipitated by population growth and often consist of abandoned pastures and croplands that have soil with excess or inadequate nutrients resulting from intensive agriculture, and often little to no pre-existing canopy cover (Vora, 1992; Padilla, 2009). Degraded semi-arid regions are being increasingly targeted for reforestation or afforestation activities and have a large carbon sequestration potential for mitigating climate change (Grunzweig et al. 2003; Bastin et al., 2019). However, restoration of native communities in these areas faces unprecedented challenges due to the compounding of ecological stressors such as drought, high irradiance, soil infertility, high temperatures and herbivory (García-Fayos & Verdú, 1998; Maestre, Cortina, Bautista, Bellot & Vallejo, 2003; Padilla et al., 2011).

One of the critical elements determining restoration success is seedling survival. Native plant revegetation usually consists of seedlings as transplants, which are extremely sensitive to environmental hazards such as water stress, extreme temperature and herbivory (Moles & Westoby, 2004; Padilla, et al. 2011). Selecting early successional species for restoration should, in theory, improve survival and overall success, as these species can maintain high growth rates under high light loads, but this is not always the case in practice (Padilla et al. 2011) This discrepancy may be due to a trade-off in seedling performance under drought versus high light

(Niinemets & Valladares 2006), both of which are prevalent in the early stages of reforestation in semi-arid areas.

Therefore, several restoration interventions (RIs) have been developed to regulate soil moisture and facilitate the survival of seedlings transplanted for restoration, including various types of artificial tree shelters (Vallejo et al. 2012) or reservoirs for holding slow-release water. Shelters and reservoirs can modify the physical environment of planted seedlings, reduce transpiration and herbivory, promote shoot growth and improve overall plant performance (Bellot et al 2002; Vallejo et al 2012; Jiménez et al., 2005; del Campo et al., 2006; Valdecantos et al., 2014). However, tree shelters may have mixed effects on enhancing seedling survival for different species (Padilla, 2011), which may be contingent on species successional strategy. For example, promoting shoot growth can lead to reduced root-to-shoot ratio, which diminishes plants' ability to withstand subsequent drought stress. Moreover, increasing shoot growth can lead to the formation of leggy stems with insufficient support to deal with wind damage when shelters are removed (Vallejo et al 2012). Hence, shifting abiotic conditions in these shelters coupled with the structural and physiological differences among species suggests species will respond to shelters differently. Further assessment is required, therefore, to understand the costs and benefits of certain interventions aimed at enhancing restoration success, especially since they account for a sizeable portion of the restoration budget when implemented at large scales (Padilla et al., 2011).

The Lower Rio Grande Valley (LRGV) of the United States and northeastern Mexico is a highly biodiverse region that supports a host of flora and fauna comprising 1,200 plant, 700 vertebrate, and 300 butterfly species, including 17 federally listed endangered and threatened species (USFWS, 2014b; Jahrsdoerfer and Leslie, 1988). However, agriculture and urbanization

led to the removal of 91-95% of the original vegetation of the LRGV and 99% in riparian areas (Tremblay et al., 2005; Jahrsdoerfer and Leslie, 1988). In historically degraded lands such as the LRGV, ecological restoration provides the opportunity to reintroduce and re-establish communities of native biota, which can promote soil conservation and mitigate biodiversity loss, forest clearance, and other emerging environmental challenges.

Since 1958, in the LRGV, facilitated succession through direct seeding or transplanting of native species has been the primary means of habitat restoration, primarily in abandoned pastures or agricultural land and over 3.3 million seedlings have been planted to date for the restoration of the Tamaulipan thornscrub (Vora, 1992; USFWS, 2014b). Herbicides and shelter tubes have been shown to enhance the survival of the thornscrub seedlings in the LRGV through controlling invasive grass cover and preventing herbivory (Alexander et al., 2016; Dick et al. 2016). However, to-date, there are no large-scale assessments of the LRGV restoration program that elucidates species-specific differences in survival as has been done in other regions (Padilla et al., 2009; Werden et al., 2018). Studies show that when vegetation restoration in arid and semi-arid regions is not tailored to the local environmental conditions, the environmental policy goals are unmet and may often lead to decreased vegetation cover and diversity, deterioration of soil ecosystems, and exacerbation of water shortages. These unintended consequences often occur due to inappropriate species selection along with unaddressed climate and landscape factors that make the site unsuitable for restoration (Cao et al., 2011). Therefore, research that elucidates species-specific responses to RIs is key for quantifying the benefits of restoration strategies and optimizing species selection.

To address these knowledge gaps, we investigated 24 different Tamaulipan thornscrub species' seedlings across different shelter types to determine species-specific and shelter-specific

variation in survival outcome. We monitored mortality and growth of 3600 seedlings belonging to these species over 12 months on a bi-monthly basis to determine species-specific, treatment-specific, and seasonal differences in survival. The relationship between survival and growth rates can be indicative of different outcomes depending on which ecological processes dominate during seedling establishment in arid land restoration. If plant traits associated with resource conservation are critical for surviving initial periods of transplant shock and subsequent abiotic stress (Reich 2014), seedling survival should decrease with growth rate. If, however, fast aboveground growth rates result in seedlings reaching a safer size faster to outgrow herbivore stress, competition and establish sufficient root systems, and thus enabling plants to access more stable resources such as deeper soil moisture (Holmgren et al., 2006; Gabler and Siemann 2013), then subsequent (vs. initial) seedling survival should increase with growth rate. These hypotheses are not mutually exclusive, and thus may counteract each other, but the direction of the survival-growth relationship can be indicative of which process dominates. So, we determined the seedling survival and growth rates of each species with and without treatment to find out which process dominates. The objective was to determine the growth rate of each species and their survival rates to ascertain the effective resource acquisition strategy (fast vs. slow) in the given set of environmental conditions at La Sal del Rey in the Lower Rio Grande Valley Wildlife Refuge. We also looked at whether interventions designed to offset aboveground and belowground abiotic and biotic stress such as water stress and herbivory can alter the effective resource acquisition strategies and confer survival benefits for some species. This will enable us to find the best performing species in the restoration of native thornscrub seedlings in the semi-arid Lower Rio Grande Valley and quantify the benefits of restoration interventions for increasing seedling survival to inform future restoration strategies.

Methods

Study site & planting methods

The study area La Sal del Rey (26°31'55"N, 98°03'50"W), in Hidalgo County, Texas and located 4 miles east of San Manuel, Texas, has been part of the Lower Rio Grande Wildlife Refuge since 1992 and has undergone reforestation efforts since 1993. In late October to early November of 2018, the US Fish & Wildlife Service & Land Life Company (<https://landlifecompany.com/>) planted over 100,000 seedlings as part of a broader Lower Rio Grande Valley National Wildlife Refuge native plant restoration project. Temperature ranges from 10-37 degrees Celsius with 23 inches of annual rainfall. The soil type consists of Brennan sandy loam and Hebbronville sandy loam with a slope ranging from 0-3%. Woody species that are commonly found in this area include *Acacia rigidula*, *Ebenopsis ebano*, *Havardia pallens*, *Cordia boissieri*, and *Karwinskia humboldtiana* (Alexander et al., 2016).

Experimental design & restoration interventions

The study consisted of an unreplicated split-plot design in which 25 seedlings of each of the 24 Tamaulipan thornscrub species were each assigned to two shelter types and control, each of which was subdivided into a mycorrhizae-biostimulant (MBS) admixture treatment and control (no MBS), for a total of 3600 seedlings (25 replicates x 24 species x 3 shelter types x 2 MBS types) (Fig. 1). Due to the opportunistic nature of this study, it was not possible to conduct a randomized block design; however, we assigned seedlings *a posteriori* to one of three blocks within each shelter treatment to control for pseudoreplication (see 'Statistical Analysis' below). Tree shelters consisted of two types (tubes and 'cocoons') designed to limit herbivory and promote seedling establishment. Tree tubes are 80 cm tall double layer of polypropylene material

with lateral ventilation and anchored with a stake to the ground at planting. ‘Cocoons’, a recently developed tree shelter consisting of a donut-shaped 5-gallon biodegradable trough (Land Life Company, Amsterdam, The Netherlands) were centered on each seedling and filled with 5 gallons of water at planting, supplying roots with slow-release moisture over 1-2 months. A 30 cm tall vented cardboard shelter surrounds the seedling above-ground. The MBS treatment was intended to facilitate rooting through increased microbial activity and nutrient supply to the roots. It consisted of a commercial pellet (Soil Moist Plant Tabs, JRM), two of which were supplied at the base of the plant at the time of planting. Each tab contained ten million spores of 5 types of ectomycorrhizal fungi, 50 spores of 7 types of endomycorrhizal fungi, organic fertilizer in a fulvic acid base, and the rooting hormone indole butyric acid. MBS tabs, however, were not designed for use in hot arid ecosystems, as they consisted predominantly of ectomycorrhizal species.

Seedling censuses

We measured growth and recorded survival of all seedlings for a year after planting. The initial monitoring occurred over 2 months from planting date (November-December 2018) and consisted of tagging each plant with a unique identifier, recording species names and intervention treatments, measuring baseline height, and recording their location. 2nd-6th monitorings occurred in January, February, March, April, July, and October 2019 respectively. These monitorings quantified vigor (proportion of green leaves left on the stem), branching (number of main branches), animal damage (whether there were signs of herbivory on the trees), and height measurement. Vigor was measured on a scale of 0-3, where 0 indicated the absence of any green healthy leaves and 3 indicated that over 75% of leaves on the plant were present and healthy. Animal damage was also measured on a scale of 0-3 where 0 = No animal damage, 1 =

slight animal damage, 2= moderate animal damage, and 3= severe animal damage. Zero vigor and severe animal damage indicated mortality of the seedlings, which was verified in subsequent surveys to avoid counting trees as dead when they were merely leafless.

Estimating growth and mortality

Relative height growth rate ($RGR_{h,i}$: $\text{cm cm}^{-1} \text{ yr}^{-1}$) of seedlings at any given census i was calculated as $RGR_{h,i} = (\log(H_i) - \log(H_{i-1})) / (t_i - t_{i-1})$ where H_i and H_{i-1} are seedling height at the current and previous census, respectively, and t_i and t_{i-1} indicate time elapsed (fractional years) since planting for the current and previous census, respectively (Alvarez-Aquino et al. 2004).

We estimated mortality (fraction of planted individuals that were dead; unitless) at the block level (within species and shelter x MBS treatment) as $(1 - N_i/N_0)$, where N_0 and N_i are the number of seedlings planted and the remaining number alive at any given census i , respectively.

We estimated the mortality rate according to Sheil & May (1996) as $1 - (N_i/N_{i-1})^{1/\Delta t}$, where N_i and N_{i-1} are the numbers of live seedlings at the current and previous census, respectively, and Δt denotes the time between two censuses (fractional years).

Statistical analysis approach

All data analyses were conducted using R (R Core Team 2019). We used the `data.table` package (Dowle & Srinivasan 2019) for manipulating the large number of individual observations ($> 25,000$) and conducting relational database operations (inner and outer joins). All graphics were prepared using the `ggplot2` package (Wickham 2016), with bracket placing (Figure 2) using the `ggrepel` package (Kassambara 2018) and text labeling on plots (Figure 6) using the `ggrepel` package (Slowikowski 2018). We employed statistical models using the response

variables seedling height (cm), RGR_h ($\text{cm cm}^{-1} \text{ yr}^{-1}$), mortality (number of live vs. dead plants), and mortality rate (number of live vs. newly dead plants). For all statistical tests on height, which was non-normally distributed, we first transformed height by taking the square root, as has been done in other studies (Alexander et al. 2016). For all statistical tests on mortality, we conducted a generalized linear model (GLM) on the live vs. dead count data, using the logit link function using the `glm()` function in R's base package. In most cases, we had to correct for overdispersion by using the quasibinomial error distribution.

We first attempted to fit the maximal model (shelter, MBS, and species identity as factors, including all pairwise and higher-order interactions) on the full dataset with linear mixed models suitable for experiments with repeated measures (Crawley, 2013a), but these models failed to converge. Therefore, we opted to fit a maximal model for mortality using all factors and their interactions based on a single, final (6th) census, which we simplified using manual stepwise deletion of factors, starting with highest-order interactions and proceeding to factors with the next least level of significance until a final minimal model with only significant factors or interactions was achieved (Crawley, 2013b). Based on these results, we used two further classes of statistical models using only factors related to RI treatments. These models respectively assessed 1) overall treatment effects independent of species identity and 2) within-species treatment effects to determine which species significantly benefitted from RIs. For the former, we identified treatment effects at specific time periods by either repeating the same statistical model at each census and applying a Bonferroni correction to the significance threshold or using a linear mixed-effects model for repeated measures.

Assessing treatment effects

To assess treatment effects on height and RGR_h (Figures 2 and 3b,c), we conducted, respectively, a two-way ANOVA and a two-way GLM for mortality, using R's `lm()` and `glm()` functions, with shelter type and MBS type as factors. We applied a Bonferroni correction to RGR_h to the significance level as $\alpha/n = 0.05/6 = 0.0083$. In these tests, data were first aggregated from individuals to the block level. We then stepped down the model as detailed above. In no test was the MBS main effect ever significant, and in only one instance was there a significant interaction between shelter and MBS factors (census 6 for RGR_h). Because this was an isolated occurrence, we deemed it likely spurious and eliminated the interaction and in the results, we therefore aggregate MBS treatments within the shelter treatments (Figures 2 and 3). Supplemental Figure S1 presents results broken down by both shelter and MBS treatment. We conducted a Tukey post-hoc test for multiple comparisons of means wherever the shelter's main effect was significant, using R's `glht()` function of the `multcomp` package (Hothorn et al. 2008). For mortality rate (Figure 3a), we fit a generalized linear mixed effects model, because of the diminishing population size and the need for increased statistical power achievable from the repeated measures. Our binary response variable (y) was the number of live vs. newly dead (relative to the previous census) individuals. Fixed effects were shelter type and census (including their interaction), with species identity as the random effect repeatedly measured each census. Our function call using the `glmer()` function from the `lme4` package (Bates et al. 2015) was of the form: `glmer(y ~ sheltertype*census + (census|SpeciesName), family=binomial)`. We used the 'bobyqa' optimizer to deal with an initial attempt when the model failed to converge. We then conducted Tukey post-hoc tests on the three shelter type treatments using the `lsmeans`

function from the emmeans package (Lenth 2019), with a call of the form: `lsmeans(model, pairwise ~ sheltertype|census)`, where 'model' was our final fitted model from `glmer()`.

To assess within-species treatment effects (Figure 6), we repeated the same two-way ANOVA and GLM as detailed above, but for each species and census separately. The only exception was that we did not apply a Bonferroni correction, due to the large number of repeated tests performed, and given that our question was not whether there was an overall significant species by treatment interaction, but rather to address the question of which species' success were significantly impacted by which RIs.

Assessing interspecific relationships between mortality and RGR_h

Finally, we assessed whether the height growth rate of live individuals (RGR_h) can predict overall mortality (Figure 7) at discrete census intervals with logistic regression of mortality on RGR_h using the `glm()` function. For a given census interval, we aggregated data to the treatment level (shelter type, MBS type, and species identity), resulting in six paired estimates of mortality and RGR_h per species. We assessed the combined inter- and intra-specific relationship by fitting a model within each treatment and across all treatments. We then assessed the intra-specific relationship by fitting the model for each species separately across all treatments.

Results

Overall mortality (fraction of individuals planted that died) increased significantly over the course of the study, from 4.1% at one month post-planting to 21.0% at 12 months, across all species and treatments, including the control. The relative difference in mortality across

treatments was large initially but declined over time (Figure 2). Both tube and cocoon shelters significantly reduced mortality at one month (2.7% and 1.7%, respectively, relative to 7.9% in the control; Figure 2a), whereas only cocoons significantly reduced mortality at 12 months (15.0% relative to 21.7% and 26.6% in tubes and controls, respectively; Figure 2b).

In contrast, the relative difference in mean plant height across treatments increased over time. Mean plant height was not significantly different between shelter types one month after planting (Figure 2c). However, at 12 months, all treatments were significantly different from each other and were tallest in tubes, followed by cocoons, and then controls (mean \pm SE for tubes, cocoons, and controls: 62 ± 3 , 51 ± 2 , and 36 ± 2 cm, respectively; Figure 2d).

Temporal patterns of relative height growth rate (RGR_h ; month⁻¹) and per capita mortality rate (year⁻¹) indicated opposing temporal trends, with the mortality rate generally decreasing when RGR_h increased (Figure 3). Mortality occurred throughout the entire period of the first year, but two distinct periods of elevated mortality were apparent: a post-transplant period (up to 3 months post-planting), and a summer period (May-August; Figure 3a). RGR_h was greatest during spring months (Jan – April), and was significantly higher for shelter treatments relative to the control for the initial five months post-planting, irrespective of whether plants with significant animal damage are included (Figure 3b,c). Relative to control, shelters did not significantly increase RGR_h from early through late summer (May – Oct); rather, tubes reduced RGR_h by a small but significant amount during late summer (July – Oct), irrespective of animal damage (Figure 3b,c).

Across the 24 species, we observed large differences in both mean plant height and growth (Figure 4) and mortality (Figure 5). Mean species-specific heights, averaged across all

treatments, varied 5-fold at both planting (range: 7 to 36 cm) and at 12 months post-planting (range: 17 to 87 cm; Figure 4d), representing a 69% to 353% increase in plant height across species. In general, across treatments, species that were tall-statured as seedlings grew the most, short-statured species grew the least, and intermediate-sized species exhibited a range of RGR_h (Figure 4). *Guaiacum angustifolium* and *Castela erecta* were among the shortest seedlings and slowest-growing species, while *Chromolaena odorata* and *Viguiera stenoloba* were among the tallest species at 12 months. Averaged across all treatments, species with the greatest relative increase in plant height were *Vachellia rigidula* and *Vachellia schaffneri* (363% and 283%, respectively). For these two species, the greatest relative height increase occurred in the tubes (470% and 403%, respectively). Species-specific mortality varied between 1% (*Condalia hookeri*, cocoon shelters) to over 80% (*Guaiacum angustifolium*: control; Figure 5). *Parkinsonia texana* and *Citharexylum berlandieri* were among the species with consistently low rates of mortality regardless of treatment, whereas *Guaiacum angustifolium* and *Viguiera stenoloba* demonstrated consistently high rates of mortality across all treatments.

Where shelter effects were significant at the treatment level, in all cases it is because benefits were distributed across many species, as opposed to large effects for a limited number of species (Figure 6a-c). The impact of shelters on species-specific responses was much more pronounced for height growth relative to mortality, with nine to 17 species having significantly greater heights but only four species (*Celtis pallida*, *Diospyros texana*, *Karwinskia hulmboldtiana*, and *Phaulothamnus spinescens*) experiencing significantly lower mortality in shelters relative to controls (Figure 6a,b,d,e).

While some species exhibited an apparent trade-off in RGR_h and survival (e.g., *Viguiera stenoloba*), others appeared to suffer increased mortality due to a failure to grow (e.g., *Guaiacum*

angustifolium). At two months post-planting, mortality decreased with increasing RGR_h across species and treatments (Figure 7a). The same relationship held true within both cocoon and tube treatments, but not controls (Figure 7a). However, at 12 months there was no significant relationship between RGR_h and mortality (Fig 7b).

Discussion

Our study highlights a few key outcomes to inform large-scale transplant-based reforestation initiatives aimed at restoring native plant biodiversity in degraded semi-arid lands. First, two distinct periods of high risk exist, as indicated by elevated mortality rates: the first 2-3 months associated with a failure to establish, and a post-establishment summer period associated with intense abiotic stress (hot and dry conditions). In contrast, damage due to mammalian herbivory was, for the most part, consistent and persistent throughout the entire study period. Second, shelters served to only minimize mortality during the establishment phase and promote height growth during the first 6 months; afterward, benefits were minimal and, in some cases, slightly detrimental to overall growth and survival. Third, large species differences in growth and survival underscore species differences in ecological strategies and palatability to herbivores. Taken together, our results suggest that the planting phase of reforestation efforts can most benefit by optimizing species selection, by targeting those species which exhibit both high growth and survival, and, when using shelters, to limit their use to periods of seedling establishment and spring growth.

Temporal dynamics of growth, mortality, and animal damage – what does it tell us?

In semi-arid ecosystems, the highest seedling mortality occurs during the post-transplant period and the first dry season (Espelta et al., 2002; Lloret et al., 2002; Close et al., 2005).

‘Transplant shock’, or the initial mortality over the first couple months when planted seedlings fail to acclimatize to stressful abiotic field conditions, is a key factor impeding restoration success (Close et al. 2005). As a result, many management practices in habitat restoration focus on introducing interventions with techniques and amendments that may help prevent transplant-shock induced mortality (Sweeney et al., 2002; Scholl et al., 2010). In our study, we saw differences in mortality for both shelters during the first month (figure 2a). Although both shelters continued to provide physical protection against herbivory for 12 months, the cocoons additionally provided moisture and protected the roots against water stress during the first month after planting. Yet, the survival benefits of the tubes tapered off over the 12 months for the tube shelters (Figure 2d), and only the cocoons continued to show reduced mortality.

How useful are shelters as RIs?

While shelters significantly impacted both height growth and mortality after one year, the relative impact of shelters was more pronounced on height growth than for mortality. At one year, the relative reduction in mortality due to shelters was 5-12%, while plant height was increased by 15-27 % (shelters relative to controls). Therefore, the effect of shelters was mostly to improve height growth, with a smaller secondary benefit of reducing mortality.

19 out of 24 species showed clear indications of growth benefits due to the use of shelters (Figure 6a, 6b). However, growth benefits conferred by shelters do not necessarily translate into survival benefits for different species (Figure 6). Three of the nine species which showed enhanced growth due to the use of cocoon shelters (figure 6a) were not benefitted in terms of survival (figure 6d). In the case of tubes shelters, facilitation of growth occurred in an even greater number of species (17), however, 15 of those 17 species did not show greater survival

(figure 6b and 6e) 12 months after planting. The lack of temporally consistent survival benefits demonstrates the importance of careful consideration in recommending the use of shelters and similar interventions for facilitating restoration in semi-arid lands.

Implications of large species differences in growth & survival

However, it is still important to note that we can still gain insights into possible mechanisms that might explain key processes from observing economic traits like growth rate. This need is highlighted in figure 7, which demonstrates the association between mortality and relative height growth rate (RGR_h) at two months (figure 7a) and 12 months (figure 7b). The presence of an association between mortality and RHGR at two months and not 12 months may be a characterization of the economic traits that guide resource acquisition and lead to certain growth survival trade-offs. Hence, it is crucial to quantify and understand the influence of these economic traits in explaining the adaptive mechanisms that underpin the ecological strategies employed by species during restoration.

While edaphic factors can shape plant adaptation to co-varying variables such as soil conditions and herbivore pressure, numerous studies show that these functional responses are largely species-specific. As a result, the significance of screening of multiple species through reforestation trials to determine site-specific suitability of species for reforestation in semi-arid areas has been long recognized (Craven et al., 2011; Bruegal et al., 2011, Butterfield, 1996, Calvo-Alvarado et al., 2007, Park et al., 2010).

Implications for Restoration & Management

Managed restoration constituting site preparation, species selection, and tree plantings is essential due to the presence of herbivores, invasive plant competitors, and limited moisture and

nutrients in semi-arid regions. The need to increase the success of restoration projects led to the introduction of interventions such as the use of shelter tubes and mycorrhizal fungi pellets to the roots. Yet, to date, no large-scale screening trials have been done to determine the viability of the 60-70 native species that are currently being propagated as part of restoration efforts to inform the planning and management of millions of seedlings that have been thus far used in restoration plantings within the Rio Grande Valley. This study addresses a much-needed gap in knowledge through determining species-specific differences in survival of 24 native species during the critical seedling stage when seedlings experience high mortality. Through the observation of large mortality differences between species across different shelter types, our findings corroborate with past studies (Wishnie et al., 2007; Weber et al., 2008, Padilla et al., 2011) which underscore species differences in optimizing for selection (figure 5).

Our findings demonstrate that while well-designed restoration interventions have a positive effect on survival, optimizing species selection is the most effective strategy for enhancing restoration success. Both types of tree shelters (cocoons and tubes) benefitted seedlings both in terms of survival and growth survival during the initial months. Tree shelters likely improved multiple abiotic and biotic factors both above and belowground. Aboveground, tree shelters reduce excessive radiation loads, reduce herbivory, and in the case of cocoons, supply moisture to the roots (Padilla et al., 2011). However, the survival benefits at 12 months remained only for cocoons. and no survival or growth benefits were observed across species and different shelters due to the inoculation of the roots with the mycorrhizal biostimulant admixture (MBS). Over the coming months, the effect of shelters may change following their planned removal (tube) and degradation (cocoons).

Limitations

One of the key limitations of giving recommendations based on these results alone is the fact that we are reporting results for 12 months only (Breugal, 2011). Despite the benefits afforded by shelters, we urge caution since the temporal patterns of performance indicate that effects on growth and survival may taper off (figure 3b, 7a) or in contrast, even accumulate over time (figure 7a, 5). These temporal patterns also identify the peak vulnerability periods of restored seedlings as the post-transplant period from October 2018-December 2018. and the first summer dry season between April 2019- July 2019 (figure 3a). Moreover, we observe that despite the 2 distinct periods of elevated mortality, mortality has yet not stabilized and continues to peak into October 2019. These results indicate that the effects of interventions beyond one year are uncertain and continued monitoring is needed to track and determine the species-specific and site-specific benefits of well-designed restoration interventions and implement better management practices.

Conclusions

Our study kickstarts a database on the performance of native thornscrub species through accumulating knowledge regarding growth and mortality to help evaluate and optimize species selection for restoration in similar habitats (Ashton et al., 2001). This information is critical for designing, planning, and implementing appropriate and effective strategies in selecting species that target key processes to match restoration objectives.

Tables and Figures

<i>Species, common name</i>	<i>Family</i>	<i>Leaf type</i>	<i>N-fixer</i>	<i>Mean height (initial) (cm)</i>	<i>Mean stem diameter (mm)</i>	<i>Growth form</i>	<i>Growth Rate</i>
1. <i>Acacia berlandieri</i> , guajillo	Fabaceae	Compound	Yes	28.96	3.29	tree	Fast
2. <i>Acacia greggii</i> Wright's acacia	Fabaceae	Compound	Yes	27.33	3.03	tree	Moderate – fast
3. <i>Amyris texana</i> , chapotillo	Rutaceae	Simple	No	13.05	3.61	shrub	Moderate-fast
4. <i>Castela erecta</i> , amargosa	Simaroubaceae	Simple	No	14.06	2.45	shrub	slow
5. <i>Celtis ehrenbergiana</i> , granjeno	Ulmaceae	Simple	No	23.07	3.45	large shrub	moderate
6. <i>Chromolaena odorata</i> , crucita	Asteraceae	Simple	No	26.10	5.96	herbaceous shrub	fast
7. <i>Citharexylum berlandieri</i> , Berlandier's	Verbenaceae	Simple	No	36.09	6.43	large shrub	fast
8. <i>Colubrina texensis</i> , hogplum	Rhamnaceae	Simple	No	24.72	3.20	shrub	moderate
9. <i>Condalia hookeri</i> , brasil	Rhamnaceae	Simple	No	23.41	3.33	tree	moderate
10. <i>Diospyros texana</i> , Texas persimmon	Ebenaceae	Simple	No	15.82	2.69	tree	moderate
11. <i>Ebenopsis ebano</i> , Texas ebony	Fabaceae	Compound	Yes	14.29	3.38	tree	moderate
12. <i>Forestiera angustifolia</i> , elbowbush	Oleaceae	Simple	No	30.56	4.41	large shrub	-
13. <i>Guaiacum angustifolium</i> , guayacán	Zygophyllaceae	Compound	Yes	6.57	2.24	large shrub	slow
14. <i>Havardia pallens</i> , tenaza	Fabaceae	Compound	No	19.30	3.37	tree	moderate
15. <i>Karwinskia humboldtiana</i> , coyotillo	Rhamnaceae	Simple	No	21.22	3.42	shrub	slow
16. <i>Parkinsonia texana</i> , palo verde	Fabaceae	Compound	No	28.24	4.28	tree	moderate
17. <i>Phaulothamnus spinescens</i> , snake eyes	Achatocarpaceae	Simple	No	19.52	3.10	large shrub	moderate
18. <i>Randia rhagocarpa</i> , crucillo	Rubiaceae	Simple	No	16.85	3.56	large shrub	slow
19. <i>Sideroxylon celastrina</i> , coma	Sapotaceae	Simple	No	17.50	3.11	tree	-
20. <i>Vachellia rigidula</i> , blackbrush	Fabaceae	Compound	Yes	15.44	2.87	large shrub	moderate
21. <i>Vachellia schaffneri</i> , huisachillo	Fabaceae	Compound	Yes	19.27	2.83	large shrub/tree	moderate
22. <i>Viguiera stenoloba</i> , skeleton-leaf golden-eye	Asteraceae	Simple	No	25.20	4.32	herbaceous shrub	fast
23. <i>Zanthoxylum fagara</i> , colima	Rutaceae	Simple	No	19.30	3.60	large shrub	moderate
24. <i>Ziziphus obtusifolia</i> , lotebush	Rhamnaceae	Simple	No	17.95	2.82	large shrub	slow

Table 2.1 Species Family Data

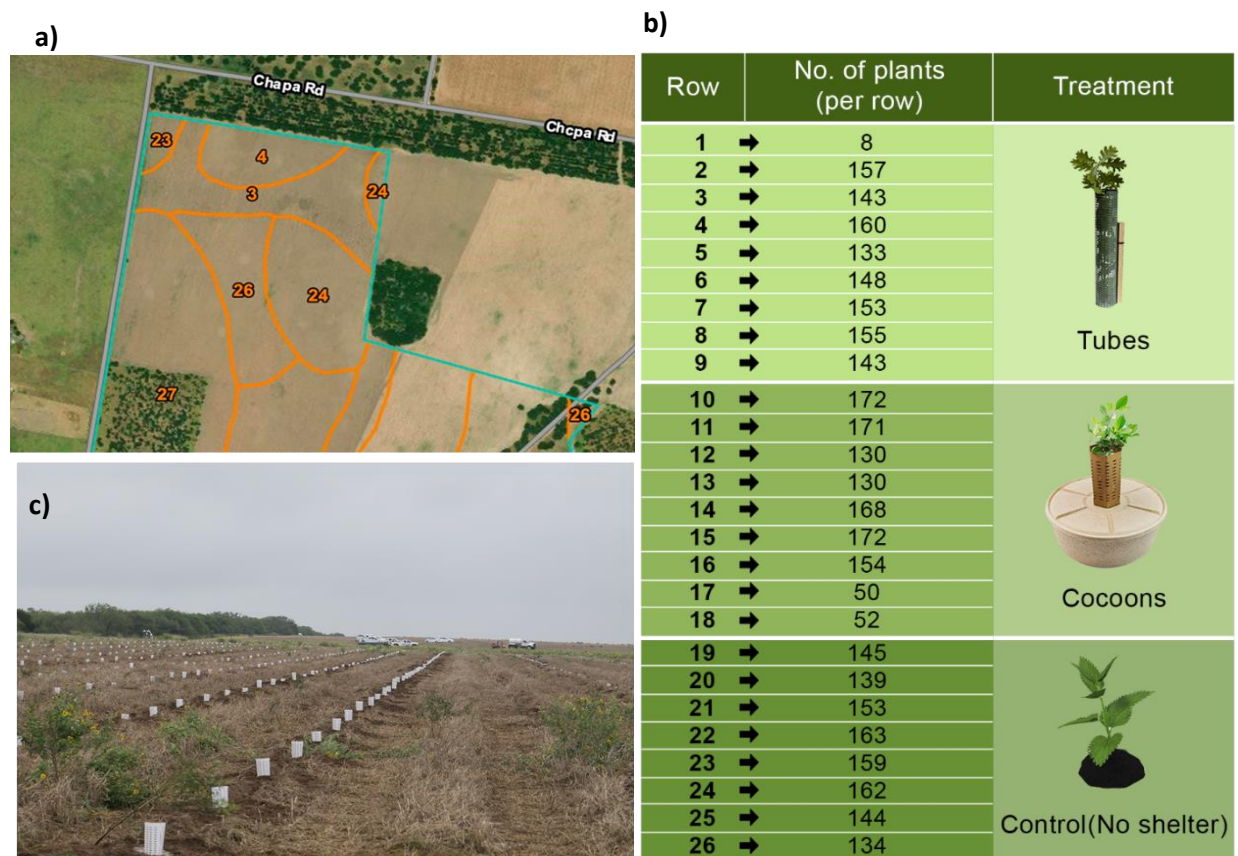


Figure 2.1. Plot Layout

- a) Study area in La Sal del Rey (Land Life Company, Netherland, Amsterdam).
- b) Layout of experimental Design encompassing 26 rows and 3 different treatments, soil amendments and shelter types
- c) I week post planting field-view of restoration site

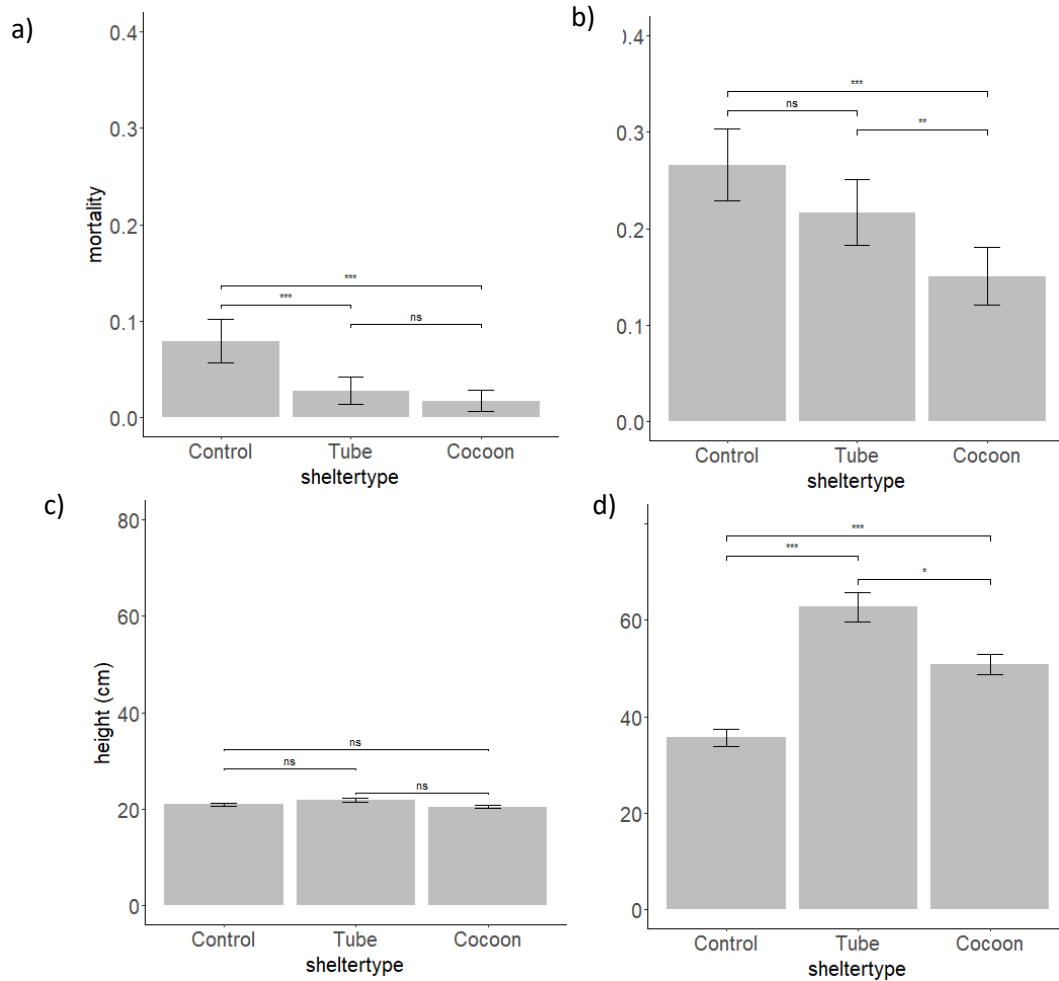


Figure 2.2 Mortality of live individuals (a, b) and height (c, d cm); fraction of planted individuals that are dead) by shelter treatment at 1 (a, c) and 12 (b, d) months post-planting of all species combined. Means are based on n = 1,200 individuals per treatment. Significance of adjusted p values from pairwise Tukey contrasts on the shelter main effect are given above the corresponding bars. Significance codes : '***' p < 0.001; '**' p < 0.01; '*' p < 0.05; 'ns' p ≥ 0.05.

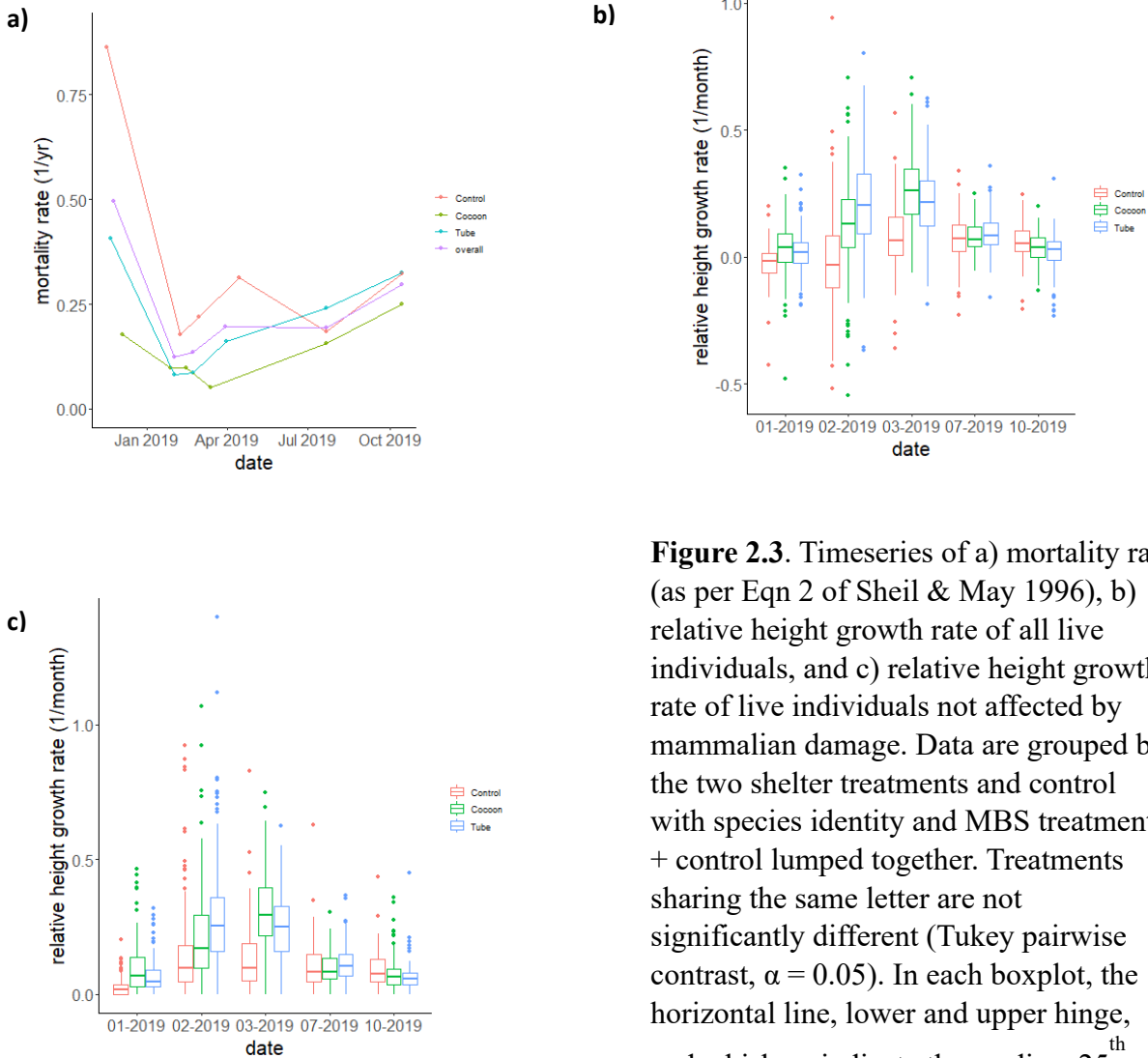


Figure 2.3. Timeseries of a) mortality rate (as per Eqn 2 of Sheil & May 1996), b) relative height growth rate of all live individuals, and c) relative height growth rate of live individuals not affected by mammalian damage. Data are grouped by the two shelter treatments and control with species identity and MBS treatment + control lumped together. Treatments sharing the same letter are not significantly different (Tukey pairwise contrast, $\alpha = 0.05$). In each boxplot, the horizontal line, lower and upper hinge, and whiskers indicate the median, 25th and 75th percentile, and 1.5 times the inter-quartile range (IQR), respectively. Outliers, defined as values greater than $1.5 \times \text{IQR}$, are plotted as individual points.

a)

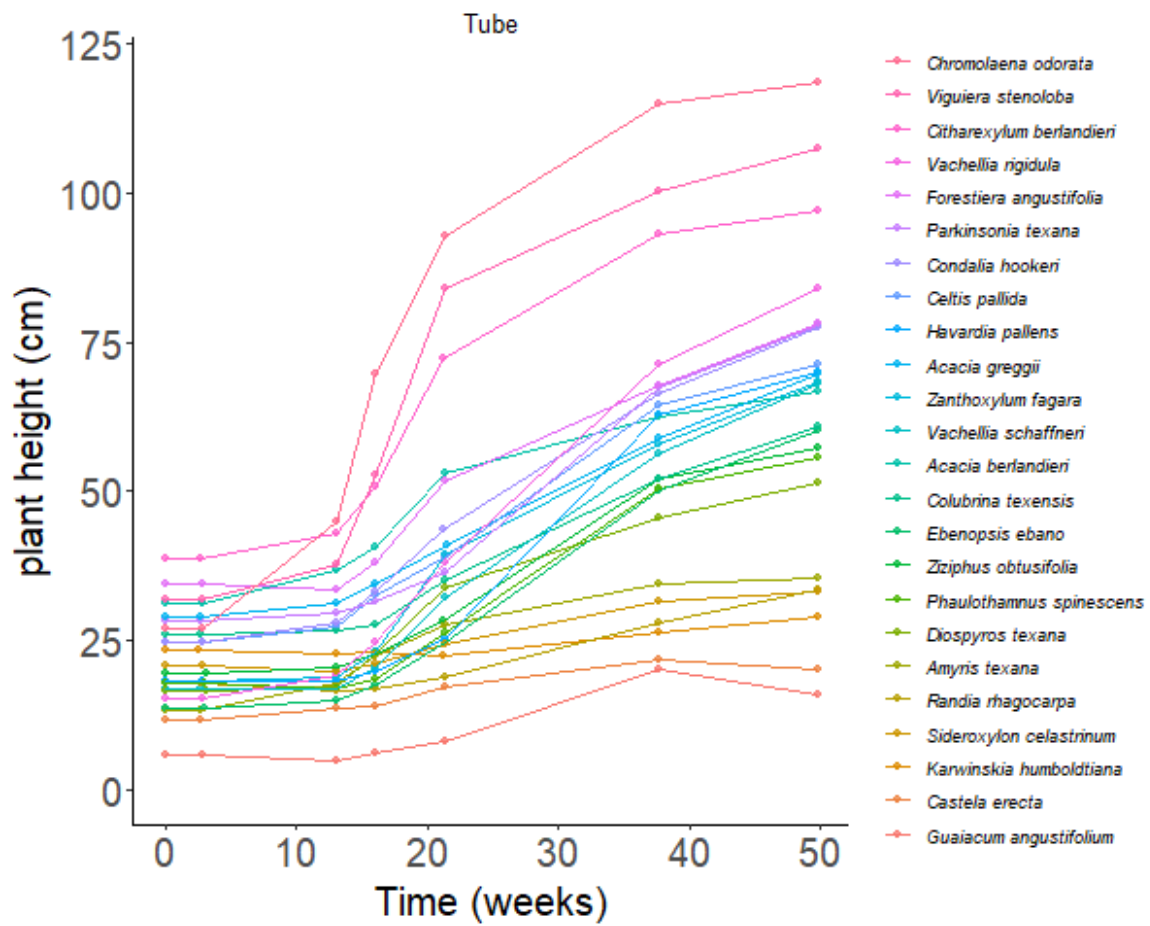


Figure 2.4. Mean height of 24 species across three shelter types: tube (a), cocoon (b), control (c), and all combined (d). Species are colored and ordered according to height in October 2019. Species height estimates are based on $n = 49-51$ individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

b)

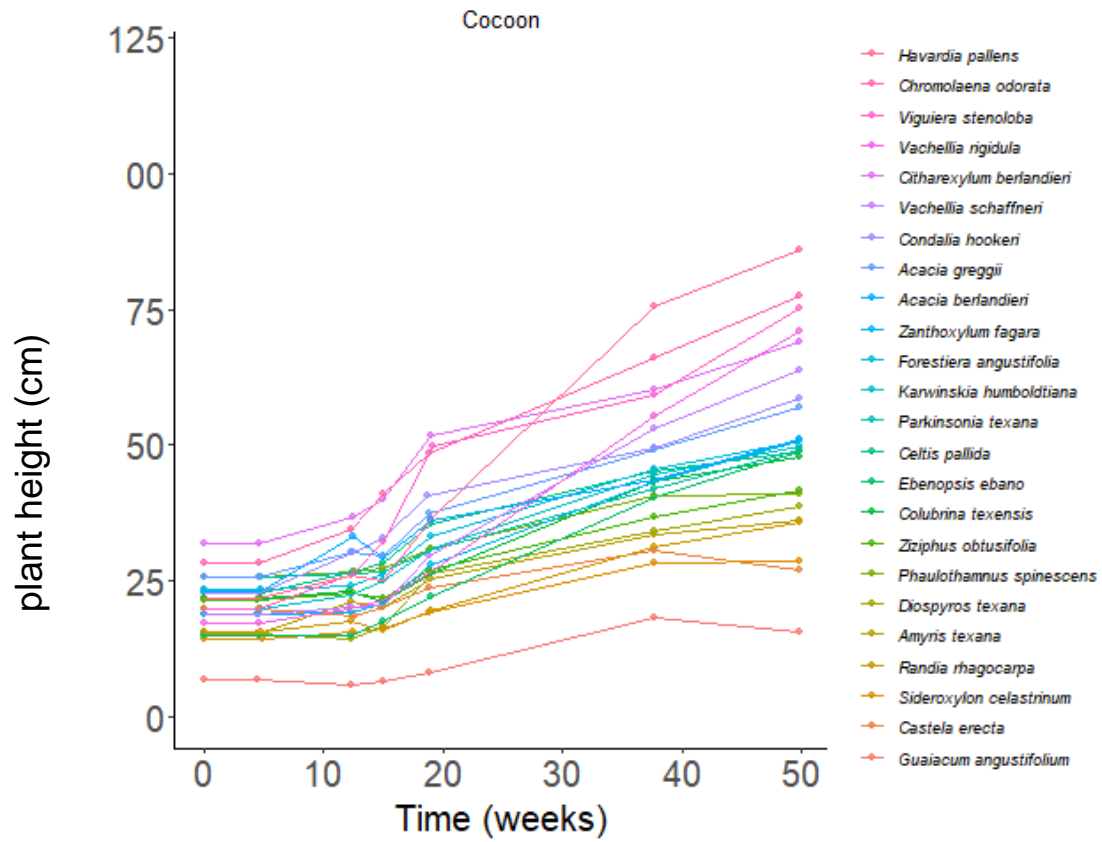


Figure 2.4. Mean height of 24 species across three shelter types: tube (a), cocoon (b), control (c), and all combined (d). Species are colored and ordered according to height in October 2019. Species height estimates are based on $n = 49-51$ individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

c)

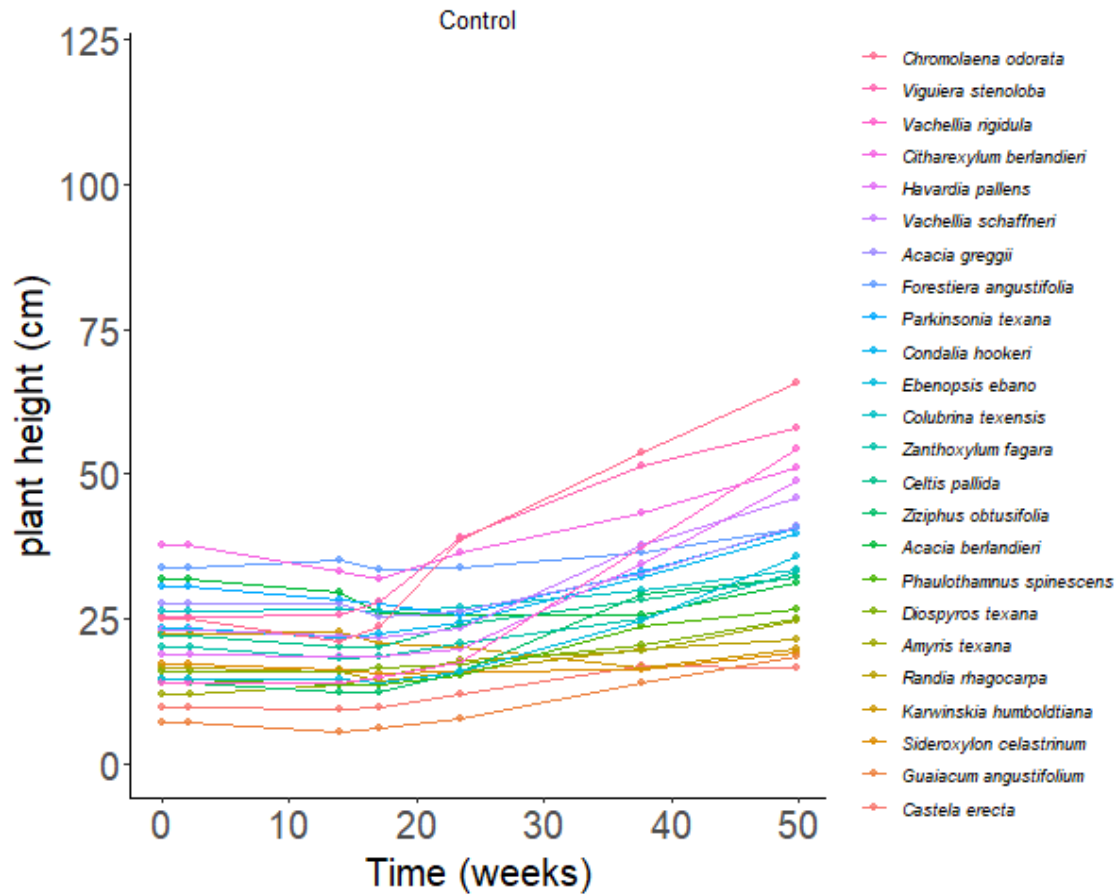


Figure 2.4. Mean height of 24 species across three shelter types: tube (a), cocoon (b), control (c), and all combined (d). Species are colored and ordered according to height in October 2019. Species height estimates are based on $n = 49-51$ individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

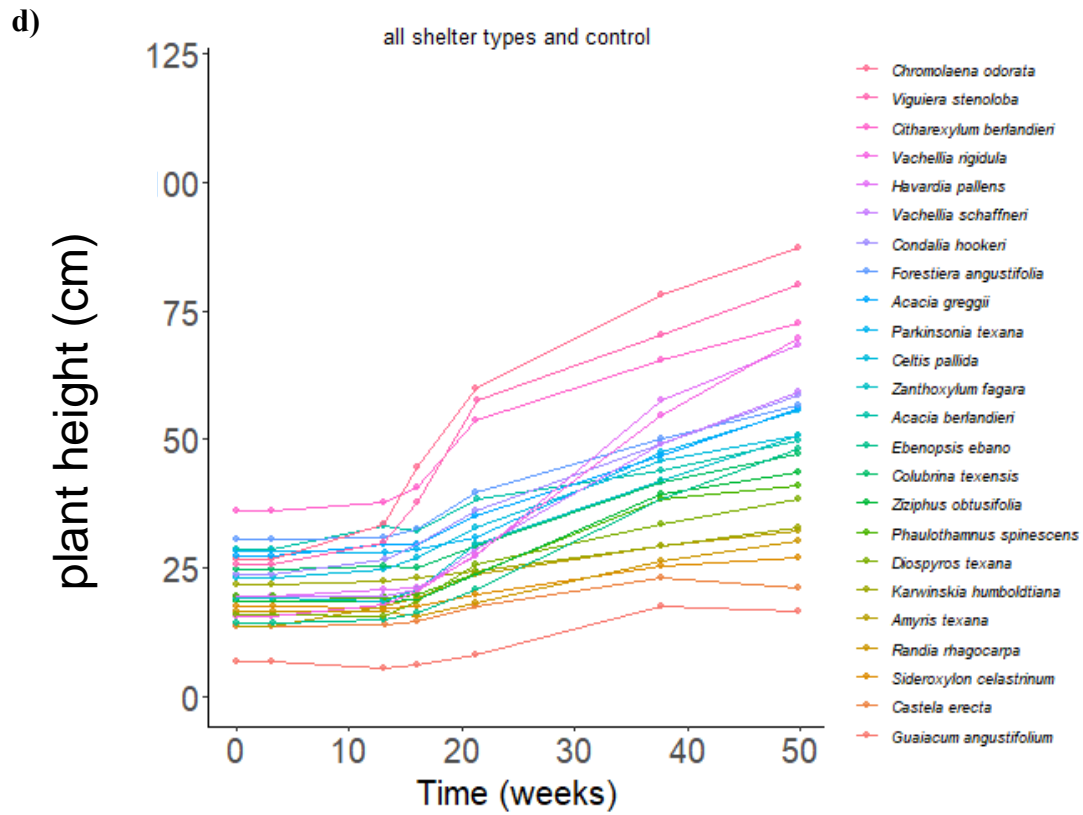


Figure 2.4. Mean height of 24 species across three shelter types: tube (a), cocoon (b), control (c), and all combined (d). Species are colored and ordered according to height in October 2019. Species height estimates are based on $n = 49-51$ individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

a)

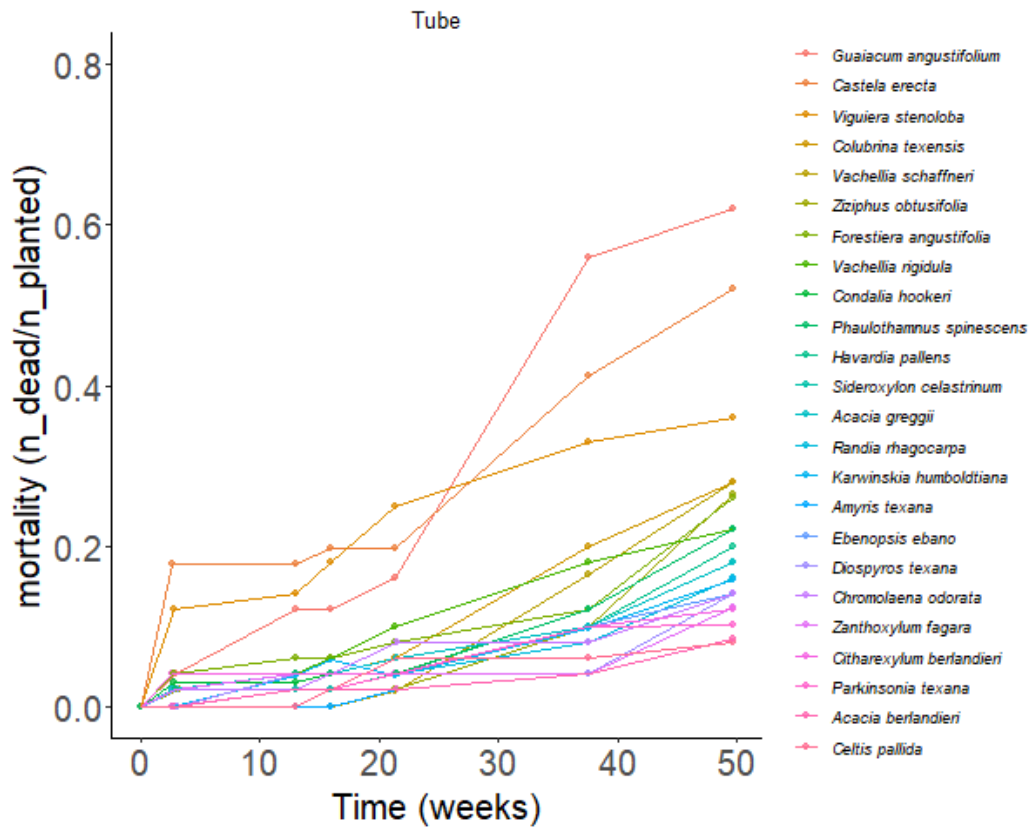


Figure 2.5. Mortality of 24 species across three shelter types: tube (a) cocoon (b), control (c), and all combined (d). Species are colored and ordered according to mortality in October 2019. Species mortality estimates are based on $n = 49$ -51 individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

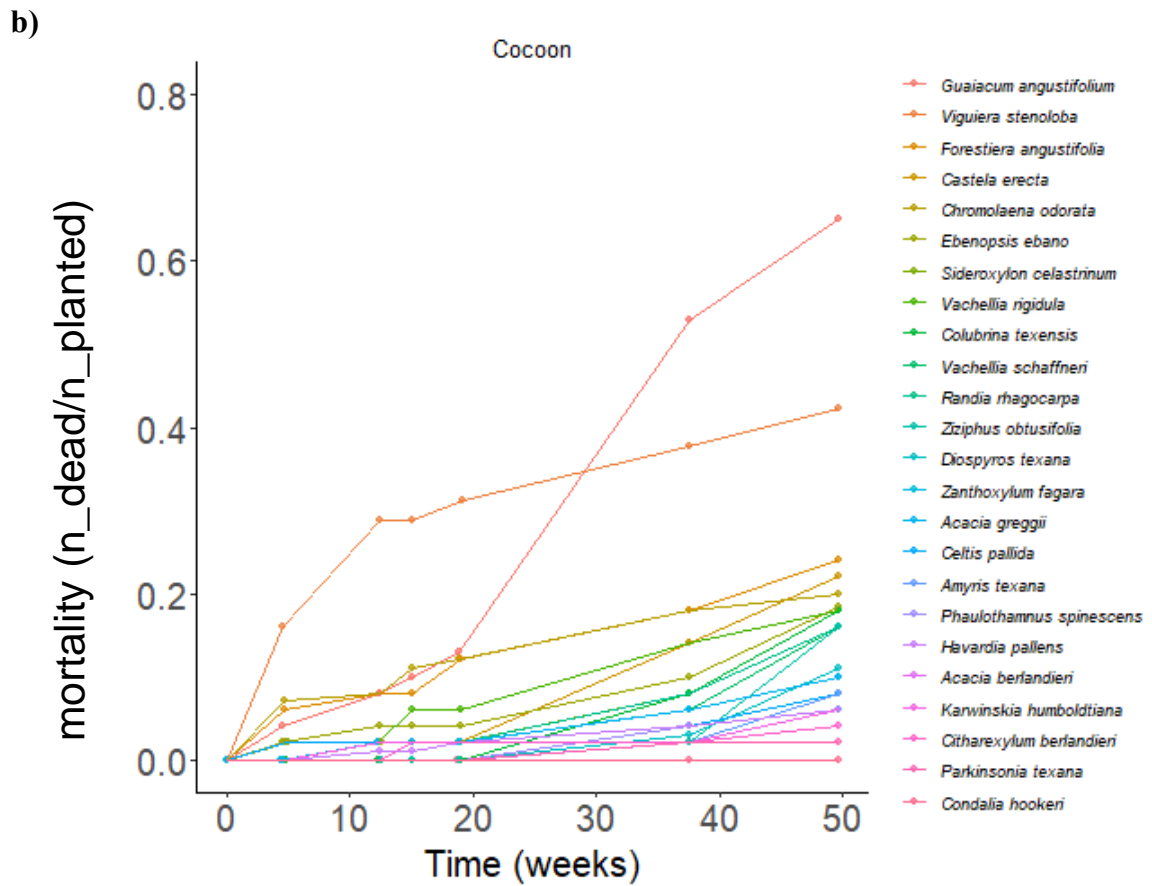


Figure 2.5. Mortality of 24 species across three shelter types: tube (a), cocoon (b), control (c), and all combined (d). Species are colored and ordered according to mortality in October 2019. Species mortality estimates are based on $n = 49-51$ individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

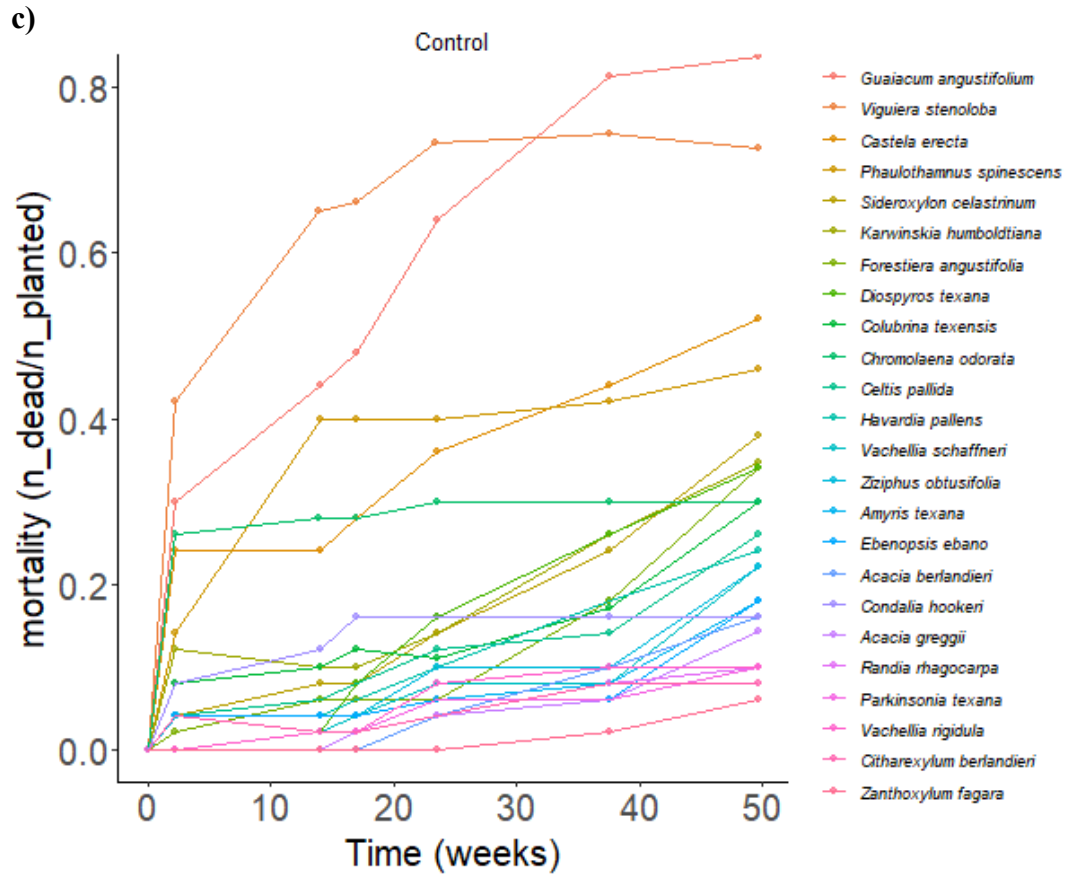


Figure 2.5. Mortality of 24 species across three shelter types: tube (a), cocoon (b), control (c), and all combined (d). Species are colored and ordered according to mortality in October 2019. Species mortality estimates are based on $n = 49-51$ individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

d)

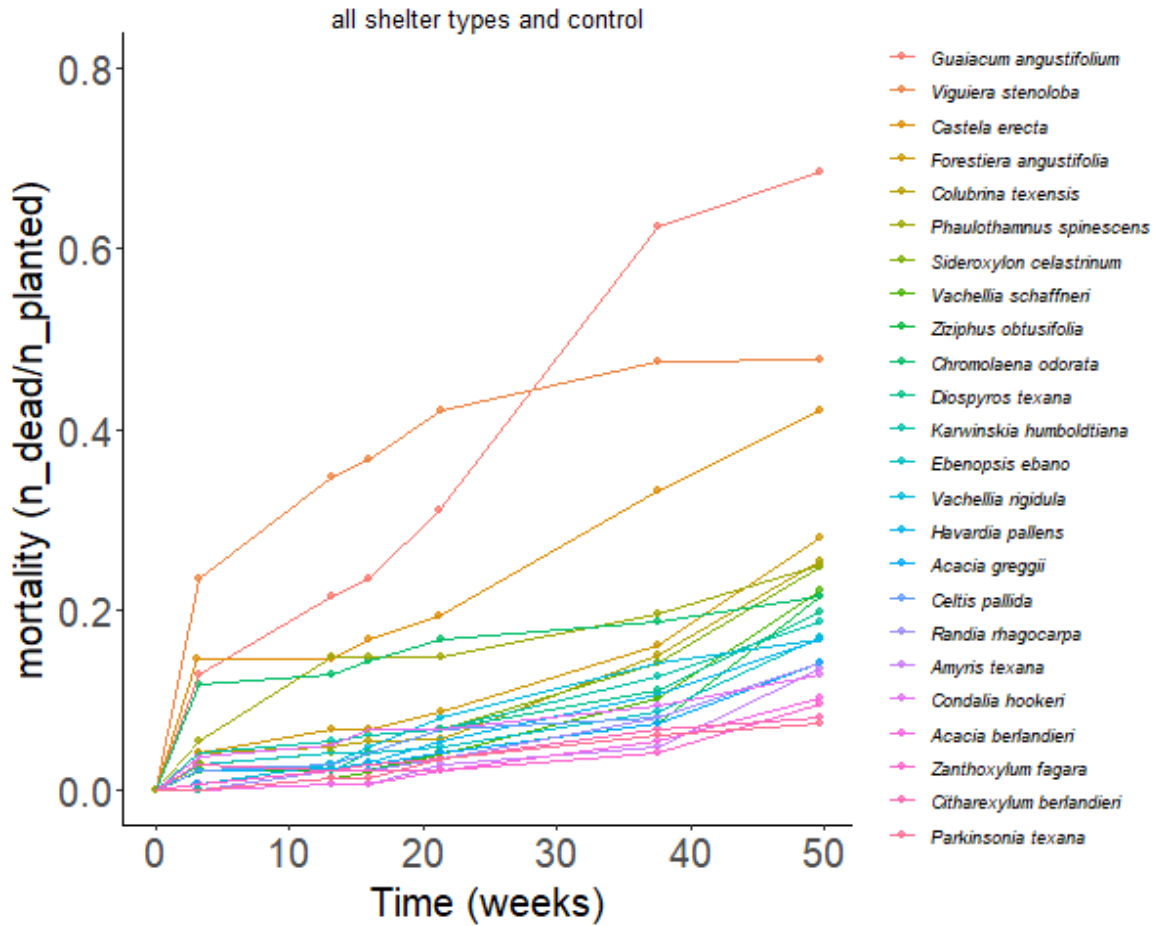


Figure 2.5. Mortality of 24 species across three shelter types: tube (a), cocoon (b), control (c), and all combined (d). Species are colored and ordered according to mortality in October 2019. Species mortality estimates are based on $n = 49-51$ individuals within each treatment and time point, except *V. stenoloba* at 50 weeks in the control ($n = 30$).

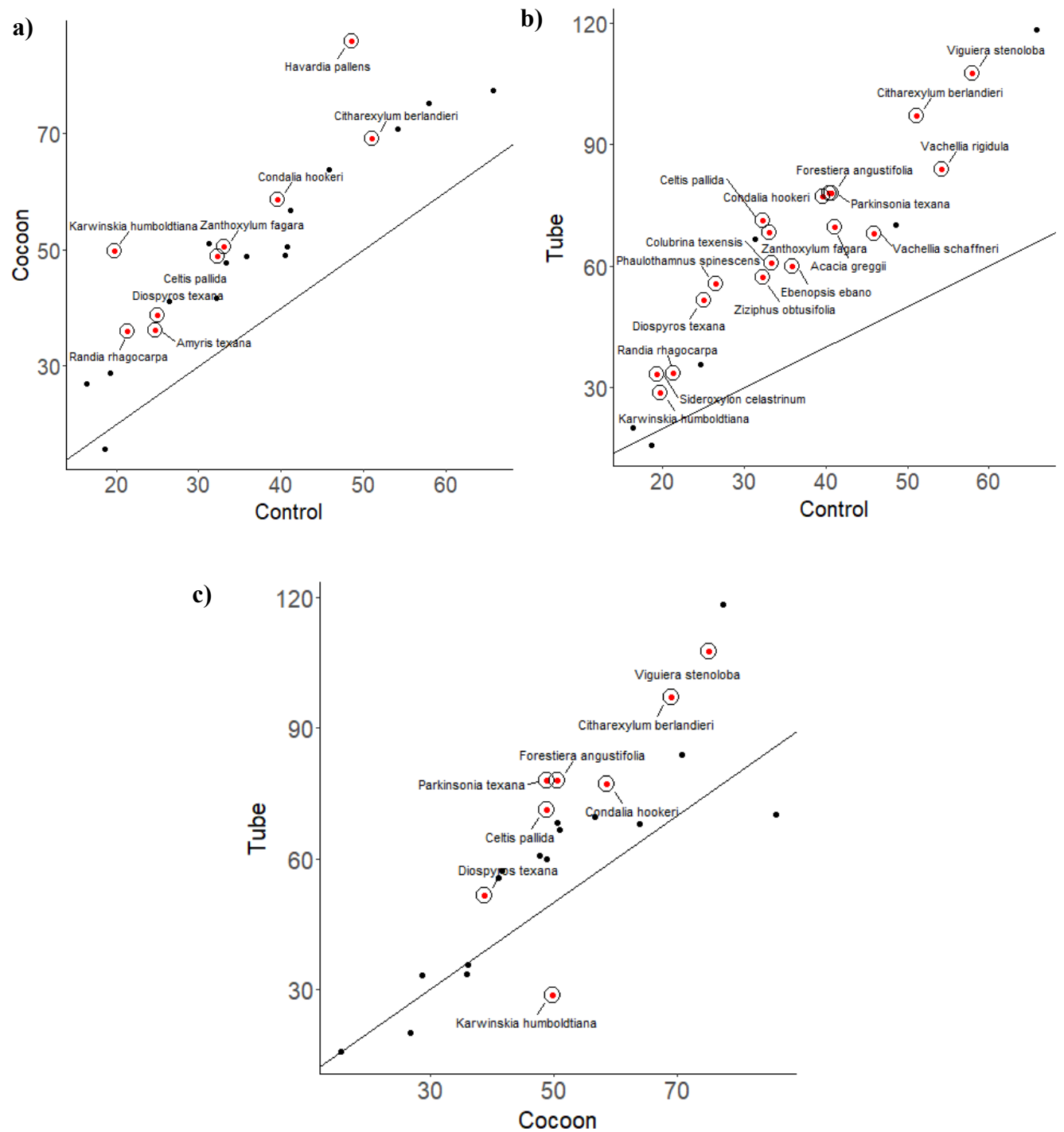


Figure 2.6. Treatment comparison of species-specific height (a) – c)) and mortality (d – f); fraction of planted individuals that are dead) at 12 months post-planting. Species with significant treatment differences (Tukey post-hoc test, $\alpha = 0.05$) are labeled. Line in each plot represents the 1:1 relationship.

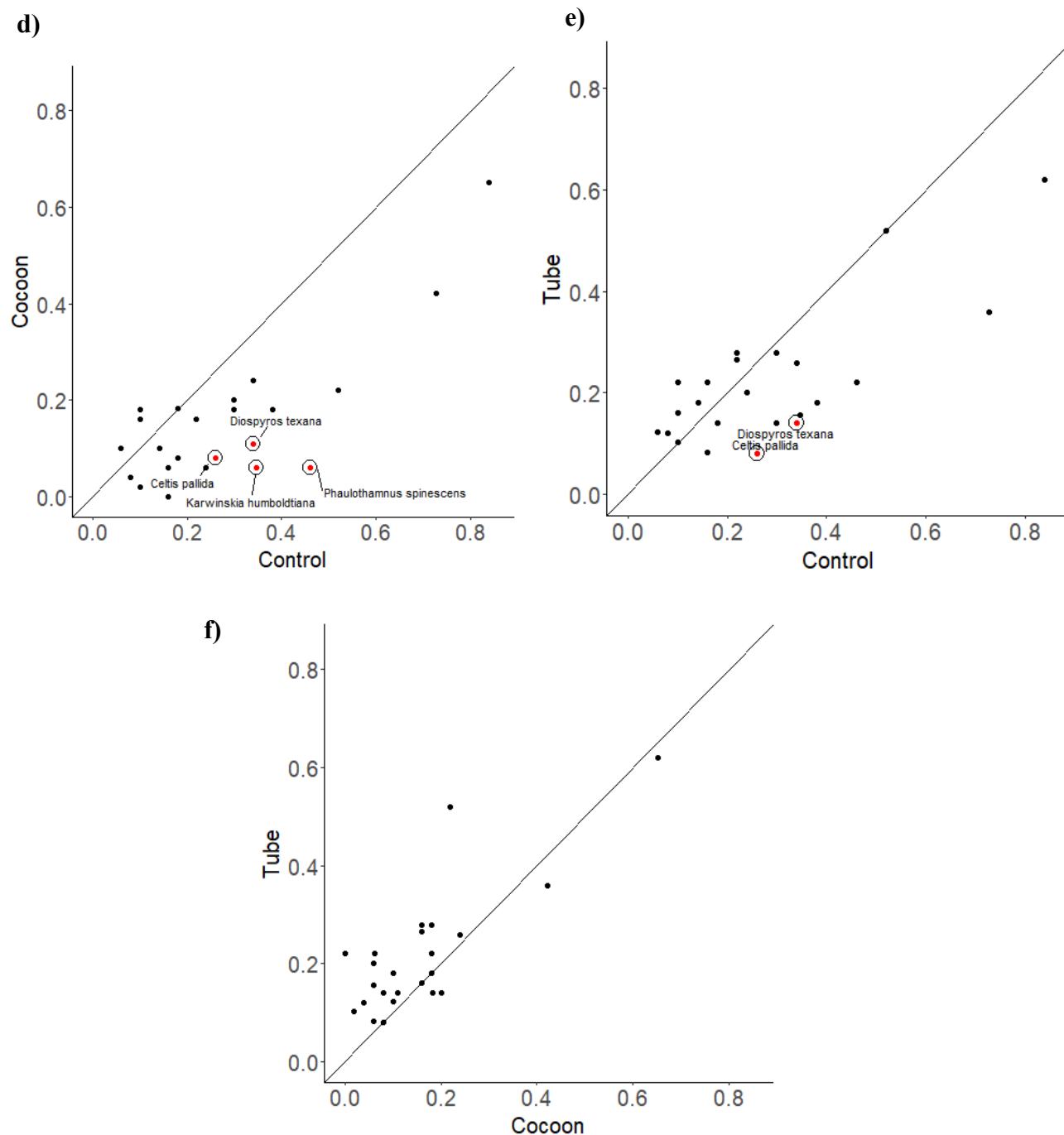


Figure 2.6. Treatment comparison of species-specific height (a) – c)) and **mortality (d) – f)**; fraction of planted individuals that are dead) at 12 months post-planting. Species with significant treatment differences (Tukey post-hoc test, $\alpha = 0.05$) are labeled. Line in each plot represents the 1:1 relationship.

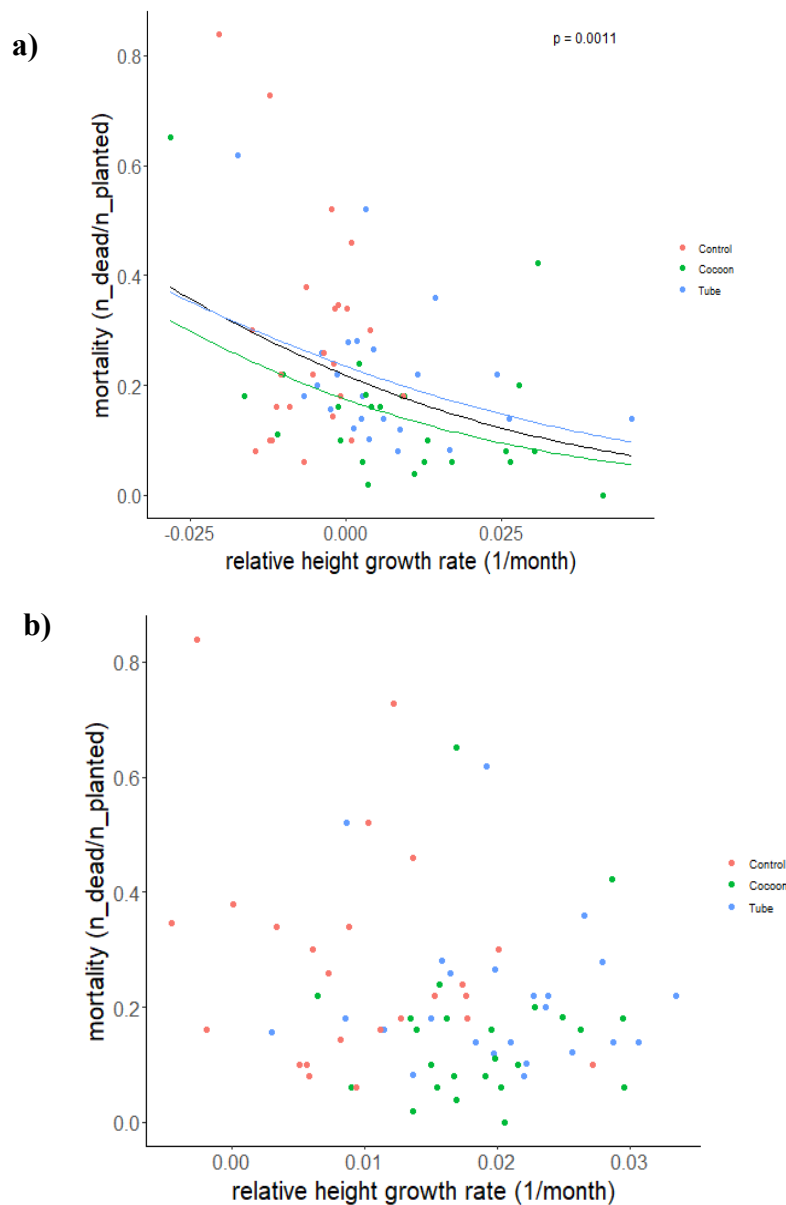


Figure 2.7. Interspecific relationship between mortality and relative height growth rate of all live individuals at 2 (a) and 12 (b) months post-planting. Logit function is plotted where significant ($p < 0.05$) and black indicates a fit through both shelter treatments and control.

CHAPTER III

CAN PLANT FUNCTIONAL TRAITS PREDICT SPECIES' SUITABILITY FOR FOREST RESTORATION? A CASE STUDY FROM SEMI-ARID SOUTH TEXAS

Abstract

Quantification of plant functional traits is essential, especially in the context of management practices such as forest restoration. Over the last couple of decades, this approach to optimizing species selection through a trait-based screening process has gained momentum and these trait-performance relationships have been explored through a variety of statistical models. However, despite the increasing use of multivariate statistics in various scientific fields for optimization, this approach in restoration ecology for the selection of species remains underutilized, and thereby, still poorly understood. In this paper, we present a case study conducted in southern Texas, where we quantified 15 initial seedling functional traits across different plant organ levels (roots, stems, and leaves) from 24 different species to determine its relationship to plant mortality during the critical establishment phase post-planting in a restoration context. We found that while singular linear relationships failed to explain the variation in species mortalities, multiple regression models encompassing trait coordination among root and stem functional traits, were able to predict the same mortalities. However, we were unable to establish any relationship between leaf traits and species mortalities.

This study shows that if plant traits are to be fully realized in their promise to predict plant performance, it is important to integrate discrete organ-level plant traits into an understanding of whole-plant function through incorporating statistical techniques that address the complexity of ecosystem-level processes impacting species performance in various management practices.

Introduction

Plant traits reflect the evolutionary underpinnings of whole plant behavior that enable them to survive and thrive in specific environments (Thorpe et al., 2011; Swenson & Enquist, 2007; Reich et. al., 2003; Ackerly et al., 2000). As a result, many studies have focused on providing a conceptual framework that links the physiology and morphology of species or taxa along an environmental gradient that explains their resource acquisition strategies (Reich, 2014; Kichenin et al., 2013; Cornwell and Ackerly, 2009). Reich's (2014) proposed "fast-slow" plant economic spectrum posits that root, stem, and leaf traits, operate in tandem to optimize resource acquisition (Reich 2014; Poorter & Bongers, 2006; Comas, Bouma & Eissenstat et al., 2002; Franco & Silvertown 1996). The overarching theme of the fast-slow plant economic spectrum is that "fast traits" confer fitness benefits in resource-rich environments whilst slow traits confer fitness benefits in resource-poor environments (Salguero-Gómez, 2017; Salguero-Gómez et al., 2016). Studies have increasingly focused on corroborating Reich et al.'s (2014) resource optimization theory to establish the functional coordination of root, stem and leaf traits with one of the three individual components of performance- growth (Menuccini et al., 2019; Perez-Harguindeguy et al., 2016; Kramer-Walter et al. 2016; Reich 2014; Carvajal et al, 2019). However, whether these coordinated functional traits can be observed during the early stages of

the plant life cycle and whether they confer enhanced fitness benefits in terms of another critical component of performance- survival, is yet to be fully understood, particularly in the case of semi-arid woody species (Foroughbakhch 2009; Shipley et al., 2016; Carvajal et al, 2019). Moreover, this relationship has important implications for management practices such as forest restoration, where selecting appropriate species with optimal functional traits is critical for meeting conservation objectives (Lavorel et al., 2012, Hamrick et al, 1991).

Over the past two decades, quantification of morphological and physiological traits of plants have become a popular approach for selecting appropriate species for reforestation programs and several studies have shown that plant traits can effectively predict the field-level performance of species in native plant restoration (Lloret et al, 1999; Jacobs et al., 2005; Tsakalidimi et al., 2013; Denton et al., 2018). These investigations have often found traits such as wood density, root-to-shoot ratio, seed size, water, and nitrogen use and other functional traits to be correlated with field performance of reforested seedlings (Grossnickle et al., 2012; Mašková et al., 2018; Messier et al., 2010; Tomar et al., 2016; Demchik et al., 2000). Most studies have increasingly relied on using single linear regression models to explore the mechanisms and relationships between survival and plant traits (Pywell et al., 2003, Lloret et al., 1999) despite evidence that the relationship between morphological and physiological attributes of plants are often non-linear and single morphological features cannot reliably and consistently predict field performance (Kramer-Walter et a., 2014; Jacobs et al., 2005). While we must acknowledge that single linear models have their benefits to generally screen for plant traits of consequence, a lot of morphological attributes, particularly relating to roots, may have an orthogonal relationship with other functional traits, and the statistical models used for inferences about species suitability should encompass the complexity of trait-trait and trait-environmental dynamics. For this

purpose, it is important to utilize multivariate statistical techniques and build models tailored for predicting field-level performance in certain sets of environmental conditions as it is more reliable and generalizable since a trait-based approach to screening plants can be applicable for species possessing similar characteristic and occurring within similar environmental gradients around the world.

Forest restoration in the semi-arid Lower Rio Grande Valley over the past four decades has resulted in the planting of over 3.3 million seedlings to revegetate the area with native thorn forests (USFWS 2014b). In a recent study, a large variation in mortality among the different species of planted seedlings was observed during the first year after planting (Mohsin et al., in preparation). While mammalian herbivory remains one of the main causes of mortality, large species-specific differences in mortality was also observed among seedlings that were protected from herbivores through physical shelters. A high proportion of this mortality occurred during the initial months after planting, suggesting that mortality was induced by transplant shock, as is the case with many transplanted seedlings used in reforestation (Demchik and Sharpe 2000; Jacobs et al. 2004; Pinto et al. 2011). However, the large variation in mortality at the species level among plants with herbivore exclusions (Mohsin et al. in prep) led us to speculate the role of functional traits at the species level which may confer fitness benefits through coordinating different functional traits along the plant economic spectrum by offsetting environmental stressors.

The purpose of this study was to determine how species' functional traits including root, stem, and leaf economic traits such as specific root length (SRL), root mass fraction, wood density, and leaf area are coordinated, and to assess which traits or combinations of traits align with field performance (mortality) to determine the adaptive significance of these traits. We

hypothesized that plant traits are highly synchronized within and between organs and thereby, incorporating multiple independent axes of trait variation will result in greater predictive power for field performance (mortality) than single plant traits in isolation. To this end, we quantified species-specific seedling mortality across 24 species through a year-long forest restoration assessment. Then we determined species-specific functional traits to evaluate relationships among mortality rates and functional traits among these 24 species to detect a subset of the linear trait-performance relationships that occur within the plant “fast-slow” economic spectrum (Reich 2014).

Methods

Species Field Demographic Estimates

We selected the 24 species (Fig. 1, Tables in Supporting Information) of recently transplanted thornscrub seedlings for which we conducted a yearlong mortality survey (November 2018-November 2019) of 3600 seedlings in La Sal del Rey (Hidalgo County, Texas) within one of Lower Rio Grande Valley National Wildlife Refuge’s restoration plot (Mohsin et al., in prep). Three separate mortality proportions were obtained from each of the species from 3 different shelter conditions including i) 80 cm tall ventilated plastic shelter tubes (TUBEX), ii) a newly developed physical seedling shelter called cocoons (Land Life Company, Amsterdam, Netherlands) which consists of a 30cm tall biodegradable physical shelter with an underground reservoir that slowly released water to the seedling roots for the initial month post-planting, and iii) seedlings without any shelters. Due to the unaccountable differences in the microclimatic environment for each of the physical seedling shelters, we quantified the mortalities for each species separately for each shelter type. We did not use mortality values of seedlings without shelters because mortality occurred in extremely high percentages for these seedlings due to

herbivory and these differences were caused by differences in palatability of leaves to herbivores, which could not be reliably quantified through this study. In total mortality rates were obtained from 2400 seedlings with an average of 50 replicates per species and shelter conditions.

Functional Trait Measurements

For trait measurements, seedlings were sourced from the Santa Ana National Wildlife Refuge's Native Plant Nursery by obtaining a subset of the seedlings used in Lower Rio Grande Valley restoration plantings. Seedlings ranged in age from 4 – 8 months, and we processed them for trait measurements within a month of obtaining them. In total, we quantified 30-40 different plant traits and 15 functional traits for each species from 125 individual seedlings of these species with an average of 5 replicates per species ($n = 3-8$). The differences in the number of measured plant traits are due to trait variability (E.g. compound vs simple leaves) and possible measurement errors. Seedling cumulative mortality, hereby referred to as mortality, was calculated for each species as $(N_D/N_{P\text{ total}})$ where N_D is the total number of seedlings dead one year following planting (Oct 2019) and $N_{P\text{ total}}$ is the total number of live seedlings at planting (Oct-Nov 2018). Between 12 to 17 photosynthetic structures (including petioles) were sampled from each plant, depending on the size per individual leaf. Vernier calipers were used to measure the thickness (mm) of five separate leaves. Fresh leaf mass (g) was obtained within an hour of harvesting, and the leaves were then dried over 48 hrs. at 70 degrees Celsius. Leaf area (cm^2) was measured on a LI-COR Biosciences LI-3100C (Lincoln, NE, USA) leaf area meter. Leaf volume(cm^3) was calculated as the product of average leaf thickness (mm) and one-sided projected leaf area. Leaf dry matter content (LDMC) was calculated as the ratio of leaf dry mass (g) to leaf fresh mass (g), specific leaf area (SLA) (cm^2/g) was calculated as fresh leaf area (cm^2)

divided by leaf dry mass (g), and leaf tissue density (g/cm^3) was calculated as leaf dry mass (g) divided by fresh leaf volume (cm^3) (Perez-Harguindeguy, 2016).

For determining stem wood density, a 2-4 centimeter section of the stem containing xylem was cut and the bark was peeled or scraped off. The diameter (mm) of the stem sections was measured using digital Vernier calipers, and fresh volume (cm^3) was calculated using the water displacement method. Fresh stem mass (g) was measured within 1 hour of harvesting, and stems were then dried to constant mass at 70°C for at least 48 h prior to measuring dry mass. Wood density (g/cm^3) was calculated as the ratio of stem dry mass (g) to stem green volume (cm^3). Total root length (cm), mean root diameter (mm), the number of tips, forks, crossing and root volume (cm^3) was calculated using WinRhizo Pro Software (Version 2017b; Regent Instruments Inc., Quebec City, QC, Canada) and an Epson Expression LA2400 scanner (Tokyo, Japan). The mean root length (cm) in each sample across species was 873 cm (range: 417–1737 cm), and the mean number of intact tips in each sample across all species was 2617 (range: 913–14167). Fresh root mass(g) of each sample was obtained after removing the surface water with paper towels. The root sections were then dried to constant mass at 100 degrees Celsius for 48 hours. Specific root length (cm/g) was calculated as root length (cm) divided by root dry mass (g). Root tissue density (g/cm^3) was calculated as root dry mass (g) divided by fresh root volume (cm^3). Root branching intensity ($\text{tips}/\text{cm}^{-1}$) (RBI) was calculated as the number of root tips divided by root length (cm).

Data Analysis

Detecting coordination of multiple traits in predicting plant mortality requires multivariate approaches and newer multivariate statistical methods such as bootstrap forest, boosted tree regressions are more deterministic and can more easily quantify both linear and non-

linear relationships through advanced assimilated mortality algorithms (Piston et al., 2019). However, it requires a very large sample size to add stochasticity to the model. Therefore, due to logistical constraints of quantifying plant traits in a large number of seedlings from each species within the forest restoration context, we sought to screen for predictor traits through single and multiple least square regression models following the precedent of Schroeder-Georgi et al. (2016), Pywell et al. (2003), Jacobs et al. (2005). We expected traits along various organ levels to be correlated. Since correlation creates chances of collinearity, we formulated regression models encompassing multiple traits only if the traits were uncorrelated since collinearity between independent variables in multiple regression models would violate the assumption of independence.

Our data met the assumptions of normality (Shapiro-Wilk's W test; $p\text{-value} > 0.085$ for all variables) and homoscedasticity (Levene, O'Brien, and Brown-Forsythe's test; $P\text{-value} > 0.0661$ for all variables). We conducted an analysis of variance (ANOVA) to establish that there were species-specific differences in root, stem, and leaf functional traits as well as mortality rates. Then we computed the Pearson correlation coefficient to test the strength of the linear relationships between these traits (Table 3.2). To determine the relationship between plant traits with species performance, we conducted simple linear regression between mortality of tube shelter and cocoon shelters seedlings (response variable) with each of the individual functional traits as explanatory variables (Schroeder-Georgi et al., 2016; Pywell et al., 2003; Jacobs et al., 2005). These were all conducted separately. Then we formed our multiple linear regression models to test the relationship of each of the functional traits to observed mortality rates using the backward elimination method to select trait variables (Jager et al., 2015). We first started with a set of 3 uncorrelated functional traits as explanatory variables (full model) and

sequentially eliminated non-significant explanatory predictor variables until only significant predictor variables remained. We applied this approach for all combinations of 3 or less uncorrelated traits based on the significant correlation values obtained in our Pearson pairwise correlation test and the obvious association between traits obtained from common measurement parameters (e.g., root length and specific root length). All analyses were conducted using SAS (JMP Pro 13).

Results

This study constituted two parts; the first was an examination of trait-trait relationships through correlations on individual-level trait correlation (Table 3.2) which looked at both intra-specific and inter-specific relationships as well as sample population-level trait correlation that determined trait coordination between species (Table 3.3). The second part looked at trait-performance (mortality) through single linear and multiple regression analyses of different combinations of uncorrelated (based on Table 3.3) functional traits as predictors of performance in terms of mortality (Jager et al., 2015). The average mortality of seedlings in tubes was 22% (Range= 8%-62%) and the average mortality in cocoon shelters was 15% (Range= 0%-65%).

Trait-trait relationship

We conducted a Pearson pairwise correlation between all measured traits. Table 3.2 shows the significant relationships that we found within our correlation matrix. Leaf tissue density is negatively associated with stem mean diameter ($r^2 = -0.276$; $p < 0.05$). Stem mean diameter has a positive association with root surface area ($r^2 = 0.331$; $p < 0.05$), root tissue density ($r^2 = 0.367$; $p < 0.05$), root volume ($r^2 = 0.245$; $p < 0.05$) and stem height ($r^2 = 0.497$; $p < 0.05$), and a negative association with specific root length ($r^2 = -0.314$; $p < 0.05$). Stem height was found to be negatively correlated with root surface area ($r^2 = 0.234$; $p < 0.05$), root tips ($r^2 = -0.241$; $p < 0.05$),

root mass fraction ($r^2=-0.252$; $p<0.05$), specific root length ($r^2= -0.254$; $p<0.05$), root branching ($r^2= -0.387$; $p<0.05$). Stem wood density was negatively associated with root tips ($r^2=-0.204$; $p<0.05$) and specific root length ($r^2=-0.214$; $p<0.05$). Root tissue density had a negative relationship with root mean diameter ($r^2= -0.380$; $p<0.05$). Root tips was found to have a negative association with root mean diameter ($r^2= -0.315$; $p<0.05$). Thus, a significant coordination within and between organ level functional traits was found within our sample.

Trait-performance relationship

Linear regression models that used a single trait as a predictor for seedling mortality found significant relationships between root branching intensity (RBI), stem wood density (WD), and specific root length (SRL) with mortality. However, through the back elimination method, we were able to make 3 distinct multiple regression models that were that yielded a significant relationship with two or more variables (Figure 3.1). While RBI ($p=0.005$, $R^2=0.32$) and SRL ($p=0.0042$, $R^2=0.33$) showed a positive association with mortality in cocoon sheltered seedlings (Fig 3.1 a,c), greater stem wood ($p=0.010$, $R^2=0.27$) density was found to be associated with lower mortality (Figure 3.1b).

We formed 3 distinct multiple linear regression models to quantify how coordinated traits function as mortality predictors. The first model constitutes two stem traits, wood density and stem height, which is an orthogonal relationship that shows that wood density has an inverse relationship with seedling mortality in cocoon shelters ($P<0.0001$) which means that as species wood density increases, an overall decrease in mortality is observed (Figure 3.2b). While stem height doesn't have an independent effect on cocoon mortality, the interaction increased stem height and wood density shows an increase in cocoon mortality ($P=0.003$) (Figure 3.2c, 3.2d)

In the second model, we observe coordination between stem and root functional traits for determining mortality in cocoon shelters (Figure 3.3). We observe a similar phenomenon as in model 1, where an increase in wood density leads to a decrease in cocoon mortality $p=0.0053$) (Figure 3.3a). However, within this model, an increase in the number of root tips leads to an increase in cocoon mortality ($p=0.0002$) (Figure 3.3b).

In the third model, we observe that an increase in root mass fraction decreases mortality of seedlings in tube shelters ($P=0.0134$), which suggests that increased root allocation decreases mortality among seedlings in tube shelters (Figure 3.4b). However, the interaction between a higher number of root tips and root mass fraction increases the mortality of seedlings in tube shelters ($P=0.0035$) (Figure 3.4d).

Discussion

We found that species' root, stem, and leaf traits are highly coordinated with each other and do indeed function in tandem to impact mortality. While some initial seedling traits such as root branching intensity, specific root length, and wood density independently predicted mortality in seedlings (figure 3.1), the strength of the associations between mortality and traits were always at least twice as much in the multiple regression mortality models. For instance, various combinations of the height of stems, wood density, root mass fraction, root tips and the interaction between root tip and root mass fraction as well as wood density and stem height were able to predict mortality in cocoons with a much greater strength of association in comparison (Figure 3.2, 3.3, 3.4) to single linear regression models (figure 3.1). There is also substantial evidence that other than being highly correlated among themselves (Table 3.2), organ traits were highly correlated between species as well (Table 3.3). This shows that coordinated traits

observable within the seedlings used in restoration are also better predictors of seedling mortality during the first year post-transplantation.

Trait-based ecology is still in its foundational stages (Laughlin, 2014). Thus, the opportunity to integrate trait-based ecological science with modern data analytical approaches has immense potential in optimizing resources to invest in appropriate management practices (Cornwell et al., 2006). As the effort to conserve and restore vegetation across the globe expands, it is essential to understand species interactions, distributions, and resilience to ecosystem processes. Our study shows that while research has established straightforward explanations of how certain traits provide fitness benefits in specific environments (Reich, 2014; Shipley et al., 2016), that is not always the case (Carvajal et al., 2019). For example, our results (on...) are in line with past studies demonstrating that in resource-limited environments, individual traits such as high root mass fraction (or root: shoot ratio) and high wood densities lead to decreased mortality among reforested seedlings (Greenwood et al., 2017; Grossnickle et al., 2012; Mašková et al., 2018; Messier et al., 2010). However, while that is partly held true in our study, we see that in the high root mass fraction shows the opposite effect in conjunction with a higher number of individual root tips (Figure 3.4). Similarly, wood density along with greater stem height results in greater mortality among seedlings (Figure 3.2). While exploring the underlying physiological principles leading to these variations in mortalities is beyond the scope of this study, the results indicate that single traits can be a misleading predictor of field performance and there should be a greater focus on developing sites specific species performance models that take into account multiple traits and environmental variables for predicting performance (Carvajal et al., 2019; Kleyer et al., 2012; Dray et al., 2014).

Linear relationships more easily measurable and interpretable, which is an important consideration since reforestation activities often involve stakeholders and decisionmakers from non-scientific backgrounds. Unlike other more multivariate approaches, it requires relatively smaller samples to form predictions (while other regression methods such as Bootstrap forest, Boosted tree regressions are more deterministic and can more easily quantify non-linear relationships as well, they require an immensely large amount of data, which is difficult and more expensive to obtain, especially if destructive trait measurements are required for trait quantification. So, quantifying desirable traits in the context of restoration through sampling seedlings used in reforestation creates a precedent for a more generalizable approach that can be more widely applicable around the world. Despite the potential of these regressions methods for trait-based screening for suitable species selection in reforestation, these methods should be used with caution since it does not have the same power to detect trait-trait coordination among multiple traits when multidimensional and non-linear relationships are involved or when stochasticity is introduced to the multi-variate approaches to diminish bias. Hence, there is a possibility that these models are too loosely interpreted and are less generalizable due to interactions between non-linear traits that haven't been accounted for. As a result, it becomes challenging to form a trait-based predictive framework for maximizing seedling establishment success during the first year based on linear trait-performance relationships only. However, trait data across the world is becoming more and more available through databases such as TRY, GLOPNET, LEDA, BROT, and quite a few other databases (Cornwell et al., 2019). This creates the opportunity for a large number of data collected around the world to be easily available for creating species selection plant trait frameworks for appropriate species selection that are more

robust and can address the multi-dimensional complexity of the interactions within plants that influence seedling establishment success.

Tables & Figures

Species	Common Name	Family	Growth form	Tube Shelter Mortality	Cocoon Shelter Mortality
<i>Acacia berlandieri</i>	Guajillo	Fabaceae	tree	8.3%	6.0%
<i>Acacia greggii</i>	Wright's Acacia	Fabaceae	tree	18.0%	10.0%
<i>Amyris texana</i>	Chapotillo	Rutaceae	shrub	14.0%	8.0%
<i>Castela erecta</i>	Amargosa	Simaroubaceae	shrub	52.0%	22.0%
<i>Celtis ehrenbergiana</i>	Granjeno	Ulmaceae	shrub	8.0%	8.0%
<i>Chromolaena odorata</i>	Crucita	Asteraceae	shrub	14.0%	20.0%
<i>Citharexylum berlandieri</i>	Fiddlewood	Verbenaceae	shrub	12.0%	4.0%
<i>Colubrina texensis</i>	Hogplum	Rhamnaceae	shrub	28.0%	18.0%
<i>Condalia hookeri</i>	Brasil	Rhamnaceae	tree	22.0%	0.0%
<i>Diospyros texana</i>	Texas Persimmon	Ebenaceae	tree	14.0%	11.0%
<i>Ebenopsis ebano</i>	Texas Ebony	Fabaceae	tree	14.0%	18.4%
<i>Forestiera angustifolia</i>	Elbowbush	Oleaceae	shrub	26.0%	24.0%
<i>Guaiacum angustifolium</i>	Guayacan	Zygophyllaceae	shrub	62.0%	65.1%
<i>Havardia pallens</i>	Tenaza	Fabaceae	tree	20.0%	6.0%
<i>Karwinskia humboldtiana</i>	Coyotillo	Rhamnaceae	shrub	15.7%	6.0%
<i>Parkinsonia texana</i>	Palo Verde	Fabaceae	tree	10.2%	2.0%
<i>Phaulothamnus spinescens</i>	Snake Eyes	Achatocarpaceae	shrub	22.0%	6.1%
<i>Randia rhagocarpa</i>	Crucillo	Rubiaceae	shrub	16.0%	16.0%
<i>Sideroxylon celastrina</i>	Coma	Sapotaceae	tree	18.0%	18.0%
<i>Vachellia rigidula</i>	Black Brush	Fabaceae	tree	22.0%	18.0%
<i>Vachellia schaffneri</i>	Huisachillo	Fabaceae	tree	27.9%	16.0%
<i>Viguiera stenoloba</i>	Goldeneye	Asteraceae	shrub	36.0%	42.2%
<i>Zanthoxylum fagara</i>	Colima	Rutaceae	shrub	12.2%	10.0%
<i>Ziziphus obtusifolia</i>	Lotebush	Rhamnaceae	shrub	26.5%	16.0%

Table 3.1 Mean values of species' mortality percentages in different shelter types

Plant Functional Traits	Root Surface Area (cm ²)	Root Mean Diameter (cm)	Root Volume (cm ³)	Root Tips	Root Mass Fraction	Specific Root Length (cm)	Root Branching (tips/cm)	Root Tissue Density (g/cm ³)	Stem Wood Density (g/cm ³)	Stem Height (cm)	Stem Mean Diameter (cm)	Leaves Total Area (cm ²)	Specific Leaf Area (cm ² /g)	Leaf Dry Matter Content	Leaf Tissue Density (g/cm ³)
Root Surface Area (cm ²)	1														
Root Mean Diameter (cm)	0.608	1													
Root Volume (cm ³)	0.840	0.780	1												
Root Tips	-0.057	-0.315	-0.102	1											
Root Mass Fraction	0.008	0.016	0.000	-0.112	1										
Specific Root Length (cm)	-0.096	-0.169	-0.116	0.359	-0.584	1									
Root Branching (tips/cm)	-0.234	-0.022	-0.048	0.751	-0.163	0.337	1								
Root Tissue Density (g/cm ³)	-0.309	-0.380	-0.174	0.115	0.139	-0.249	-0.060	1							
Stem Wood Density (g/cm ³)	0.092	0.176	0.089	-0.204	0.086	-0.214	-0.145	-0.006	1						
Stem Height (cm)	0.234	0.072	0.144	-0.241	-0.252	-0.254	-0.387	0.094	0.084	1					
Stem Mean Diameter (cm)	0.331	0.088	0.245	0.088	-0.021	-0.314	-0.119	0.367	0.047	0.497	1				
Leaves Total Area (cm ²)	0.088	-0.059	-0.021	-0.065	-0.184	-0.083	-0.168	0.047	-0.068	0.341	0.328	1			
Specific Leaf Area (cm ² /g)	-0.017	-0.158	-0.066	0.015	0.041	-0.016	-0.079	0.051	-0.107	0.050	0.190	0.320	1		
Leaf Dry Matter Content	-0.135	-0.024	-0.028	-0.097	-0.045	0.006	-0.053	0.128	0.073	0.040	-0.040	-0.078	-0.547	1	
Leaf Tissue Density (g/cm ³)	-0.062	0.001	-0.024	-0.044	0.030	-0.034	0.060	0.000	0.036	-0.008	-0.276	-0.150	-0.347	0.352	1

Table 3.2: Pearson's correlation matrix showing intra-specific and interspecific correlation of laboratory quantified plant traits. Correlation matrix was formulated from raw data of 125 seedling samples of 24 species.

Plant Functional Traits	Root Length (cm2)	Root Surface Area (cm2)	Root Mean Diameter (cm)	Root Volume (cm3)	Root Tips	Root Mass Fraction	Specific Root Length (cm)	Root Branching (tips/cm)	Root Tissue Density (g/cm3)	Stem Wood Density (g/cm3)	Stem Height (cm)	Stem Mean Diameter (cm)	Leaves Total Area (cm2)	Specific Leaf Area (cm2/g)	Leaf Dry Matter Content	Leaf Tissue Density (g/cm3)
Root Length (cm)	1															
Root Surface Area (cm2)	0.5084	1														
Root Mean Diameter (cm)	-0.763	-0.0334	1													
Root Volume (cm3)	-0.2272	0.4998	0.6975	1												
Root Tips	0.6101	0.25	-0.3375	0.0286	1											
Root Mass Fraction	-0.1851	0.0804	0.2141	0.1189	-0.1358	1										
Specific Root Length (tips/cm)	0.4284	-0.2103	-0.3809	-0.3885	0.5135	0.5133	1									
Root Branching (tips/cm)	0.0905	0.0083	0.209	0.3505	0.7946	0.0524	0.3405	1								
Root Tissue Density (g/cm3)	0.2271	-0.2907	-0.321	-0.1015	0.1689	0.0751	-0.0715	0.1447	1							
Stem Wood Density (g/cm3)	-0.0365	0.1676	0.1017	0.167	-0.3212	0.3103	-0.3993	-0.2991	0.1018	1						
Stem Height (cm)	0.0114	0.5843	0.2041	0.5118	-0.2345	0.3016	-0.3412	-0.276	-0.2809	0.1768	1					
Stem Mean Diameter (cm)	0.1793	0.6648	0.1622	0.7291	0.2512	0.0135	-0.4367	0.2759	0.1778	0.2106	0.4597	1				
Leaves Total Area (cm2)	0.1244	0.2996	-0.1106	0.1547	-0.0871	0.3136	-0.114	-0.1189	-0.0236	-0.1328	0.3149	0.3029	1			
Specific Leaf Area (cm2/g)	0.0616	0.0779	-0.1156	-0.0585	-0.0539	0.1324	-0.1825	-0.1075	0.0997	-0.063	0.1616	0.21	0.5274	1		
Leaf Dry Matter Content	-0.1799	-0.27	0.007	-0.1028	-0.1712	0.0927	0.1506	-0.0969	-0.01	0.1228	-0.1831	-0.1764	-0.2067	-0.4882	1	
Leaf Tissue Density (g/cm3)	-0.1135	-0.0967	0.0152	-0.1025	-0.0946	0.326	-0.0912	-0.0038	0.0757	0.211	-0.0812	-0.1422	-0.3294	-0.5213	0.3821	1

Table 3.3: Pearson's correlation matrix showing interspecific correlation between mean trait values of 24 species. The correlation matrix was formulated by plotting the average plant traits of 24 species

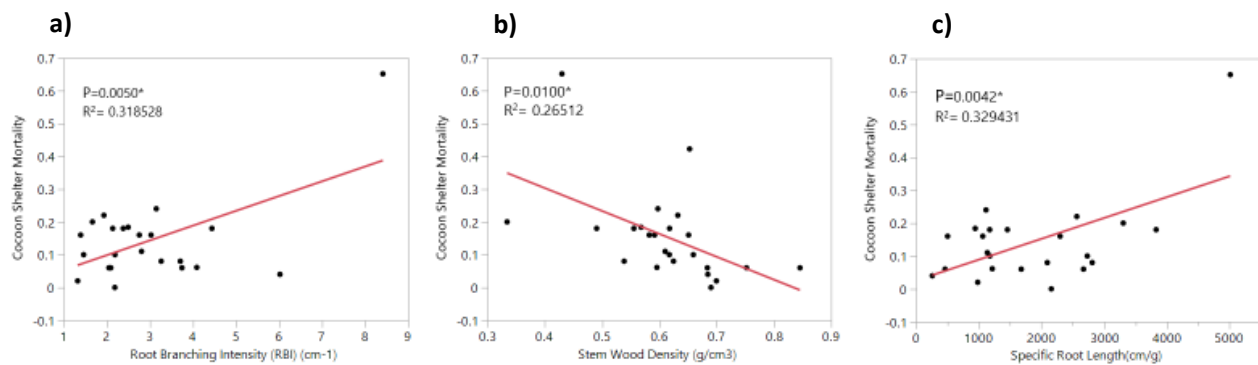


Figure 3.1: Bivariate relationships between seedling mortality in cocoon shelters and root branching intensity, stem wood density and specific root length. Solid lines indicate significant regression lines. Coefficients of determination (R^2) and p-values are shown have a combined effect on mortality of seedlings in cocoon shelters

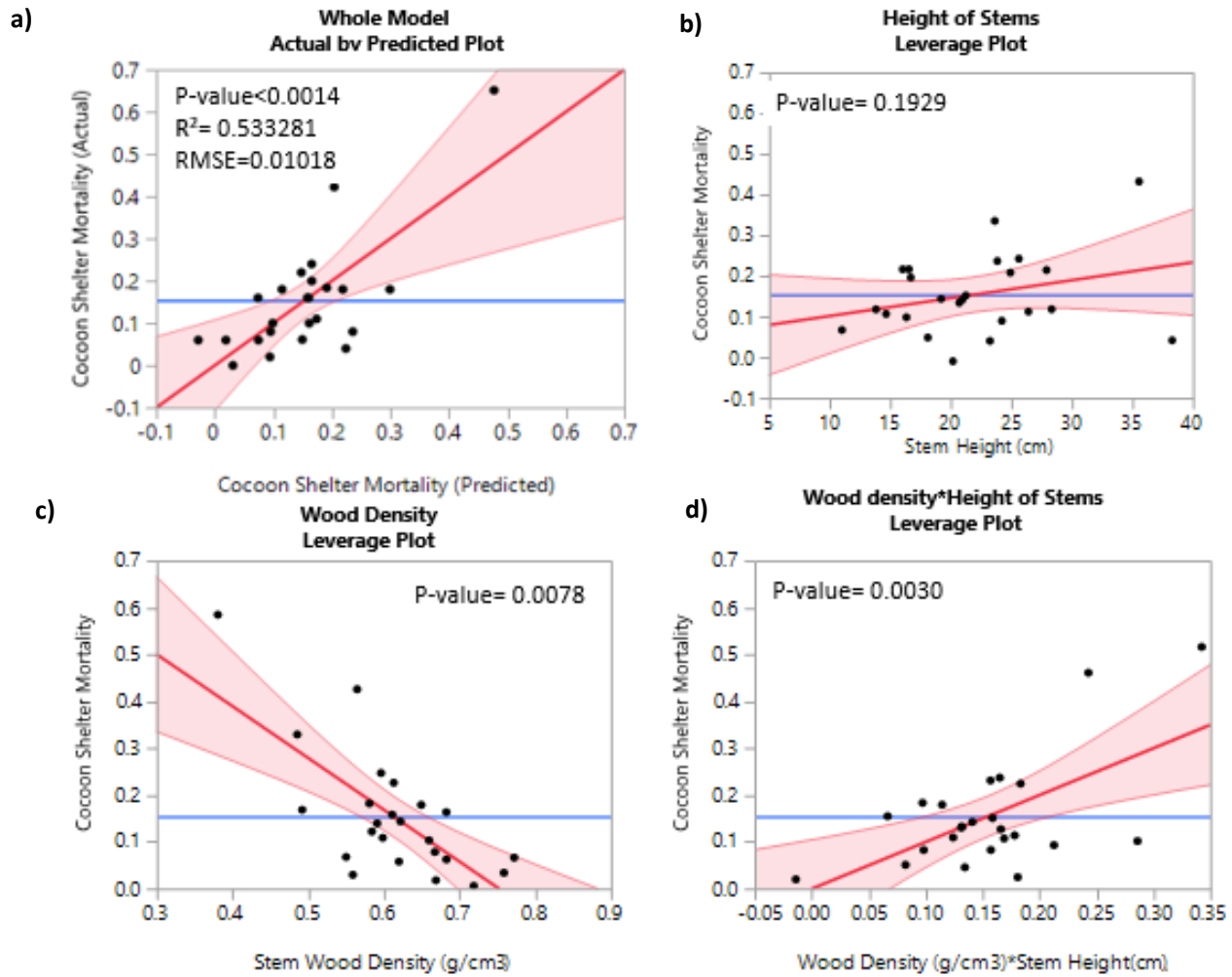


Figure 3.2. The model shows the goodness of fit of the multiple regression model formed with height of stems, wood density, and interaction between wood density and height of stems as predictor variables for mortality in cocoon shelters. (a) The actual vs predicted plot shows that the observed model is a good fit since the observed vs the predicted values are highly correlated ($R^2=0.533281$; p-value<0.0014) (b) The leverage plot of the height of stems shows that stem height and mortality in cocoons are associated, although insignificantly (p-value=0.1929) (c) The leverage plot of wood density shows negative association with mortality in cocoons (p-value= 0.0078) (c) The leverage plot of the interaction between wood density and height of stems (p-value= 0.0030) show that increased wood density and height of stems is associated with greater mortality.

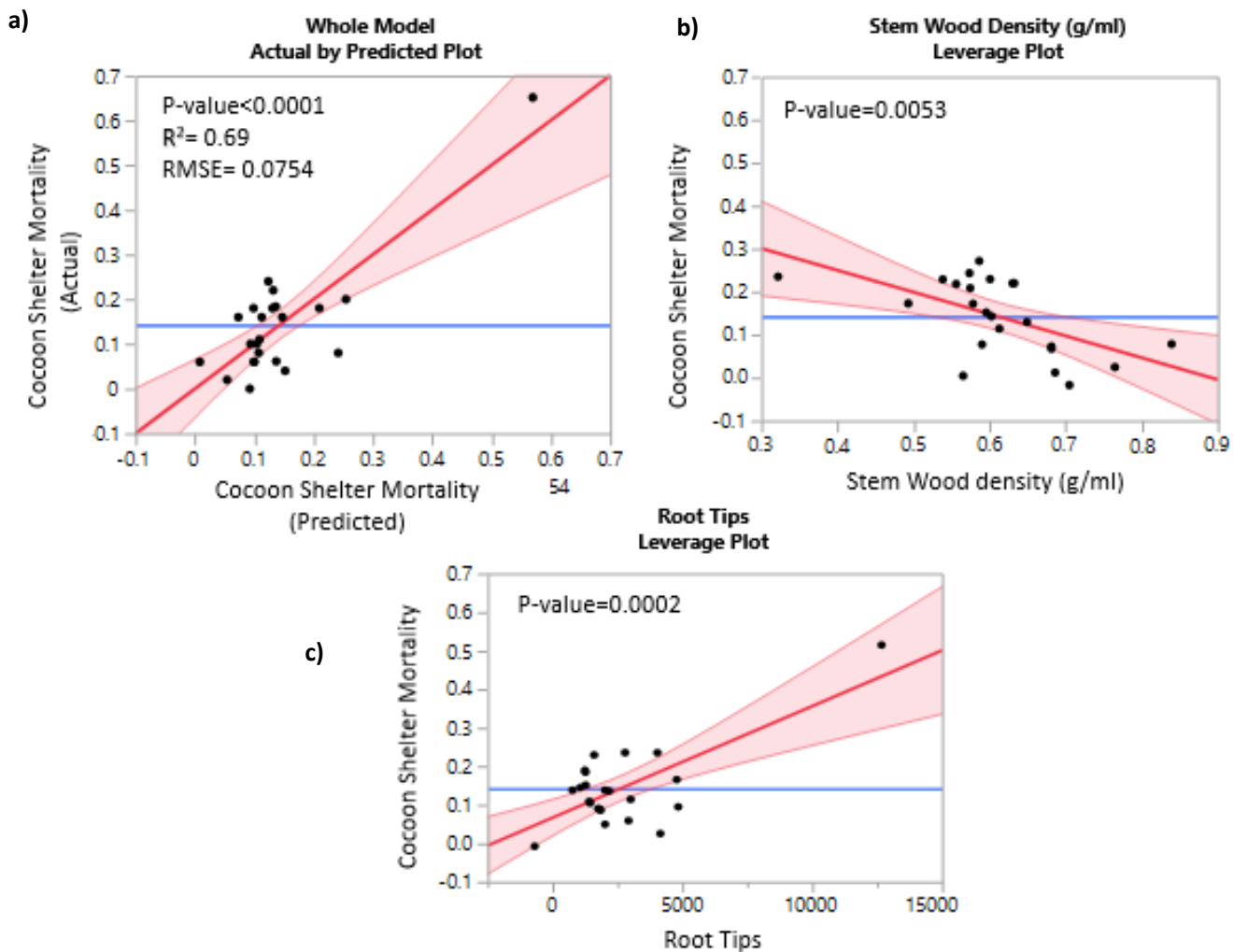


Figure 3.3 (a) The model shows the goodness of fit of the multiple regression model formed with wood density, root tips as predictor variables for mortality in cocoon shelters. (a) The model is a good fit since the observed vs the predicted values are highly correlated ($R^2=0.69$; p-value<0.0001) (b) The leverage plot of the wood density (p-value= 0.0053) (c) The leverage plot of the wood density (p-value= 0.0078) shows WD effects tube mortality positively

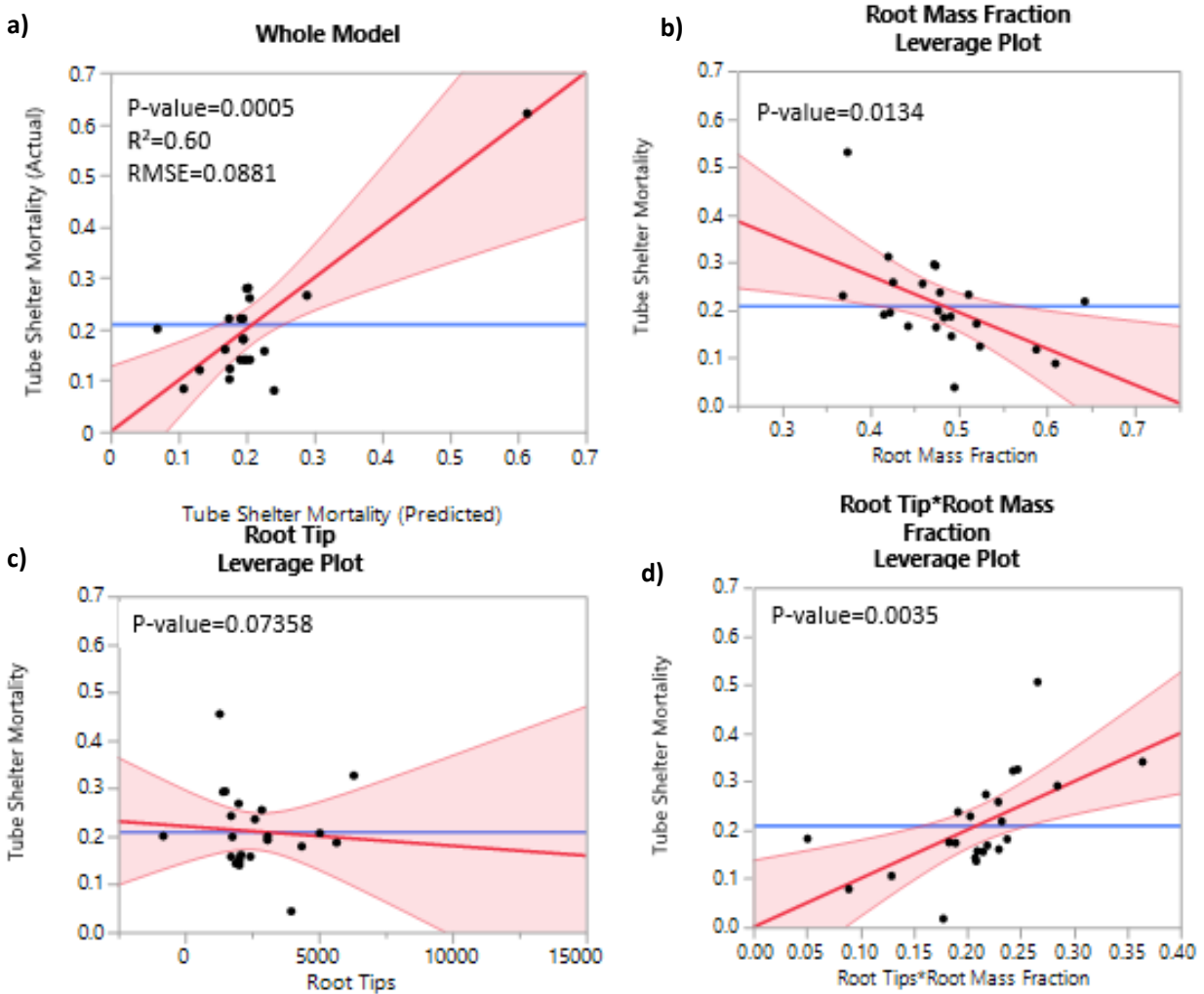


Figure 3.4. (a) The model is a good fit since the observed vs the predicted values are highly correlated ($R^2=0.60$; p-value=0.0005) (b) The leverage plot of the root mass fraction (p-value=0.0134) showing a negative association between RMF and mortality in shelter tubes (c) The leverage plot of the root tips (p-value=0.07358) showing root tips do not independently effect tube mortality (d) Plotted leverage of the interaction between root tips and root mass fraction (p-value=0.0035) showing that the two variable have a combined effect on mortality in shelter tubes

Species	Root Length (cm)	Root Surface Area (cm ²)	Root Mean Diameter (cm)	Root Volume (cm ³)	Root Tips	Root Forks	Root Crossings	Root Mass Fraction	Specific Root Length (cm/g)	Root Branching Intensity (tips/cm)	Root Tissue Density (g/cm ³)
<i>Acacia berlandieri</i>	648.41	302.44	0.15	11.57	2400.60	4378.60	466.00	0.61	460.16	3.74	0.14
<i>Acacia greggii</i>	668.02	302.63	0.16	11.59	1390.60	3821.80	528.00	0.51	1175.85	2.19	0.07
<i>Amyris texana</i>	507.83	197.95	0.15	7.94	1639.60	2508.00	297.80	0.38	2812.45	3.26	0.10
<i>Castela erecta</i>	1338.04	379.04	0.10	9.34	2611.20	10914.60	1943.20	0.36	2565.19	1.93	0.10
<i>Celtis ehrenbergiana</i>	1265.40	285.15	0.07	5.57	4749.00	11513.40	2869.40	0.45	2093.62	3.71	0.17
<i>Chromolaena odorata</i>	1014.19	345.74	0.11	9.51	1609.40	8083.00	1413.60	0.27	3308.26	1.66	0.03
<i>Citharexylum berlandieri</i>	686.44	477.50	0.28	77.63	4225.43	5273.29	314.00	0.51	256.54	6.02	0.11
<i>Colubrina texensis</i>	635.26	292.69	0.15	11.18	1209.60	3996.00	582.20	0.53	1173.26	2.14	0.05
<i>Condalia hookeri</i>	1043.04	222.70	0.07	4.09	2266.33	6385.00	1496.00	0.47	2158.01	2.18	0.18
<i>Diospyros texana</i>	509.63	336.17	0.21	18.99	1420.67	2074.00	297.00	0.55	1135.72	2.80	0.04
<i>Ebenopsis ebano</i>	637.38	189.26	0.10	5.25	1629.80	2997.00	412.80	0.49	942.38	2.49	0.21
<i>Forestiera angustifolia</i>	518.74	197.06	0.18	12.11	1712.40	2986.40	430.20	0.38	1114.32	3.15	0.15
<i>Gualacum angustifolium</i>	1691.98	341.71	0.06	5.51	14166.60	15823.80	3652.00	0.43	5018.80	8.41	0.11
<i>Havardia pollens</i>	1736.63	403.52	0.07	7.51	3605.67	12611.00	2682.00	0.56	1678.13	2.09	0.14
<i>Karwinskia humboldtiana</i>	1090.38	334.66	0.11	8.54	2085.00	7557.60	1566.60	0.39	2672.71	2.05	0.09
<i>Parkinsonia texana</i>	852.36	389.57	0.15	14.28	1114.25	6799.75	703.25	0.41	981.77	1.32	0.06
<i>Phaulothamnus spinescens</i>	528.98	283.21	0.17	12.28	2145.80	5078.60	747.20	0.51	1215.36	4.09	0.07
<i>Randia rhagocarpa</i>	746.78	298.20	0.13	9.74	2260.40	5576.20	990.20	0.52	1063.07	3.03	0.08
<i>Sideroxylon celastrina</i>	1203.99	366.30	0.10	10.50	2806.14	5305.14	1014.71	0.47	1456.34	2.38	0.16
<i>Vachellia rigidula</i>	417.71	140.74	0.23	11.08	1224.00	2246.25	474.25	0.47	3833.27	4.44	0.13
<i>Vachellia schaffneri</i>	446.97	234.65	0.19	11.13	1228.60	2330.00	287.40	0.52	2298.97	2.75	0.05
<i>Viguiera stenoloba</i>								0.36			
<i>Zanthoxylum fagara</i>	1227.02	341.03	0.09	7.64	1769.50	5697.50	1230.50	0.57	2733.72	1.46	0.09
<i>Ziziphus obtusifolia</i>	672.10	328.72	0.16	13.17	913.00	4200.40	577.00	0.71	500.31	1.39	0.10

Table 3.4: Mean root structural and functional traits

Species	Stem Wood Density (g/cm ³)	Stem Height (cm)	Stem Mean Diameter (cm)
<i>Acacia berlandieri</i>	0.684	22.94	0.333
<i>Acacia greggii</i>	0.617	26.96	0.265
<i>Amyris texana</i>	0.625	15.80	0.265
<i>Castela erecta</i>	0.632	26.34	0.280
<i>Celtis ehrenbergiana</i>	0.539	17.20	0.326
<i>Chromolaena odorata</i>	0.334	35.48	0.271
<i>Citharexylum berlandieri</i>	0.685	36.64	0.607
<i>Colubrina texensis</i>	0.618	17.44	0.286
<i>Condalia hookeri</i>	0.690	19.72	0.259
<i>Diospyros texana</i>	0.610	28.84	0.304
<i>Ebenopsis ebano</i>	0.568	19.83	0.351
<i>Forestiera angustifolia</i>	0.598	24.05	0.289
<i>Guaiacum angustifolium</i>	0.430	11.20	0.328
<i>Havardia pallens</i>	0.752	21.00	0.320
<i>Karwinskia humboldtiana</i>	0.846	27.18	0.369
<i>Parkinsonia texana</i>	0.700	25.84	0.361
<i>Phaulothamnus spinescens</i>	0.596	17.86	0.268
<i>Randia rhagocarpa</i>	0.582	12.32	0.362
<i>Sideroxylon celastrina</i>	0.491	18.75	0.388
<i>Vachellia rigidula</i>	0.556	6.38	0.156
<i>Vachellia schaffneri</i>	0.592	18.86	0.189
<i>Viguiera stenoloba</i>	0.653	35.10	0.336
<i>Zanthoxylum fagara</i>	0.659	22.90	0.269
<i>Ziziphus obtusifolia</i>	0.651	18.64	0.287

Table 3.5 Mean stem structural and functional traits

Species	Leaves Total Area (cm ²)	Total Leaflets	Total Leaves	Leaves Mean Thickness (cm)	Specific Leaf Area (cm ²)	Leaf Dry Mass Content	Leaf Tissue Density (g/cm ³)
<i>Acacia berlandieri</i>	18.4930	1066	3	0.0122	1.9423	0.3808	0.8932
<i>Acacia greggii</i>	15.4604	211	22	0.0214	2.0748	0.3094	0.4231
<i>Amyris texana</i>	25.2974		32	0.0144	1.8041	2.3878	0.9801
<i>Castela erecta</i>	54.5854		260	0.0270	2.0582	0.2537	0.4564
<i>Celtis ehrenbergiana</i>	14.3840		44	0.0190	2.2370	0.2086	0.3241
<i>Chromolaena odorata</i>	72.1942		44	0.0234	2.2737	0.2615	0.2376
<i>Citharexylum berlandieri</i>	47.8766		43	0.0408	1.9639	0.2831	0.2761
<i>Colubrina texensis</i>	8.3490		23	0.0204	2.2546	0.2515	0.2900
<i>Condalia hookeri</i>	55.8912		247	0.0093	2.3557	0.2600	0.5304
<i>Diospyros texana</i>	39.6798		16	0.0145	2.6251	0.2225	0.2238
<i>Ebenopsis ebano</i>	35.7448	384	141	0.0142	2.1114	0.5044	0.5246
<i>Forestiera angustifolia</i>	24.3705		31	0.0205	2.1117	0.3798	0.5453
<i>Guaiacum angustifolium</i>	14.1106		24	0.0346	1.9268	0.2081	0.4425
<i>Havardia pallens</i>	27.7013		5	0.0144	2.0226	0.5568	0.4941
<i>Karwinskia humboldtiana</i>	48.4718		14	0.0180	2.4526	0.2070	0.2513
<i>Parkinsonia texana</i>	25.1640		159	0.0319	1.7704	0.7210	1.1482
<i>Phaulothamnus spinescens</i>	71.0748		118	0.0241	2.1705	0.2301	0.2914
<i>Randia rhagocarpa</i>	41.4802		37	0.0162	2.2810	0.2446	0.3295
<i>Sideroxylon celastrina</i>	60.6279		108	0.0116	2.4884	0.1637	0.5360
<i>Vachellia rigidula</i>	5.0216	102	11	0.0136	1.9905	0.3943	0.8421
<i>Vachellia schaffneri</i>	3.1526	488	11	0.0113	1.3802	0.5252	4.6318
<i>Viguiera stenoloba</i>	10.9978		96	0.0277	2.2547	0.1363	0.3308
<i>Zanthoxylum fagara</i>	7.4158	45	10	0.0111	1.5442	0.9107	4.2234
<i>Ziziphus obtusifolia</i>	19.3926		17	0.0267	2.1300	0.3139	0.3297

Appendix 3.5: Mean leaf structural and functional traits

CHAPTER IV

CONCLUSION

In the restoration of native forests, there are clear winners (Figure 4.1) and losers (Figure 4.2) evidenced by the large variations in the mortalities of the 24 species. While some species had less than 1% mortality % (*Condalia hookeri*, cocoon shelters), others had greater than 80% (*Guaiacum angustifolium*: control). This variation indicates that several species-specific factors may be largely responsible for seedling performance. These factors are often a combination of plant genes' interaction with the environment to produce phenotypes that end up responding to environmental cues with different levels of tolerance (Sthultz et al., 2009). Since the outcome of reforestation depends upon the phenotypic expression resulting from these interactions, it makes sense to quantify species' successes in restoration using plant traits, which are dependable indicators of phenotypic expression. Other species aspects such as detecting genetic markers of mortality may potentially be able to better predict performance, however, they are expensive and time-consuming. Thus, the method of selecting appropriate species for restoration using functional traits as predictors can be largely standardized for selecting species through determining which traits are dependable predictors of mortality. Through our study, not only did we kickstart a database of successful species in Tamaulipan thorn forest restoration that would aid in selecting appropriate species for reforestation in the valley, but we also identified potential predictors of performance for woody species in the Rio Grande Valley.

These findings are important for restoration managers in not only optimizing species selection but also for optimizing intervention selection to facilitate restoration.

As the global population grapple with the exacerbating challenges of climate change, induced by unmitigated and unregulated industrial growth, management practices such as forest restoration are becoming more and more common, due to their multifold benefits to the economy and the environment. The Lower Rio Grande Valley's forest restoration program is a perfect example of such a program that encompasses the environmental and economic milieu. However, since so many resources are invested in restoring native habitats for conservation and economic purposes, it is important to come up with scientifically salient interventions and general frameworks that address the challenges of restoring habitats in the rapidly changing and often increasingly harsh environments where restoration occurs. Our study shows that forest restoration interventions such as shelters provide such an opportunity to manage the impacts of herbivory, whereas trait-based screenings allow resource optimization through appropriate species selection. What is clear from this study is that to mitigate challenges encountered in largescale conservation efforts, while certain investments pay off (shelters), others may not (mycorrhizae). The good news is that often the approaches that end up working are ones that require minimal investment such as appropriate species selection. Hence, management practices in forest restoration should involve appropriate planning to make scientifically informed decisions that will minimize the cost and maximize the number of restoration objectives met.

Tables & Figures

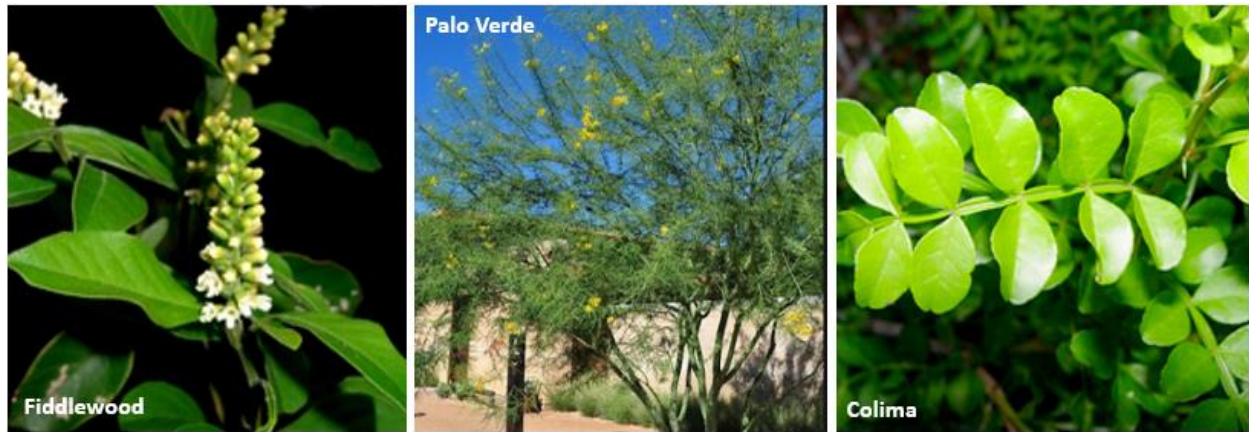


Figure 4.1 Species with lowest mortality overall: *Citharexylum berlandieri* (Fiddlewood) 8%, *Parkinsonia texana* (Palo verde) 7%, *Zanthoxylum fagara* (Colima) 9%.



Figure 4.2 Species with highest mortality overall: *Castela erecta* (Amargosa) 42%, *Guaiacum angustifolium* (Guayacán); 69%, *Viguiera stenoloba* (Skeleton leaf golden eye), 47%

REFERENCES

- Ackerly, D. D., Dudley, S. A., Sultan, S. E., Schmitt, J., Coleman, J. S., Linder, C. R., ... & Lechowicz, M. J. (2000). The evolution of plant ecophysiological traits: recent advances and future directions: new research addresses natural selection, genetic constraints, and the adaptive evolution of plant ecophysiological traits. *Bioscience*, 50(11), 979-995.
- Alexander, H. D., Moczygemba, J., & Dick, K. (2016). Growth and survival of thornscrub forest seedlings in response to restoration strategies aimed at alleviating abiotic and biotic stressors. *Journal of Arid environments*, 124, 180-188.
- Alvarez-Aquino, C., Williams-Linera, G., & Newton, A. C. (2004). Experimental native tree seedling establishment for the restoration of a Mexican cloud forest. *Restoration Ecology*, 12(3), 412-418.
- Ashton, M. S., Gunatilleke, C. V. S., Singhakumara, B. M. P., & Gunatilleke, I. A. U. N. (2001). Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *Forest ecology and management*, 154(3), 409-430.
- Bartlett, M. K., Scoffoni, C., & Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology letters*, 15(5), 393-405.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67(1), 1-48.
- Bellot, J., De Urbina, J. O., Bonet, A., & Sánchez, J. R. (2002). The effects of treeshelters on the growth of *Quercus coccifera* L. seedlings in a semiarid environment. *Forestry*, 75(1), 89-106.
- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., ... & Anderson, J. J. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, 102(42), 15144-15148.
- Butterfield, R. P. (1996). Early species selection for tropical reforestation: a consideration of stability. *Forest Ecology and Management*, 81(1-3), 161-168.
- Calvo-Alvarado, J. C., Arias, D., & Richter, D. D. (2007). Early growth performance of native and introduced fast growing tree species in wet to sub-humid climates of the Southern region of Costa Rica. *Forest Ecology and Management*, 242(2-3), 227-235.

- Cao, S., Chen, L., Shankman, D., Wang, C., Wang, X., & Zhang, H. (2011). Excessive reliance on afforestation in China's arid and semi-arid regions: lessons in ecological restoration. *Earth-Science Reviews*, 104(4), 240-245.
- Carvajal, D. E., Loayza, A. P., Rios, R. S., Delpiano, C. A., & Squeo, F. A. (2019). A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies. *Journal of Ecology*, 107(3), 1079-1092.
- Chao, K. J., Phillips, O. L., Gloor, E., Monteagudo, A., Torres-Lezama, A., & Martínez, R. V. (2008). Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology*, 96(2), 281-292.
- Close, D. C., Beadle, C. L., & Brown, P. H. (2005). The physiological basis of containerised tree seedling ‘transplant shock’: a review. *Australian Forestry*, 68(2), 112-120.
- Comas, L., Bouma, T., & Eissenstat, D. (2002). Linking root traits to potential growth rate in six temperate tree species. *Oecologia*, 132(1), 34-43.
- Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79(1), 109-126.
- Cornwell, W. K., Pearse, W. D., Dalrymple, R. L., & Zanne, A. E. (2019). What we (don't) know about global plant diversity. *Ecography*, 42(11), 1819-1831.
- Cornwell, W. K., Schwilk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87(6), 1465-1471.
- Craven, D., Dent, D., Braden, D., Ashton, M. S., Berlyn, G. P., & Hall, J. S. (2011). Seasonal variability of photosynthetic characteristics influences growth of eight tropical tree species at two sites with contrasting precipitation in Panama. *Forest Ecology and Management*, 261(10), 1643-1653.
- Crawley, M.J. (2013). "Mixed-effects models," in *The R Book*, ed. M.J. Crawley. (Chichester, United Kingdom: John Wiley & Sons).
- Crawley, M.J. (2013). "Statistical modelling," in *The R Book*, ed. M.J. Crawley. (Chichester, United Kingdom: John Wiley & Sons).
- del Campo, A. D., Navarro, R. M., Aguilera, A., & González, E. (2006). Effect of tree shelter design on water condensation and run-off and its potential benefit for reforestation establishment in semiarid climates. *Forest ecology and management*, 235(1-3), 107-115.
- Demchik, M. C., & Sharpe, W. E. (2000). The effect of soil nutrition, soil acidity and drought on northern red oak (*Quercus rubra* L.) growth and nutrition on Pennsylvania sites with high and low red oak mortality. *Forest Ecology and Management*, 136(1-3), 199-207.

- Denton, E. M., Smith, B. S., Hamerlynck, E. P., & Sheley, R. L. (2018). Seedling defoliation and drought stress: variation in intensity and frequency affect performance and survival. *Rangeland Ecology & Management*, 71(1), 25-34.
- Dick, K., Alexander, H. D., & Moczygamba, J. D. (2016). Use of shelter tubes, grass-specific herbicide, and herbivore exclosures to reduce stressors and improve restoration of semiarid thornscrub forests. *Restoration Ecology*, 24(6), 785-793.
- Dowle, M., and Srinivasan, A. (2019). "data.table: Extension of `data.frame`". R package version 1.12.2 ed. (<https://CRAN.R-project.org/package=data.table>)
- Espelta, J. M., Rodrigo, A., Habrouk, A., Meghelli, N., Ordóñez, J. L., & Retana, J. (2002). Land use changes, natural regeneration patterns and restoration practices after a large wildfire in NE Spain: challenges for fire ecology and landscape restoration. *Fire and Biological Processes. Backhuys Publishers, Leiden*, 315-324.
- Foroughbakhch, R., Hernández-Piñero, J. L., Alvarado-Vázquez, M. A., Céspedes-Cabriales, E., Rocha-Estrada, A., & Cárdenas-Ávila, M. L. (2009). Leaf biomass determination on woody shrub species in semiarid zones. *Agroforestry Systems*, 77(3), 181-192.
- Franco, M., & Silvertown, J. (1996). Life history variation in plants: an exploration of the fast-slow continuum hypothesis. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351(1345), 1341-1348.
- Gabler, C. A., & Siemann, E. (2013). Timing of favorable conditions, competition and fertility interact to govern recruitment of invasive Chinese tallow tree in stressful environments. *PloS one*, 8(8).
- García-Fayos, P., & Verdú, M. (1998). Soil seed bank, factors controlling germination and establishment of a Mediterranean shrub: *Pistacia lentiscus* L. *Acta Oecologica*, 19(4), 357-366.
- Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., ... & Kraft, N. J. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, 20(4), 539-553.
- Grossnickle, S. C. (2012). Why seedlings survive: influence of plant attributes. *New Forests*, 43(5-6), 711-738.
- Grünzweig, J. M., Lin, T., Rotenberg, E., Schwartz, A., & Yakir, D. (2003). Carbon sequestration in arid-land forest. *Global Change Biology*, 9(5), 791-799.
- Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D., & McCulloh, K. A. (2001). Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, 126(4), 457-461.
- Hamrick, J. L., Godt, M. J. W., Murawski, D. A., & Loveless, M. D. (1991). Correlations between species traits and allozyme diversity: implications for conservation biology. *Genetics and conservation of rare plants*, 3, 30.

- Holmgren, M., López, B. C., Gutierrez, J. R., & Squeo, F. A. (2006). Herbivory and plant growth rate determine the success of El Niño Southern Oscillation-driven tree establishment in semiarid South America. *Global Change Biology*, 12(12), 2263-2271.
- Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal* 50(3), 346-363.
- Jacobs, B. F. (2004). Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 359(1450), 1573-1583.
- Jacobs, D. F., Salifu, K. F., & Seifert, J. R. (2005). Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings. *New Forests*, 30(2-3), 235-251.
- Jager, M. M., Richardson, S. J., Bellingham, P. J., Clearwater, M. J., & Laughlin, D. C. (2015). Soil fertility induces coordinated responses of multiple independent functional traits. *Journal of Ecology*, 103(2), 374-385.
- Jahrsdoerfer, S. E., & Leslie Jr, D. M. (1988). Tamaulipan brushland of the Lower Rio Grande Valley of south Texas: description, human impacts, and management options. *Oklahoma Cooperative Fish and Wildlife Research Unit Stillwater*.
- Jiménez, M. N., Navarro, F. B., Ripoll, M. Á., Bocio, I., & De Simón, E. (2005). Effect of shelter tubes on establishment and growth of *Juniperus thurifera* L.(Cupressaceae) seedlings in Mediterranean semi-arid environment. *Annals of forest science*, 62(7), 717-725.
- Judd, F. W. (2002). Tamaulipan biotic province. *The Laguna Madre of Texas and Tamaulipas*, 38-58.
- Leslie Jr, D. M. (2016). *An international borderland of concern: conservation of biodiversity in the Lower Rio Grande Valley* (No. 2016-5078). US Geological Survey.
- Kassambara, A. (2018). "ggpubr: 'ggplot2' Based Publication Ready Plots". R package version 0.2 ed. (<https://CRAN.R-project.org/package=ggpubr>).
- Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., & Freschet, G. T. (2013). Contrasting effects of plant inter-and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, 27(5), 1254-1261.
- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R. J., Strauss, B., ... & Lavorel, S. (2012). Assessing species and community functional responses to environmental gradients: which multivariate methods?. *Journal of Vegetation Science*, 23(5), 805-821.
- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R. J., Strauss, B., ... & Lavorel, S. (2012). Assessing species and community functional responses to environmental gradients: which multivariate methods?. *Journal of Vegetation Science*, 23(5), 805-821.

- Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. 2006. World map of the KöppenGeiger climate classification. *Meteorologische Zeitschrift* 15(3):259-263.
- Kramer, P. J., & Boyer, J. S. (1995). *Water relations of plants and soils*. Academic press.
- Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., & Laughlin, D. C. (2016). Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, 104(5), 1299-1310.
- Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, 102(1), 186-193.
- Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, 102(1), 186-193
- Lavorel, S., & Grigulis, K. (2012). How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, 100(1), 128-140.
- Lenth, R. (2019). "emmeans: Estimated Marginal Means, aka Least-Squares Means". R package version 1.4.3.01 ed. (<https://CRAN.R-project.org/package=emmeans>).
- Leslie Jr, D. M. (2016). An international borderland of concern: Conservation of biodiversity in the Lower Rio Grande Valley (No. 2016-5078). US Geological Survey.
- Lloret, F., Calvo, E., Pons, X., & Díaz-Delgado, R. (2002). Wildfires and landscape patterns in the Eastern Iberian Peninsula. *Landscape Ecology*, 17(8), 745-759.
- Lloret, F., Casanovas, C., & Penuelas, J. (1999). Seedling survival of Mediterranean shrubland species in relation to root: shoot ratio, seed size and water and nitrogen use. *Functional Ecology*, 13(2), 210-216.
- Maestre, F. T., Cortina, J., Bautista, S., Bellot, J., & Vallejo, R. (2003). Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. *Ecosystems*, 6(7), 630-643.
- Mathis, M., & Matisoff, D. (2004). A characterization of ecotourism in the Texas Lower Rio Grande Valley. *Valuing nature in Texas: discussion paper*. Houston Advanced Research Center, Houston, Texas, USA.
- Mašková, T., & Herben, T. (2018). Root: shoot ratio in developing seedlings: How seedlings change their allocation in response to seed mass and ambient nutrient supply. *Ecology and Evolution*, 8(14), 7143-7150.
- Mencuccini, M., Rosas, T., Rowland, L., Choat, B., Cornelissen, H., Jansen, S., ... & Reich, P. B. (2019). Leaf economics and plant hydraulics drive leaf: wood area ratios. *New Phytologist*, 224(4), 1544-1556.
- Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology letters*, 13(7), 838-848.

- Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology letters*, 13(7), 838-848.
- Moles, A. T., & Westoby, M. (2004). Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, 92(3), 372-383.
- Niinemets, Ü., & Valladares, F. (2006). Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological monographs*, 76(4), 521-547.
- Padilla, F. M., Miranda, J. D. D., Ortega, R., Hervás, M., Sánchez, J., & Pugnaire, F. I. (2011). Does shelter enhance early seedling survival in dry environments? A test with eight Mediterranean species. *Applied Vegetation Science*, 14(1), 31-39.
- Padilla, F. M., Ortega, R., Sánchez, J., & Pugnaire, F. I. (2009). Rethinking species selection for restoration of arid shrublands. *Basic and Applied Ecology*, 10(7), 640-647.
- Park, A., van Breugel, M., Ashton, M. S., Wishnie, M., Mariscal, E., Deago, J., ... & Hall, J. S. (2010). Local and regional environmental variation influences the growth of tropical trees in selection trials in the Republic of Panama. *Forest Ecology and Management*, 260(1), 12-21.
- Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... & Urcelay, C. (2016). Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of botany*, 64(8), 715-716.
- Pinto, J. R., Marshall, J. D., Dumroese, R. K., Davis, A. S., & Cobos, D. R. (2011). Establishment and growth of container seedlings for reforestation: A function of stocktype and edaphic conditions. *Forest Ecology and Management*, 261(11), 1876-1884.
- Poorter, L., & Bongers, F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, 87(7), 1733-1743.
- Pywell, R. F., Bullock, J. M., Roy, D. B., Warman, L. I. Z., Walker, K. J., & Rothery, P. (2003). Plant traits as predictors of performance in ecological restoration. *Journal of applied Ecology*, 40(1), 65-77.
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, 102(2), 275-301.
- Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, 164(S3), S143-S164.
- Rotenberg, E., & Yakir, D. (2010). Contribution of semi-arid forests to the climate system. *Science*, 327(5964), 451-454.

- Salguero-Gómez, R. (2017). Applications of the fast–slow continuum and reproductive strategy framework of plant life histories. *New Phytologist*, 213(4), 1618-1624.
- Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., ... & Buckley, Y. M. (2016). Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences*, 113(1), 230-235.
- Schimel, D. S. (2010). Drylands in the earth system. *Science*, 327(5964), 418-419.
- Scholl, A. E., & Taylor, A. H. (2010). Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecological Applications*, 20(2), 362-380.
- Schroeder-Georgi, T., Wirth, C., Nadrowski, K., Meyer, S. T., Mommer, L., & Weigelt, A. (2016). From pots to plots: hierarchical trait-based prediction of plant performance in a mesic grassland. *Journal of Ecology*, 104(1), 206-218.
- Sheil, D., and May, R.M. (1996). Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84(1), 91-100.
- Shindle, D. B., & Tewes, M. E. (1998). Woody species composition of habitats used by ocelots (*Leopardus pardalis*) in the Tamaulipan Biotic Province. *The Southwestern Naturalist*, 273-279.
- Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180(4), 923-931.
- Sthultz, C. M., Gehring, C. A., & Whitham, T. G. (2009). Deadly combination of genes and drought: increased mortality of herbivore-resistant trees in a foundation species. *Global Change Biology*, 15(8), 1949-1961.
- Struve, D. K. (2009). Tree establishment: a review of some of the factors affecting transplant survival and establishment. *Arboriculture & Urban Forestry*, 35(1).
- Sweeney, B. W., Czapka, S. J., & Yerkes, T. (2002). Riparian forest restoration: increasing success by reducing plant competition and herbivory. *Restoration Ecology*, 10(2), 392-400.
- Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, 94(3), 451-459.
- Thorpe, A. S., Aschehoug, E. T., Atwater, D. Z., & Callaway, R. M. (2011). Interactions among plants and evolution. *Journal of Ecology*, 99(3), 729-740.
- Tomar, R. S. S., Tiwari, S., Naik, B. K., Chand, S., Deshmukh, R., Mallick, N., ... & Tomar, S. M. S. (2016). Molecular and morpho-agronomical characterization of root architecture at

- seedling and reproductive stages for drought tolerance in wheat. *PloS one*, 11(6), e0156528.
- Tremblay, J. P., Thibault, I., Dussault, C., Huot, J., & Côté, S. D. (2005). Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. *Canadian Journal of Zoology*, 83(8), 1087-1096.
- US Fish and Wildlife Service. (2014). Environmental conservation online system.
- Valdecantos, A., Fuentes, D., Smanis, A., Llovet, J., Morcillo, L., & Bautista, S. (2014). Effectiveness of low-cost planting techniques for improving water availability to *Olea Europaea* seedlings in degraded drylands. *Restoration ecology*, 22(3), 327-335.
- Vallejo, V. R., Smanis, A., Chirino, E., Fuentes, D., Valdecantos, A., & Vilagrosa, A. (2012). Perspectives in dryland restoration: approaches for climate change adaptation. *New Forests*, 43(5-6), 561-579.
- van Breugel, M., Hall, J. S., Craven, D. J., Gregoire, T. G., Park, A., Dent, D. H., ... & Cedeño, N. (2011). Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. *Forest Ecology and Management*, 261(10), 1580-1589.
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. *Oikos*, 116(5), 882-892.
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, 277(5325), 494-499.
- Vora, R. S. (1992). Restoration of native vegetation in the Lower Rio Grande Valley, 1984-87. *Ecological Restoration*, 10(2), 150-157.
- Werden, L. K., Alvarado J, P., Zarges, S., Calderón M, E., Schilling, E. M., Gutiérrez L, M., & Powers, J. S. (2018). Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols. *Journal of Applied Ecology*, 55(2), 1019-1028.
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.
- Wishnie, M. H., Dent, D. H., Mariscal, E., Deago, J., Cedeno, N., Ibarra, D., ... & Ashton, P. M. S. (2007). Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. *Forest Ecology and Management*, 243(1), 39-49.
- Wright, I. J., Westoby, M., & Reich, P. B. (2002). Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal of ecology*, 90(3), 534-543.

BIOGRAPHICAL SKETCH

Faeqa Mohsin received her B.Sc. degree in Biological Sciences from Asian University for Women in 2017 in her hometown of Chittagong, Bangladesh. She worked as a Knowledge Management professional at United Nations World Food Programme with food insecure communities near the Myanmar-Bangladesh border during the Rohingya refugee crisis. She also collaborated with faculty, colleagues and peers from around the world to conduct community development projects through grants obtained from the US Dept. of State's Bureau of Educational and Cultural Affairs and Takahashi Foundation. Faeqa came to the US in August 2018 to pursue a conservation-related master's project culminating from her passion for evolutionary biology and desire to improve human society through protecting the environment. She completed her Master of Science degree in Biology in August 2020. You can contact her at faeqa.mohsin@gmail.com.