

ENVIRONMENTAL FACTORS INFLUENCING THE SPREAD AND
INVASION POTENTIAL OF *ARUNDO DONAX*
IN CENTRAL TEXAS

by

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A thesis submitted to the Graduate Council of
Texas State University in partial fulfillment
of the requirements for the degree of
Master of Science
with a Major in Aquatic Resources
December 2022

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ACKNOWLEDGEMENTS

I would like to express my deepest appreciation to my mentor and the chair of my committee for providing me with support and guidance throughout this experience. This journey would not have been possible without the expertise of my committee members who provided invaluable feedback and direction. Many thanks to Texas State faculty and staff who instructed and counseled me throughout my program. I am also so grateful to my fellow lab mates and peers whose help with my experiment was indispensable. Special thanks to Texas Parks and Wildlife Department who provided data critical to the completion of this experiment. Lastly, I'd like to acknowledge and thank my family and husband for their unwavering support and confidence as I pursued my degree.

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ABSTRACT

Invasive species are a global concern and a significant contributor to anthropogenic global change. As invasive species continue to invade new regions, they impact natural ecosystem function and displace native species. The success and impact of invasive species can be tied to species biology and the attributes of the invaded ecosystem. A two-step experimental approach using a greenhouse experiment and remote sensing methodology was used to develop an understanding of the environmental conditions where *Arundo donax*, a large-statured invasive wetland species, performs best and how it may colonize new areas. I predicted that *Arundo* would exhibit higher values of performance-related traits such as aboveground biomass (AGB), belowground biomass (BGB), net photosynthesis, and total tiller length under high light, high soil moisture, and high nutrient conditions because there would be fewer factors limiting growth for this species. I also predicted that the spread of *Arundo* would be closely tied to major flood events when the transportation of propagules downstream and the scouring of banks leads to colonization opportunities. Eight of the eleven response variables analyzed, including AGB, BGB, total tiller length, and net photosynthesis showed a significant interaction between soil moisture and light with plants grown in saturated, high light conditions having the highest values for performance related traits. Nutrients were found to influence biomass allocation patterns, with plants grown with added nitrogen and phosphorous exhibiting higher shoot:root and stem:leaf ratios; however nutrients were not found to significantly influence performance related traits. Major flood events were

shown to positively influence the rate of spread of *Arundo* in the studied stretches of the Guadalupe and Medina rivers in Texas. Understanding how invasive species respond to changes in abiotic factors and what influences their ability to colonize new areas is necessary to make predictions about species expansion and prioritize management efforts and can provide necessary information for the development of ecological models.

I. ABIOTIC FACTORS INFLUENCING THE PERFORMANCE OF *ARUNDO*

Introduction

Invasive Plant Species

Invasive species are a significant component of human-mediated global change and are of state and national concern in the United States. Invasive species are those nonindigenous species that do not naturally occur in a geographical area whose introduction is likely to cause economic or environmental harm or harm to the health of humans, plants, or animals. (Exec. Order No. 13751, 2016, Keddy 2016). Evidence suggests that the introduction and spread of nonindigenous invasive species has been accelerated by globalization and free trade resulting from the removal of natural barriers (Lockwood 2005, McNeely 2006). The rate of invasion continues to increase globally due to global trade and the human-facilitated introduction of species for use in ornamental and horticultural activities (Seebens 2017). Invasive species have been estimated to cause \$314 billion in damages per year (Pimentel 2001). In addition, invasive species can cause environmental harm, displacing native species and, in some instances altering ecosystem processes (Zedler 2004, Lambert 2010, Pyšek 2012, USDA 2016). For example, invasive cheatgrass (*Bromus tectorum*) in western rangelands has been found to displace native plant species and encourage more frequent and intense fires, fundamentally changing how invaded rangelands function and facilitating further invasion (Hull 1947, Knick 1997, Link 2006). Invasive species are believed to be the second-largest cause of biodiversity loss following habitat elimination (Vitousek 1997). In some instances, such as with cattail (*Typha angustifolia*), invasive species have been found to hybridize with native species producing adept invaders, e.g., *Typha* × *glauca*.

The success and impact of invasive species is closely related to their biology as well as the attributes of the invaded ecosystem (Vilà 2004). In a meta-analysis of traits related to invasiveness, Van Kleunen (2010) found that invasive plant species generally have higher values of performance-related characteristics, including but not limited to growth rate, size, and fitness. Furthermore, invasive plant species' impact on ecosystem productivity was found to be dependent on height. Invasive species taller than 1.2 meters significantly affected the productivity of plant and animal communities (Pyšek 2012). In some cases, a higher relative growth rate (RGR), especially during the establishment phase, has been shown to predict the success of invasive species (James 2007, Reichmann 2016). A study conducted on invasive forbs of eastern Oregon found that invasive species had a higher RGR than native species due to greater specific leaf area and leaf area ratio (James 2007). Moreover, invasive species have been found to increase RGR in high nitrogen conditions (Quinn 2011, Matzek 2013). Biomass allocation in invaders may also play an essential role in establishment success. Quinn (2006) found that *Arundo* grown in pots treated with nitrogen allocated more biomass to aboveground biomass and root tissues. Invasive shrub *Rhus typhina* allocated more resources to increasing height than its non-invasive counterparts (Xiangfeng 2012). Dong (2012) found that invasive grasses tended to allocate biomass to the roots and the crown. This pattern does not, however, hold true for all invasive species. Nackley (2017) found that *Arundo* grown in CO₂ and N-enriched environments allocated more biomass to rhizomes. Invasive Hawaiian rainforest species were also found to exhibit no difference in biomass allocation under different light regimes (Pattison 1997).

There is conflicting evidence surrounding differences in physiological attributes such as water use efficiency (WUE) and photosynthetic rate between invasive and native species. Water use efficiency, the ratio of water used for metabolism to water lost through transpiration, has been found, under resource-limited conditions, to be higher in native species than in their invasive counterparts (Matzek 2011). However, many studies have shown little difference between the physiological attributes of invasive and native plant species. In a study comparing invasive and native species of the intermountain west in resource-poor environments, both native and invasive species exhibited similar physiological responses to changes in nitrogen and water availability (Drenovsky 2010). Similar results emerged from a study comparing the physiological attributes of native and invasive species in non-resource poor tallgrass prairie habitats. Invasive species were found to have higher SLA but overall demonstrated little difference in physiological traits, such as maximum photosynthetic rate, apparent quantum yield, and dark respiration (Smith 2001). A comparison of invasive and native genotypes of *Phalaris arundinacea* revealed that physiological characteristics of native and invasive genotypes were not significantly different, except for photosynthetic rate and stomatal conductance being higher in the native genotype (Broderson 2008). In a study of five phylogenetically related pairs of invasive and native species in Hawaii, Funk (1996) found invasive species to have differences in physiological traits compared to their native counterparts; however, no consistent directional pattern was observed in these differences. Invasive species showed higher plasticity in performance-related traits in response to nutrient availability suggesting that plasticity may be more important in species success than physiological attributes (Funk 1996). Other research indicates that some invasive and

native species may differ in their physiological traits, primarily among plants in the same genus. Studies of species in the genera *Eupatorium* and *Rubus* found that invasive species within these genera had higher photosynthetic nutrient use efficiency and WUE (McDowell 2002, Feng 2008). In studies conducted on *Imperata cylindrica*, an invasive grass, it was found that the invader retained more N per hectare than native species and that most of the N captured was stored in the belowground organs (Daneshgar 2009). Analysis of *Arundo* litter revealed that compared to native species, percent nitrogen was significantly lower in the invader (Going 2008). However, another study suggests that there may be no difference between invasive and native species in area-based leaf nitrogen content, chlorophyll, or total protein (Matzek 2011). The same study found that invaders had higher photosynthetic nitrogen use efficiency (Matzek 2011). However, no consistent pattern has been found between the physiological attributes of native and invasive species suggesting that the success of invasive species may be related to plasticity in physiological traits. The physiological attributes of invasive and native species appear to be primarily dependent on the environmental conditions to which the organism is subjected. The lack of consensus surrounding the physiological attributes of invasive and native species suggests that the physiological characteristics of plants are context-dependent and may not exhibit consistent patterns. Further research is needed to determine the relationship between the physiological attributes of invasive and native species and what role trait plasticity may play in invader success.

Though species characteristics play a significant role in the establishment and spread of invasive species, increasing evidence suggests that factors outside of species traits play a role in invasion. Propagule pressure, composed of two key components, the

number of propagules (i.e., rate of propagules introduced per unit time) and propagule size (i.e., number of individuals per introduction event), has been shown to be closely tied to establishment success (Lockwood 2005, Simberloff 2009). A theory of ecosystem invasibility proposed by Davis (2000) suggests that the invasibility of ecosystems may be increased by nutrient enrichment and its temporal relation to disturbance events and propagule introduction. This theory can be further supported by findings suggesting that influxes of nutrient-rich stormwater, which simultaneously causes disturbance and enriches systems with nutrients, facilitates invasion by *Phalaris arundinacea* (Maurer 2003). Another theory surrounding the mechanisms of ecosystem invasion, the enemy release hypothesis, suggests that some successful invasive species experience decreased regulation from native competitors, herbivores, and disease in the introduced range, which allows for the species to proliferate (Keane 2002). The theory of native community resistance suggests that an invader may be less likely to establish in a given area if a species with similar traits fills the invader's niche in an ecological community. Therefore, diverse native communities reduce the number of unoccupied niches that invaders can exploit (Funk 2008). Though many experiments have pointed to invasion being inversely related to diversity, some evidence suggests that species identity, or the functional role that a species plays in an ecosystem, may play a more significant role in resistance than was initially thought (Elton 1958, Kennedy 2002, Dodd 2004, Smith 2004). Thus, it is likely that species diversity and species identity play an essential role in the susceptibility of ecosystems to invasion. The characteristics of invaded ecosystems, as well as the timing and number of propagules introduced during invasion events, play a significant role in how successful any given invader may be in an area.

Disturbance is often cited as one of the leading facilitators of exotic plant invasions (Hobbs 1992, Hierro 2006, Eschtruth 2009). Invasion has been associated with increases in bare ground caused by disturbance and consequent increases in available light (Baruch 2000, Perry 2006). In many instances, particularly in communities vulnerable to invasion following disturbance, light availability may be equal to or more important than nutrient availability in deciding the likelihood of invasion (Perry 2006). This becomes increasingly important in recently disturbed ecosystems where vegetation has been removed. Some studies suggest that plant height may play a role in invasive species' success (Williamson 1996, Goodwin 1999, Wang 2021). This, combined with the trend of higher RGR in invasive species (Pattinson 1998, James 2007), indicates that early and continued access to sunlight may allow invasive species to attenuate light more successfully than shorter, slower-growing plants in the same area. In a study of *Solidago canadensis* and *Conyza canadensis*, it was found that the invasiveness of these species was influenced mainly by plant height and, thus, higher competitiveness for sunlight acquisition. Plant height was found to be a more significant contributor to overall invasiveness than leaf photosynthetic area, especially under heavy invasion (Wang 2021).

Invasive species continue to invade new regions impacting natural ecosystem function and displacing native species (Vitousek 1997, Zedler 2004, USDA 2016). Functional traits of these species and ecosystem attributes are known to play a role in the success of invasive species (Davis 2000, Kennedy 2002, Van Kleunen 2010), though the importance of each likely varies among invasions. To better understand the processes and factors that influence a specific invasion, it is necessary to understand what factors play the most significant role in influencing invasive species' performance. By gaining insight

into the elements that influence the performance of invasive species, we can better anticipate sites that may be more prone to invasion and implement proper management strategies.

Giant Reed (Arundo donax)

Arundo donax (hereafter *Arundo*) is a perennial invasive grass that has been introduced in the southern part of the continental United States as well as Hawaii, Puerto Rico, and the Virgin Islands (USDA 2020). *Arundo* was historically introduced for erosion control and cultivated for musical reed production (Perdue 1958, Ahmad 2008). *Arundo* is hypothesized to have originated in Asia and diffused into the Mediterranean, from whence it was introduced to North America in the early 1800s (Ahmad 2008, Hardion 2014). Genetic analysis of individuals in North America revealed that all sampled *Arundo* were genetically identical, except for one sample in Texas that exhibited a single mutation (Ahmad 2008). Further investigation into the reproductive mechanisms of *Arundo* shows that the North American invader is sterile and incapable of reproducing via seed. Post-meiotic mutations of the ovule and pollen were found to render the plant infertile (Mariani 2010). The spread of *Arundo* through North America can be attributed to human-mediated introductions and asexual vegetative reproduction via layering, rhizomes, and fragmentation (Decruyenaere 2001, Boland 2006, Ahmad 2008). Layering is a mode of spread by which adventitious roots form from a stem node in contact with the ground, while fragmentation occurs when stem fragments, due to some disturbance, disperse and establish downstream (Bell 1993, Boland 2006). *Arundo* rhizomes can spread laterally underground and produce new roots and shoots at nodes. This lateral growth has been shown to increase under high nitrogen conditions (Decruyenaere 2005).

The current theory surrounding the spread of *Arundo* is that rhizome and stem fragments are dispersed through flood events that carry propagules downstream, allowing them to establish in areas that have been disturbed (Bell 1997, Mariani 2010). Alternative theories propose that flooding may not be the primary driver of *Arundo* spread, attributing the species' expansion to fragmentation caused by bulldozing and layering (Boland 2006, Boland 2008).

The fast growth of *Arundo*, along with its lack of significant natural enemies, has made the species an aggressive and successful invader. *Arundo* can grow up to 10 meters tall, forming dense monotypic stands associated with lower species richness in stream banks and floodplains and has been linked to decreased streamflow in the Nueces River (Cushman 2010, USDA 2014, Jain 2015). The height of this species confers a competitive advantage over shorter-statured native species. The species is typically found along disturbed stream beds, lakes, and other wet areas and can grow 30-70 cm per week under ideal conditions (Perdue 1958, Bell 1997). The fast growth rate and height of *Arundo* allows it to displace native species, especially under high nitrogen and ideal soil moisture regimes. Currently, there is no evidence that *Arundo* acts as a significant food source or habitat for wildlife (Bell 1997). The C:N ratio of *Arundo* tissues in California was found to be less than the range of C:N ratios considered favorable by aquatic herbivores (Mattson 1980, Spencer 2005), which might make it a less desirable food source.

Attempts at biological control of *Arundo* have been made using *Rhizaspidiotus donacis*, an armored scale, and *Tetramesa romana*, a stem-galling wasp, frequently found within the native range of *Arundo* (Moore 2010). These biological control agents have

thus far had limited negative impacts on *Arundo* populations, decreasing biomass by 22-32% (Goolsby 2016), and do not exert significant control. Management efforts using chemical, biological, and mechanical methods have all been used in an attempt to control *Arundo* (Bell 1997, Moore 2010). Management of *Arundo* can take multiple years, and the success of any given method of control is largely dependent upon the characteristics of the ecosystem being managed. Programs to manage *Arundo* in Texas have been put into place by Texas Parks and Wildlife Department and the Texas State Soil and Water Conservation Board throughout central and southern Texas; however, these programs are geographically limited. Even with biological control and *Arundo* management programs in place, this species continues to invade susceptible ecosystems.

Invasion by *Arundo* has been found to impact arthropod communities by changing the vegetation structure of native habitats. The exotic cattle tick *Rhipicephalus (Boophilus)* spp. was shown to be more successful under the abiotic and biotic conditions created by stands of *Arundo* (Racelis 2012). This invasive tick is a known vector of cattle parasites, such as those that cause cattle fever in southern Texas (Busch 2014). Invasion by large-statured invasive grasses, such as *Arundo*, is known to alter vegetation structure and reduce arthropod diversity, which leads to decreased avian diversity (Herrera 2003, Kisner 2004, Osbrink 2018). More research is needed to comprehend the impact of *Arundo* on native and domestic animal communities.

Arundo can be found in a wide range of soils, from dense clays to loose sand, and is tolerant of high salinity conditions (Perdue 1958, DiMola 2018). Though capable of withstanding extreme drought and excessive soil moisture, *Arundo* seems to be most successful in areas with well-drained soil and ample moisture (Perdue 1958). The growth

of *Arundo* has been found to be closely correlated to soil moisture (Quinn 2006, Nackley 2014). In a study performed by Quinn in 2006, it was found that *Arundo* exhibited a positive response to soil moisture and disturbance (Quinn 2006). As is the case with many competitive species, *Arundo* thrives in disturbed areas and is tolerant of conditions that may be detrimental to native species.

Though able to subsist in infertile conditions, *Arundo* performs the best in high nitrogen conditions (Perdue 1958). The plant seems to favor nitrogen delivered as NH_4^+ or $\text{NH}_4^+ \text{NO}_3^-$ instead of solely NO_3^- (Tho 2017). Under low nitrogen regimes, *Arundo* tends to exhibit greater distance between buds on the rhizome and more extensive underground structures (Perdue 1958). As is the case with many invasive species, *Arundo* shows higher biomass and spread in response to increased nitrogen (Quinn 2007, Nackley 2017, Tho 2017). Studies indicate that fast-growing invasive species like *Arundo* may gain a competitive advantage over native species when N is increased. It is suggested that this may lead to a positive feedback loop in which invasive species are able to, through faster growth and larger size, outcompete native species for resources, mainly light (Mangla 2011). This idea is supported by the success of many large-statured wetland species grown in high nitrogen conditions, such as *Phragmites australis*, *Typha domingensis*, and *Phalaris arundinacea* (Green 2001, Minchinton 2003, Escutia-Lara 2007).

The presence of established native communities and competitors has not been studied at length in *Arundo*. Still, the literature indicates that *Arundo* is mostly unaffected by native community composition or the presence of a competitor. In a study conducted by Quinn in 2007, *Arundo* biomass was not significantly affected by competition with

Schoenoplectus pungens though tiller production was slightly reduced. This study indicates that nitrogen enrichment may compensate for the adverse effects of competition in *Arundo* establishment (Quinn 2007). A separate study revealed that the establishment success of *Arundo* was unaffected by the composition of native communities consisting of *Schoenoplectus pungens*, *Baccharis salicifolia*, and *Salix gooddingii* (Quinn 2009). Though clearly a strong competitor, studies to date have yet to address how different soil moisture regimes interact with nutrient loading to impact the competitive ability of *Arundo*.

In an experiment conducted to determine the response of *Arundo* to intermittent shading over two years, it persisted even at a 90% reduction of light levels. Even in low light conditions, the success of this plant suggests that it can take advantage of limited sunlight available from gaps in the overstory (Spencer 2012). *Arundo* was found to be plastic for several traits, including but not limited to leaf chlorophyll content, leaf N content, total leaf area, and plant height (Spencer 2012). The experiment did not consider how nutrients and soil moisture may play a role in the ability of *Arundo* to harvest light. The photosynthetic capacity of *Arundo* has made it a species of particular interest to biofuel researchers (Mack 2008, Krička 2017, Cappelli 2021). A study assessing the photosynthetic capacity of *Arundo* found that although a C3 species *Arundo* has a photosynthetic capacity comparable to C4 bioenergy grasses. Photosynthetic capacity was determined to be high in both low and high light conditions (Webster 2016). Studies suggest that in *Arundo*, shoot emergence may be inversely related to photosynthetically active radiation (PAR), while shoot height and shoot survival exhibit a positive relationship to PAR (Quinn 2008). *Arundo* grown in the Mediterranean showed

high evapotranspiration rates at 1100 mm and a water use efficiency value of 3.2 g L⁻¹, whereas *Miscanthus giganteus* evapotranspiration rates were only 900 mm with a water use efficiency value of 3.1 g L⁻¹ (Triana 2015). In comparison, a 60-ha switchgrass field in Canada was found to have a total annual evapotranspiration rate of about 562 mm (Eichelmann 2015)

Given the characteristics of *Arundo* growth combined with its lack of significant natural enemies in North America and extreme tolerance to disturbance, the species has become a significant threat to wetland and upland habitats. This study will provide insight into how *Arundo* is impacted by its environment's abiotic factors during its establishment. In comprehending the factors that influence the performance of *Arundo*, we can better predict the sites where the species may establish and more efficiently implement management strategies. Understanding what factors may play a role in *Arundo* invasion has the potential to aid in the development of a comprehensive control plan for the species.

Hypotheses

This study aims to understand how soil moisture, nutrients, and light interact to influence the morphological and physiological attributes of *Arundo*. While these factors' impact on *Arundo* have been assessed individually, no crossed factor experiments have been conducted with these variables. A three-way factorial analysis of soil moisture, nutrients, and light, characteristics that commonly vary in the field, was conducted to understand better the interactions that may occur during the invasion process.

Understanding the mechanisms by which *Arundo* is able to invade and under what conditions it is most successful has implications for future management strategies and may provide insight into how this species functions as an invader.

Nutrient availability, in particular nitrogen and phosphorous, is known to control primary productivity. According to Zedler's Efficient Use Hypothesis, invasive species may make more efficient use of nutrients (Zedler 2004). Thus, a positive response in performance-related traits to nutrient addition is expected. Given the known affinity for soil moisture of *Arundo*, I predict that high nutrients and soil moisture will have a multiplicative effect on *Arundo* growth, increasing overall biomass.

Hypotheses:

- 1) *Arundo* will have higher values for performance-related traits, such as height and photosynthetic rate, when grown under high nutrient, saturated soils without shading because the plant as a large statured invasive species is particularly adept at taking advantage of conditions where growth limiting factors are minimal.
- 2) *Arundo* will have higher photosynthetic rate and lower nitrogen use efficiency (NUE) and WUE when grown in saturated, high-nutrient soils. The excess nitrogen and water will allow the plant to photosynthesize at a higher rate with lower efficiency.
- 3) *Arundo* will have lower biomass and number of stems when grown in the shade because shade lowers the ability of the plant to assimilate carbon that would be used for biomass and tiller production.
- 4) *Arundo* will exhibit growth-related responses indicating nutrient colimitation with N and P because both nutrients are essential to plant growth.

5) *Arundo* will allocate more biomass to stem tissues to aid in light capture and root tissues to aid in nutrient uptake as opposed to leaf and rhizome tissues when grown in high nutrient, saturated soils without shading to take advantage of optimal growing conditions.

Methods

Experimental Design

To better control *Arundo* invasions, it is necessary to understand how soil moisture, nutrient limitation, and light availability, three factors known to affect *Arundo* growth, influence the success of *Arundo*. I conducted a 4x3x2 factorial experiment of soil moisture, nutrients, and light availability to understand better how these factors may interact to affect invasion success by *Arundo*. This experiment investigates nutrient colimitation of nitrogen and phosphorus at four levels, soil moisture at three levels, and shading at two levels, with five replicates of each treatment (n = 120).

Plants were grown in 22.7-liter (5-gallon) pots filled with commercially available locally sourced topsoil and sand at a 1-part sand to 3-parts topsoil ratio. *Arundo* rhizomes were harvested on March 5th and March 30th, 2021, from the Blanco Shoals Natural Area in San Marcos, Texas. Due to the genetic homogeneity among *Arundo* populations (Ahmad 2008), one site was used for the collection of all *Arundo* rhizomes; therefore, site will not be considered a factor in the experiment. Rhizomes were washed, had their roots trimmed, and cut into fragments weighing 20-90 g with at least one bud present (n=150). Fragments were buried 5 cm apart and 3 cm deep in 57.15 cm x 40 cm x 12.7 cm tubs containing moist soil (1:3 sand to topsoil) and allowed to germinate until sprouting was observed (4 -15 days). Once most fragments sprouted, wet weight was be recorded, and

sprouted fragments were transferred to experimental pots. One fragment per pot was buried approximately 3 cm deep in the soil. Plants were grown in the Texas State University Research Greenhouse for three months.

One week after *Arundo* planting, fertilizer treatments were administered at four levels, control (0 g m⁻² y⁻¹ of nitrogen & phosphorous), nitrogen addition as ammonium nitrate (34.5% N; 15 gN m⁻² y⁻¹), phosphorous addition as triple superphosphate (46% P₂O₅; 15 gP m⁻² y⁻¹), and nitrogen + phosphorous addition (15 gP m⁻² y⁻¹ + 15 gN m⁻² y⁻¹). This treatment regime follows procedures used by Smith and Slater (2010). Fertilizer was dissolved in 25ml water and applied to the base of the plant with a syringe. In a review of N fertilization rates in the current literature for *Arundo donax* L., *Panicum virgatum* L., and *Miscanthus* spp., N fertilization rates in a variety of environmental conditions were found to range most commonly from 0-30 gN m⁻² y⁻¹. (Monti 2019).

Moisture levels for pots were maintained at three different levels, dry (watered every third day with 350 ml of water, ~25% soil moisture), wet (watered every other day with 350 ml of water, ~32% soil moisture), and saturated (pot placed in a tray of standing water and refilled when water levels drop below 2 cm, ~40% soil moisture).

Five shade tents representing dense canopy cover in riparian areas in central Texas (Crawford 2020) with an average reduction in PAR of 80%, measuring 114 cm x 152 cm x 165 cm, were constructed using PVC and shade cloth and randomly placed across three greenhouse benches. One set (12 pots) of each of the five replicates of each nutrient and moisture treatment combination (60 pots total) were placed under the shade cloth after being allowed to establish in experimental pots for one week, while another set of each treatment combination were left unshaded. Pots were assigned a stratified random

position on the greenhouse benches. Every other week, the plants were relocated to a new position in the greenhouse using a stratified random placement in which shaded and non-shaded sub-units (cohorts) remained grouped to minimize the effects of temperature and light gradients within the greenhouse.

Data Collection & Harvest

Throughout the duration of the experiment, the number of *Arundo* leaves, and tillers and the height of tillers was recorded every other week. During the last week of the experiment, gas exchange and chlorophyll fluorescence measurements were taken on the third leaf from the apex of the tallest stem in each pot. Due to time restrictions, chlorophyll fluorescence measurements were only recorded on 12 of the 24 treatment combinations for a total of 60 measurements. Samples were representative of all shade and soil moisture treatments but were only taken on plants receiving no nutrients and plants receiving both nitrogen and phosphorous (treatment combinations that include only N or only P addition were not sampled). This subsample was selected to provide insight into how the physiological photosynthetic processes of *Arundo* change in response to nutrient addition, the effects of nutrient colimitation were not investigated.

Measurements were taken the week of August 1st, 2021, between 9 am and 5 pm with the CIRAS-3 Portable Photosynthesis System at 38° C with a light intensity of 1200 $\mu\text{mol m}^{-2}\text{s}^{-1}$ and a CO₂ concentration of 400 μmol . Chlorophyll fluorescence measurements were taken independently from gas exchange measurements, which were taken from 10 am to 4 pm at 38° C with ambient light. All photosynthetic measurements were taken within the same week. The chlorophyll fluorescence measure of quantum yield of photosystem II activity (PSII) is calculated as $(F_m' - F_s) / F_m'$ where F_s is the

light-adapted fluorescence at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ immediately before multiple saturating pulses of $4000 \mu\text{mol m}^{-2} \text{s}^{-1}$, $5000 \mu\text{mol m}^{-2} \text{s}^{-1}$, and $6000 \mu\text{mol m}^{-2} \text{s}^{-1}$ are applied for 0.3 s at each step (PP Systems 2018, Tshapa 2021).

Harvest took place 159 days from the start of the experiment. The number of tillers, number of leaves, and cumulative height of all tillers were recorded for each pot. *Arundo* aboveground biomass (AGB) was cut at the base of the stem (at the soil surface), and the leaves were removed. Stems and leaves were placed in separate, labeled paper bags. The top three leaves from the tallest tiller were removed and submitted for analysis in a separate study, after which they were dried and weighed, and added to the total leaf biomass for that pot. *Arundo* belowground biomass (BGB) was removed from each pot, and remaining soil was removed by gentle washing with tap water. Roots were separated from rhizomes, and each was placed in a separate, labeled paper bag. Bags containing ABG and BGB were placed in a drying oven at 80°C for a minimum of 48 hours. A subsample of soil from the experimental pots was collected from all pots and sent to A&L Great Lakes Laboratories for nutrient analysis.

After drying, leaves, stems, roots, and rhizomes were weighed on a top-loading scale and measured to the nearest 1/100 of a gram. The shoot:root ratio of *Arundo* was determined by dividing AGB by BGB for each pot. Leaf, stem, root, and rhizome dry biomass of each plant was ground using a Wiley mill. A subset of 3 replicates of full sunlight dry and saturated treatments of all nutrient treatments (n=96) samples was then analyzed on an elemental analyzer to determine the percent nitrogen and percent carbon of plant tissues and the C:N ratio. This sampling methodology was chosen to show the effects of nutrient addition to C:N allocation in plants grown under natural sunlight

conditions in both dry and saturated soils. Nitrogen use efficiency (NUE) of plant organs was calculated by multiplying total organ mass by percent nitrogen to determine total grams of nitrogen in a given organ. Total organ biomass (g) was then divided by total nitrogen content (g) to determine how many grams of biomass were produced per unit of nitrogen assimilated. Another subset of 3 replicates of full sunlight, dry and saturated treatment, and only control and P+N nutrient treatments were analyzed for particulate phosphorous (n=48, results in appendix). This sampling methodology was chosen to show the effects of P and N addition to the total phosphorous content of plants grown under natural sunlight conditions in dry and saturated soils.

Statistical Analysis

This experiment was conducted as a 4x3x2 factorial experiment. Morphological response variables analyzed include cumulative tiller height, aboveground biomass (AGB), belowground biomass (BGB), shoot:root ratio, number of tillers, total tiller length, average tiller length, stem:leaf ratio, and the biomass allocation of plant organs. Physiological response variables analyzed include %N, C:N ratio, and %P of leaves, stems, roots, and rhizomes (results in appendix), WUE, maximum quantum yield of PSII, operating efficiency of PSII (Fv/Fm), and net photosynthesis.

Data were analyzed for normality and heteroscedasticity using visual analysis. Cumulative tiller height, AGB, number of tillers, total tiller length, and stem:leaf ratio were log-transformed. BGB, shoot:root ratio, and maximum quantum yield of PSII were square-root transformed. Net photosynthesis was log₁₀ transformed. WUE, operating efficiency of PSII (Fv/Fm), percent nitrogen, carbon:nitrogen ratios, total nitrogen, and

NUE were unable to be transformed, and therefore non-parametric tests were used for these variables.

A general linear mixed-effects model was performed using initial rhizome mass as a covariant and cohort as a random effect to see if any response variables differ significantly across soil moisture, nitrogen, and shade treatments. Soil moisture, shade, and nutrients were treated as fixed factors. Regression analyses were performed on initial rhizome weight x BGB, initial rhizome weight x AGB (results in appendix), and net photosynthesis x average tiller length to determine if relationships between variables were present. MANOVA was used on the percent of total biomass represented by different plant organs to determine if there were differences in organ biomass allocation between or among groups in response to the independent variables. Non-parametric tests were used for variables which could not meet the assumptions of parametric tests. An aligned rank transformation test was used to analyze WUE, and Kruskal Wallis tests were used to analyze the operating efficiency of PSII (F_v/F_m), percent nitrogen, carbon:nitrogen ratios, total nitrogen, percent phosphorus, and carbon phosphorus ratios. R (version 4.1.0) was used for all analyses.

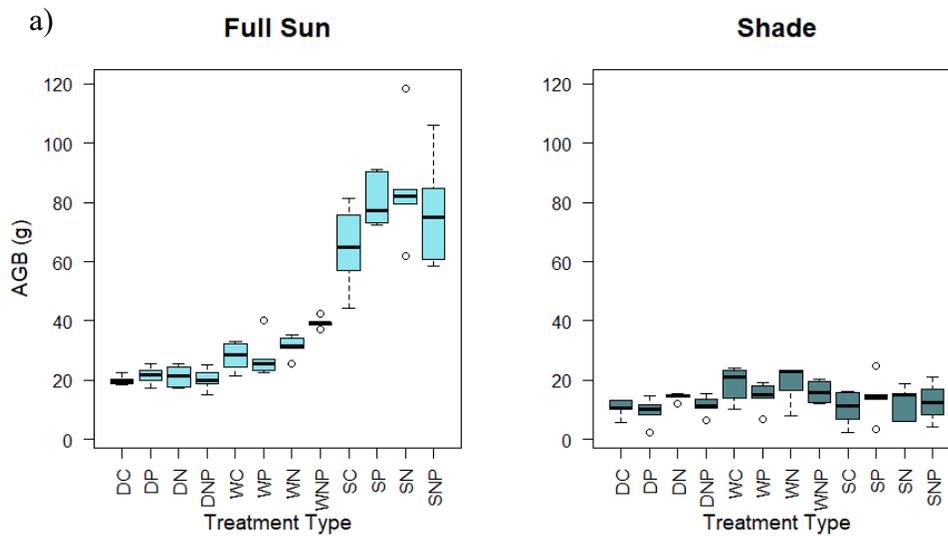
Results

Linear Mixed-Effects Model

Aboveground biomass & Belowground biomass

In full sun treatments, across nutrient levels, *Arundo*'s AGB increased with soil moisture, while AGB did not vary across treatments grown in shade (2-way interaction – light x moisture, $P < 0.0001$, Table 1, Figure 1). Plants grown in saturated soils had greater AGB than those grown in dry and wet treatments (main effect of moisture, P

<0.0001, Table 1). Plants grown in full sun had greater AGB than those grown in shade treatments (main effect of light, $P < 0.0001$, Table 1, Figure 1). In full sun treatments, across nutrient levels, *Arundo*'s BGB increased with soil moisture, while BGB did not vary across treatments grown in shade (2-way interaction – light x moisture, $P < 0.0001$, Table 1, Figure 1). Plants grown in saturated soils had greater BGB than those grown in dry and wet treatments (main effect of moisture, $P < 0.0001$, Table 1, Figure 1). Plants grown in full sun had greater BGB than those grown in shade treatments (main effect of light, $P < 0.0001$, Table 1).



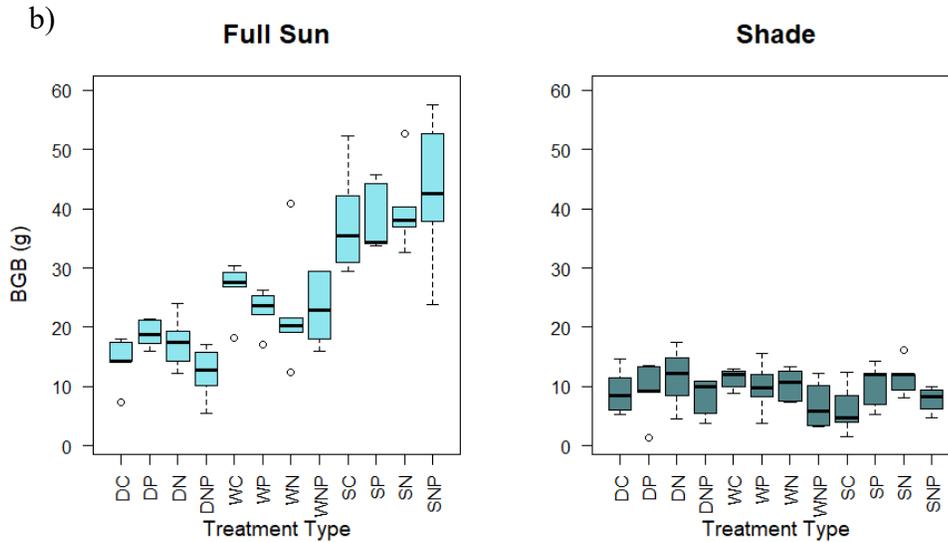


Figure 1

Box and whisker plots of (a) AGB, and (b) BGB of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C=control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Shoot:Root Ratio & Stem:Leaf Ratio

Plants grown in soils with added nitrogen and phosphorus tended to have greater shoot:root ratio than those grown in soils without nutrients (main effect of nutrients, $P = 0.0049$, Table 1, Figure 2), while plants grown in saturated soils tended to have greater shoot:root ratio than those grown in dry and wet treatments (main effect of moisture, $P = 0.0177$, Table 1, Figure 2). *Arundo*'s stem:leaf ratio increased with soil moisture, while stem:leaf ratio did not vary across treatments grown in shade treatments across nutrient levels. (2-way interaction – light x moisture, $P < 0.0001$, Table 1, Figure 2). Plants grown in soils with added nitrogen and phosphorus had a greater stem:leaf ratio than those grown in soils without nutrients (main effect of nutrients, $P = 0.0451$, Table 1, Figure 2). Plants grown in saturated soils had greater stem: leaf ratio than those grown in dry, and wet treatments (main effect of moisture, $P < 0.0001$, Table 1, Figure 2).

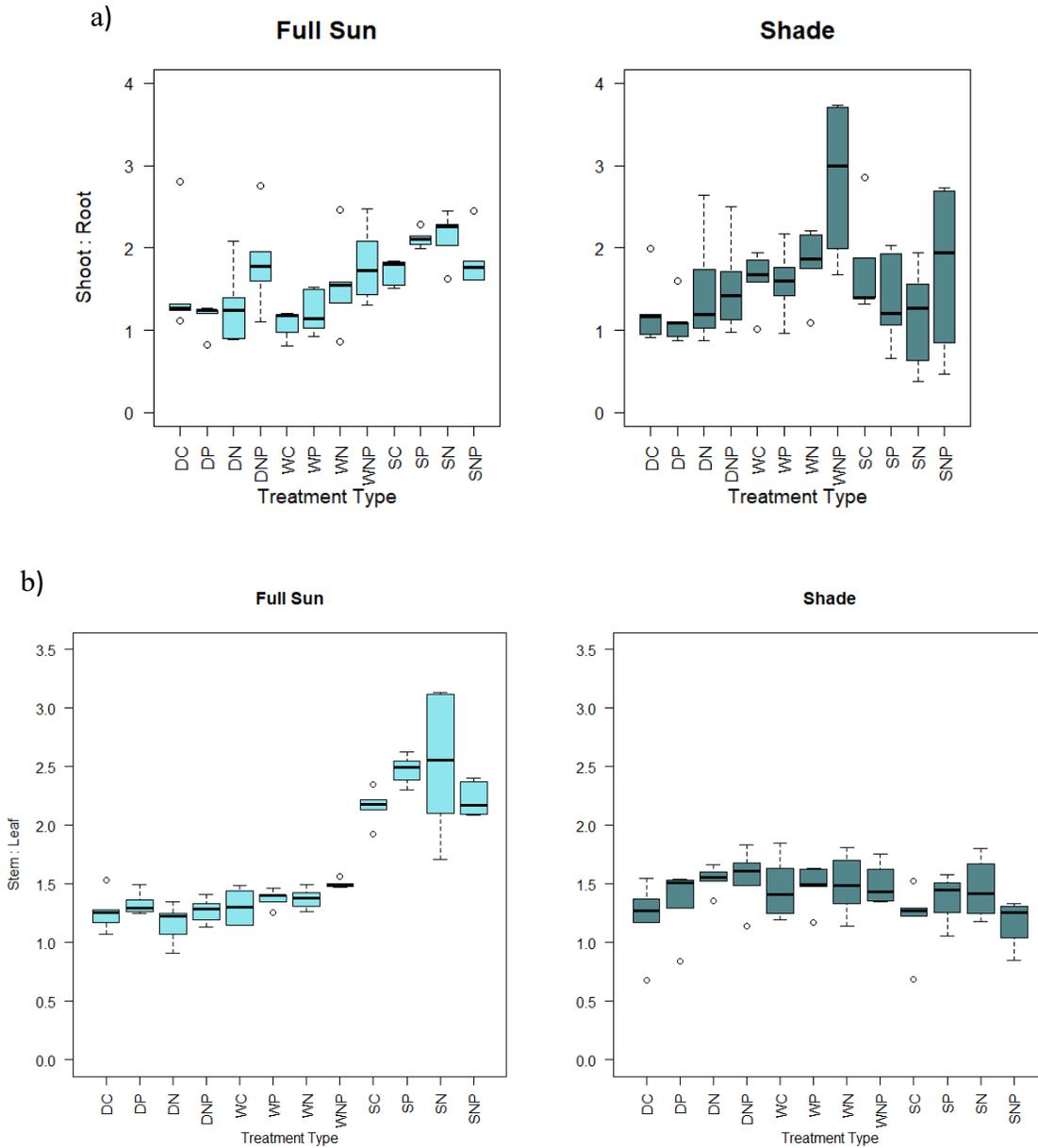


Figure 2

Box and whisker plots of (a) Shoot:Root Ratio, and (b) Stem:Leaf Ratio of *Arundo donax* grown in full sun and shade conditions at three moisture levels and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Number of Tillers

Plants grown in saturated soils exhibited a greater number of tillers than those grown in dry and wet treatments (main effect of moisture, $P < 0.0001$, Table 1, Figure 3). Plants grown in full sun had a greater number of tillers than those grown in shade treatments (main effect of shade, $P = 0.0026$, Table 1, Figure 3).

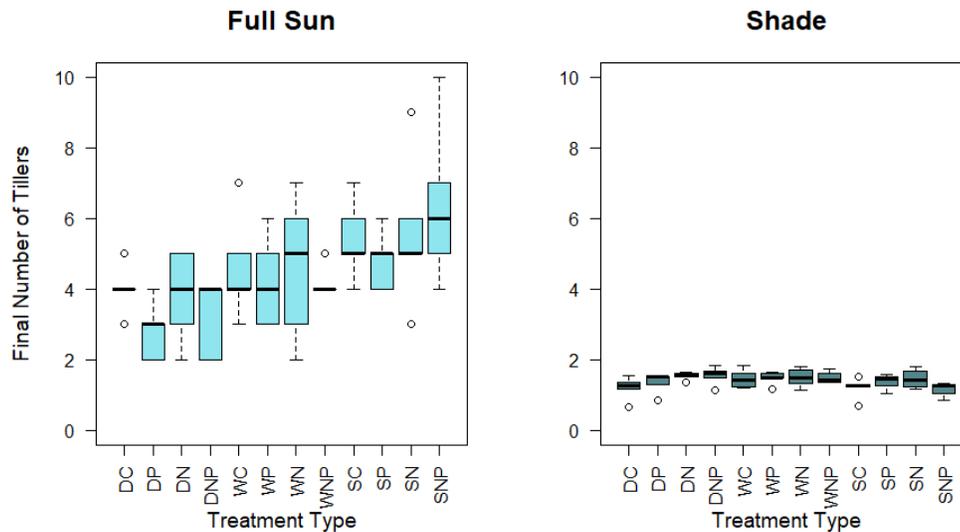


Figure 3

Box and whisker plots of the final number of tillers of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C=control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Total Tiller Length & Average Tiller Height

Across nutrient levels in full sun treatments, *Arundo*'s total tiller length increased with soil moisture, while total tiller length did not vary across treatments grown in shade. (2-way interaction – light x moisture, $P < 0.0001$, Table 1, Figure 4). Plants grown in saturated soils had greater total tiller length than those grown in dry and wet treatments (main effect of moisture, $P < 0.0001$ Table 1, Figure 4). Plants grown in full sun exhibited

greater total tiller length than those grown in shade treatments (main effect of light, $P = 0.0029$, Table 1, Figure 4). In full sun treatments, across nutrient levels, *Arundo*'s average tiller height increased with soil moisture. Total tiller height did not vary across treatments grown in shade. (2-way interaction– light x moisture, $P < 0.0001$, Table 1, Figure 4). Plants grown in saturated soils had greater average tiller height than those grown in dry and wet treatments (main effect of moisture, $P = 0.0067$, Table 1, Figure 4).

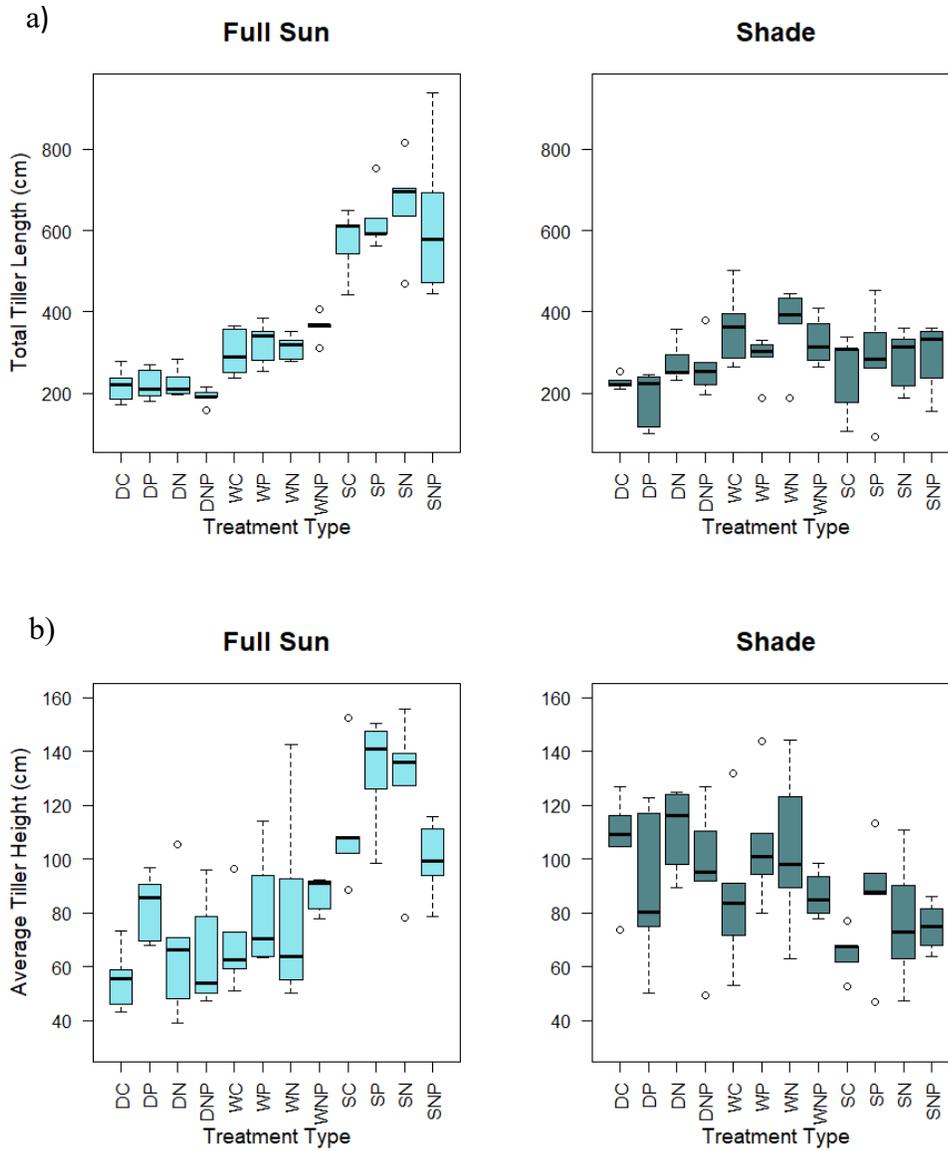


Figure 4

Box and whisker plots of (a) Total Tiller Length, and (b) Average Tiller Height of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Photochemical Efficiency of PSII

Plants grown in saturated soils (especially those grown in full sun) tended to have greater photochemical efficiency of PSII than plants grown in dry and wet treatments (main effect of moisture, $P=0.0486$, Table 1, Figure 5).

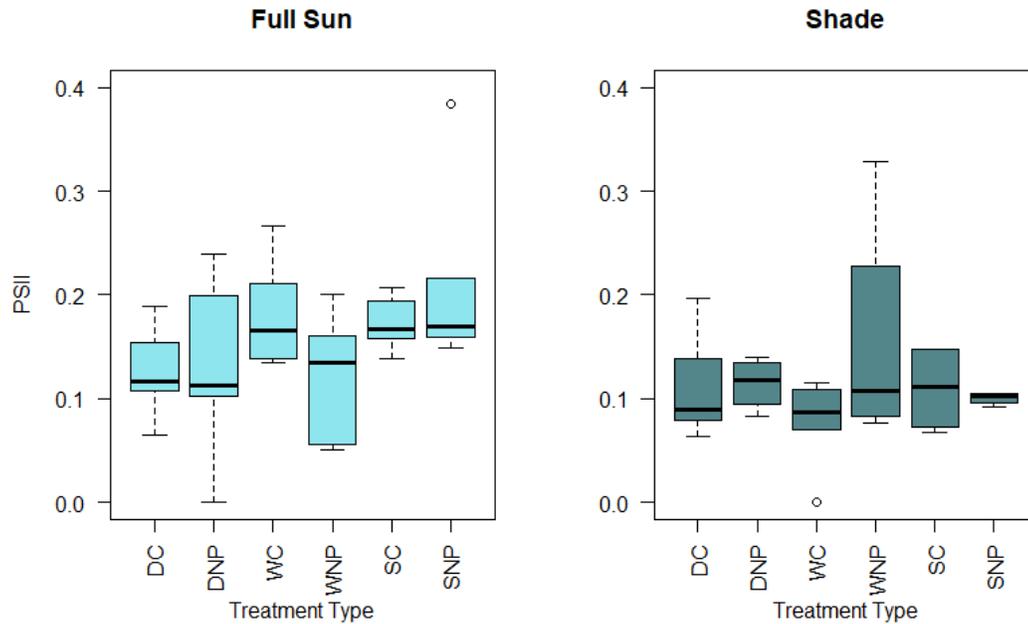


Figure 5

Box and whisker plots of the photochemical efficiency of photosystem two ($\frac{Fm' - Fs}{Fm'}$) where Fm' = maximum fluorescence signal yield in an illuminated sample and Fs = steady state fluorescence yield in an illuminated sample of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and two nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, NP=nitrogen & phosphorus.

Net Photosynthesis

Arundo's net photosynthesis in full sunlight treatments across nutrient levels increased with soil moisture, while net photosynthesis did not vary across treatments grown in shade. (2-way interaction – light x moisture, $P < 0.0001$, Table 1, Figure 6).

Plants grown in saturated soils exhibited greater net photosynthesis than those grown in dry and wet treatments (main effect of moisture, $P < 0.001$, Table 1, Figure 6).

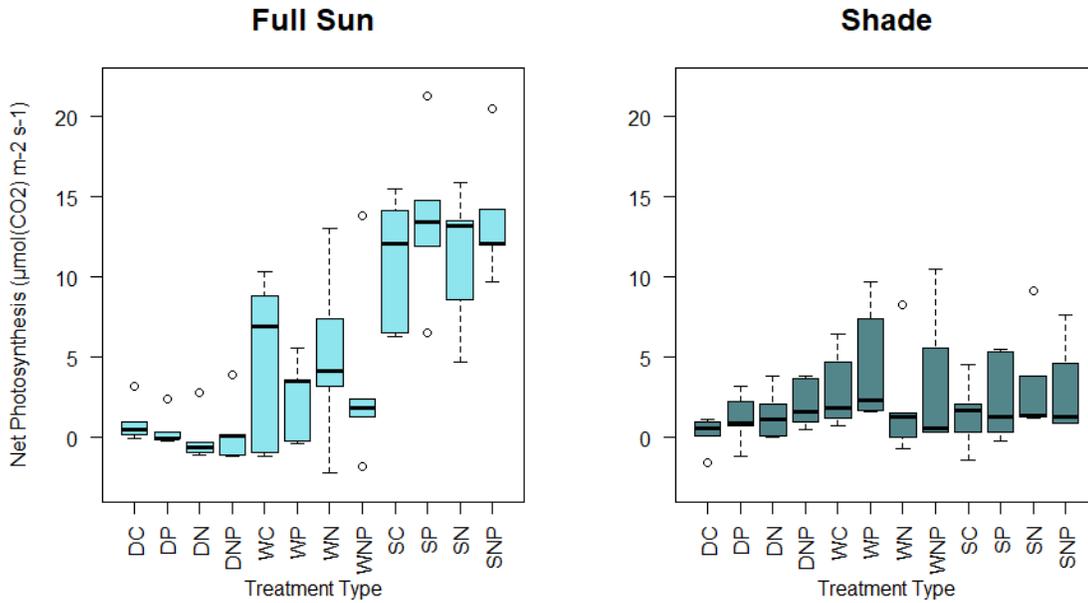


Figure 6
 Box and whisker plots of net photosynthesis of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Table 1

F-values and significance levels for general linear mixed-effects model using initial rhizome mass as a covariant, and cohort as a random effect, for the effect of nutrients, soil moisture, and shade on aboveground biomass (AGB), belowground biomass (BGB), shoot: root ratio, stem: leaf ratio, final number of tillers, total tiller length, average tiller length, Photochemical Efficiency of PSII, and net photosynthesis.

* $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$

Source	AGB	BGB	Shoot:Root	Stem:Leaf	Number of Tillers	Total Tiller Length	Average Tiller Length	PSII	Net Photosynthesis
Nutrients	3.38	0.01	8.28**	4.11**	0.36	3.07	0.53	0.30	0.31
Moisture	54.61***	100.03***	5.81*	48.28***	36.68***	87.57***	7.65**	4.14*	51.17***
Shade	152.04***	271.05***	0.20	17.91**	18.48**	17.74**	0.37	4.58	2.14
N:M	0.07	0.39	0.13	1.01	0.63	0.08	0.54	0.43	0.17
N:S	0.08	0.29	0.07	0.70	1.14	0.42	0.22	1.67	1.49
M:S	50.07***	100.75***	2.25	71.01***	0.54	52.82***	52.27***	0.49	28.63***
N:M:S	0.23	0.00	0.89	2.55	1.94	0.40	1.29	0.13	1.10

MANOVA

Full Model

In full sun treatments across nutrient levels, *Arundo* allocated its biomass differently depending on if it was growing in saturated or dry soils (2-way interaction – light x moisture, $P < 0.001$, Table 2). *Arundo* grown in shade allocated biomass to different organs than it did when grown in light (main effect of light, $P < 0.001$, Table 2). Plants grown in saturated soils tended to allocate biomass differently than plants grown in dry soils (main effect of moisture, $P < 0.001$, Table 2).

Percent Leaf Tissue

In full sun treatments, across nutrient levels, *Arundo* allocated less biomass to leaf tissue in saturated treatments than in dry or wet treatments. Leaf biomass allocation did not vary across treatments grown in shade. (2-way interaction– light x moisture, $P < 0.0001$, Figure 7). Plants grown in shade tended to allocate more biomass to leaf tissue than those grown in full sun (main effect of light, $P = 0.047$, Table 2, Figure 7). Plants grown in saturated conditions allocated less biomass to leaf tissue than in dry or wet treatments (main effect of moisture, $P = 0.019$, Table 2, Figure 7).

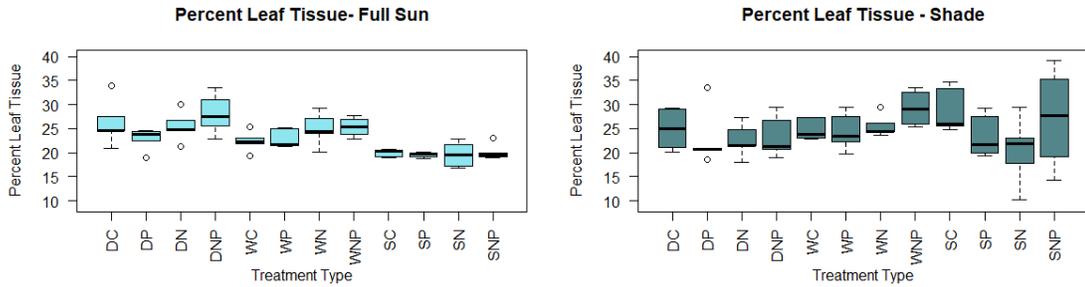


Figure 7

Box and whisker plots of percent leaf tissue of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Percent Stem Tissue

Across nutrient levels in full sun, *Arundo* tended to allocate more biomass to stem tissue in saturated treatments than in dry or wet treatments. Stem biomass allocation did not vary across treatments grown in shade. (2-way interaction– light x moisture, $P < 0.0001$, Table 2, Figure 8). Plants grown in shade allocated less biomass to stem tissue than those grown in full sun (main effect of light, $P = 0.008$, Table 2, Figure 8). Plants grown in saturated conditions were observed to allocate more biomass to stem tissue than in dry or wet treatments (main effect soil moisture, $P < 0.0001$, Table 2, Figure 8). *Arundo* grown in pots with added nitrogen and phosphorus allocated more biomass to stem tissue than those grown in control treatments (main effect nutrients, $P = 0.014$, Table 2, Figure 8)

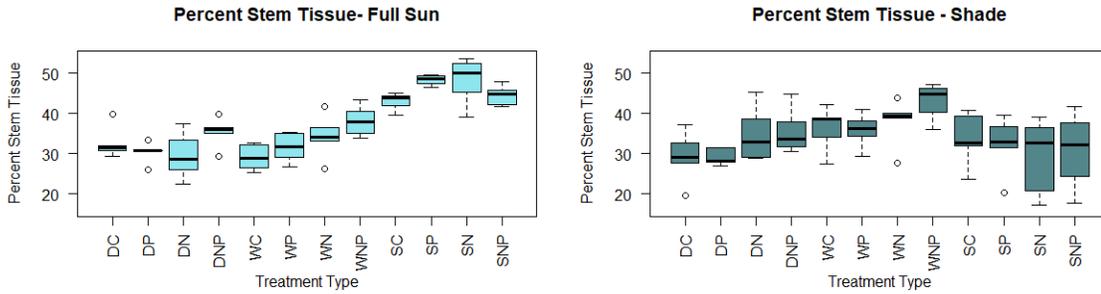


Figure 8

Box and whisker plots of percent stem tissue of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Percent Rhizome Tissue

In full sunlight treatments, across nutrient levels, *Arundo* allocated less biomass to rhizome tissue in saturated treatments than in dry or wet treatments (2-way interaction–light x moisture, $P=0.015$, Figure 9). *Arundo* grown in shade allocated more biomass to rhizome tissue than plants grown in full sun (main effect light, $P<0.0001$, Table 2, Figure 9). Plants grown in saturated conditions tended to allocate less biomass to rhizome tissue than in dry or wet treatments (main effect moisture, $P=0.007$, Table 2, Figure 9).

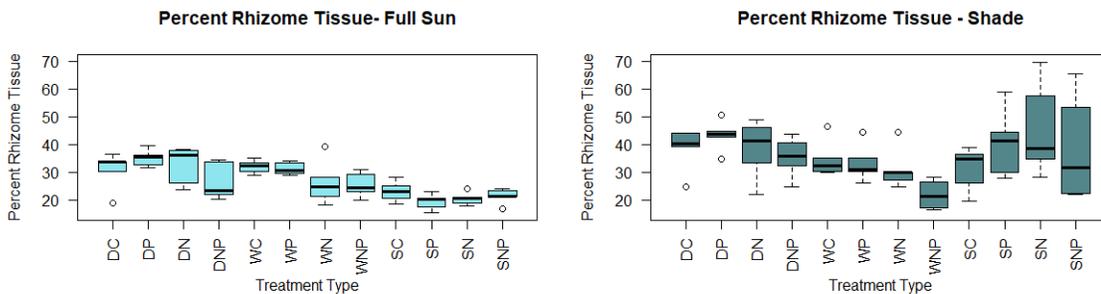


Figure 9

Box and whisker plots of percent rhizome tissue of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Percent Root Tissue

Arundo tended to, in full sunlight treatments, across nutrient levels, allocate more biomass to root tissue in saturated treatments than in dry or wet treatments, while root biomass allocation did not vary across treatments grown in shade. (2-way interaction—light x moisture, $P = 0.028$, Figure 10). *Arundo* grown in shade allocated less biomass to root tissue than plants grown in full sun (main effect light, $P < 0.0001$, Table 2, Figure 10).

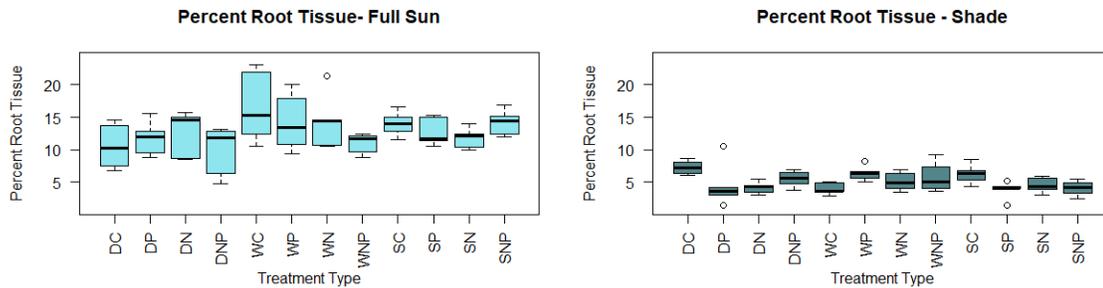


Figure 10

Box and whisker plots of percent root tissue of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Table 2

F-values and significance levels for MANOVA, for the effect of nutrients, soil moisture, and shade on percent leaf tissue, percent stem tissue, percent rhizome tissue, and percent root tissue.

* p<0.05, ** p<0.01, ***p<0.001

Source	Full Model	Percent Leaf	Percent Stem	Percent Rhizome	Percent Root
Moisture	13.88***	5.59*	23.90***	7.39**	1.61
Nutrients	2.05	0.36	6.11*	2.00	3.84
Shade	68.30***	4.02*	7.29**	32.34***	218.73***
M:N	0.89	0.27	1.60	1.19	0.03
M:S	22.72***	15.06***	26.24***	6.00*	4.90*
N:S	0.56	0.91	0.00	0.03	0.81
M:N:S	0.97	0.00	2.46	1.28	0.03

Regressions

Net photosynthesis x Average tiller length

Net photosynthesis was found to be a significant predictor of average tiller height (P =0.0003, Figure 11). Average tiller height accounted for about 10% of the variability in photosynthetic rate. This suggests that higher net photosynthesis is associated with greater average tiller height.

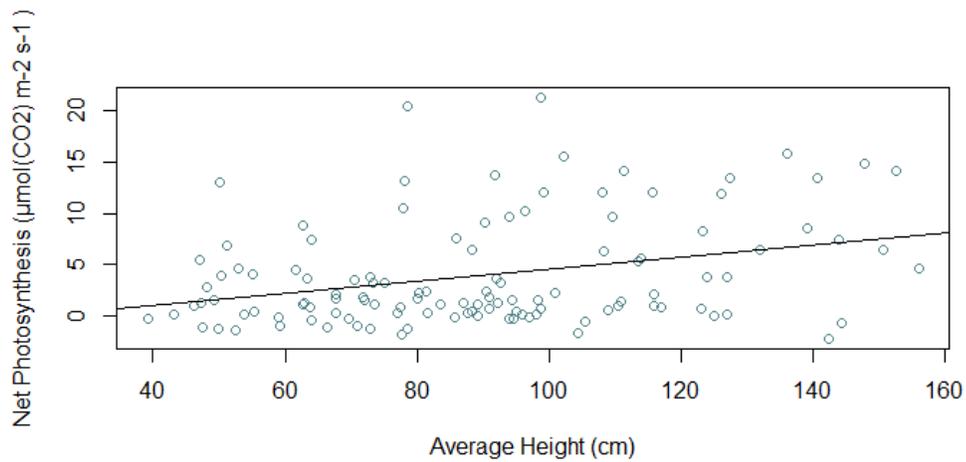


Figure 11
Plot of Average Tiller Height as a function of Net Photosynthesis. $R^2=0.10$

Non-Parametric Tests

WUE

Using an aligned rank transformation test, it was found that in full sunlight treatments, across nutrient levels, the water use efficiency of *Arundo* increased with soil moisture, while water use efficiency did not vary across treatments grown in shade and tended to be higher than the full sun treatment. (2-way interaction - light x moisture, $P=0.0013$, Table 3, Figure 12). Plants grown in saturated soils tended to have greater water use efficiency than those grown in dry and wet treatments (main effect moisture, $P=0.001$, Table 3, Figure 12).

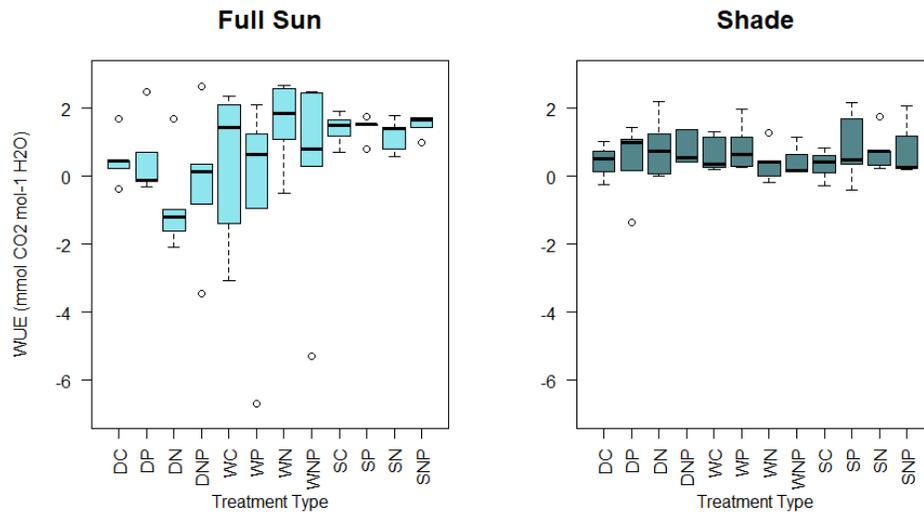


Figure 12

Box and whisker plots of water use efficiency ($\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and four nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=phosphorus, N=nitrogen, NP=nitrogen & phosphorus.

Table 3

Degrees of freedom, F-values and significance levels for ART test, for the effect of nutrients, soil moisture, and shade on WUE.

* $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$

Source	Degrees of Freedom	F Value
Nutrients	3	0.02
Moisture	2	7.40**
Shade	1	0.02
N:M	6	0.99
N:S	3	0.39
M:S	2	7.07**
N:M:S	6	0.10

Operating Efficiency of PSII (Fv/Fm)

Using a Kruskal-Wallis test, it was found that plants grown in full sunlight exhibited higher values for Fv/Fm (main effect light, P =0.01, Table 4, Figure 13).

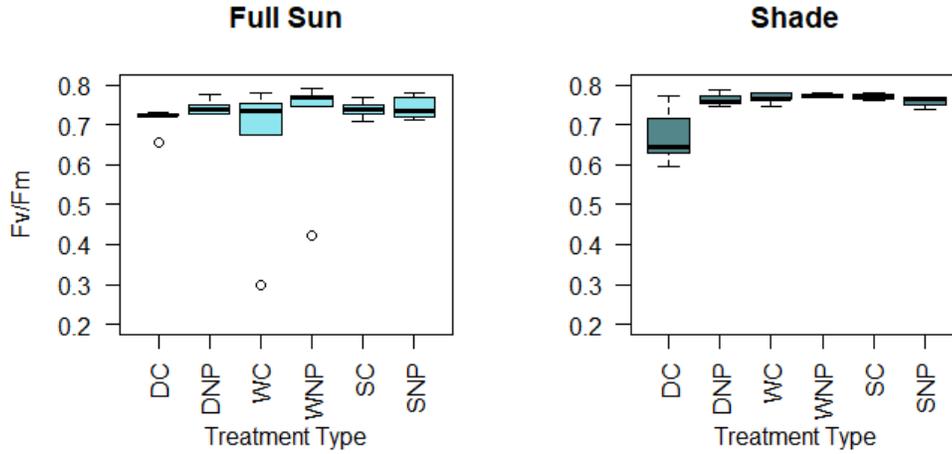


Figure 13

Box and whisker plots of Fv/Fm of *Arundo donax* grown in full sun and shade conditions at three moisture levels, and two nutrient levels. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, NP=nitrogen & phosphorus.

Table 4

Chi-squared values and significance levels for Kruskal-Wallis test, for the effect of nutrients, soil moisture, and shade.

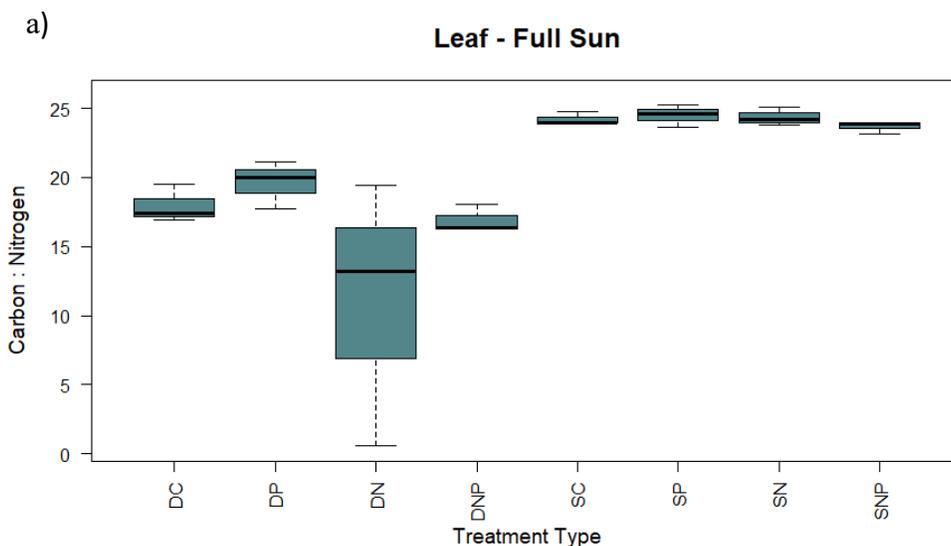
* p<0.05, ** p<0.01, ***p<0.001

Source	Operating Efficiency of PSII (Fv/Fm)
Nutrients	0.1129
Moisture	1.6498
Shade	5.5994*

Percent Nitrogen & Carbon:Nitrogen

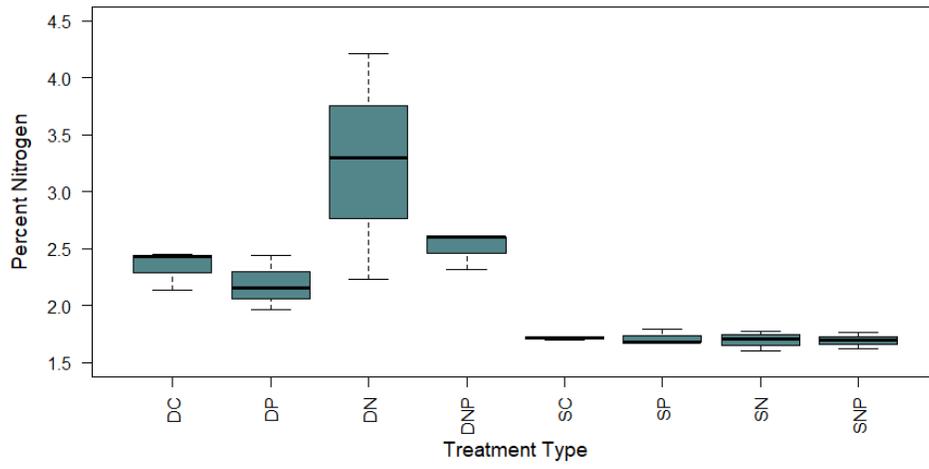
Leaves

Plants grown in saturated conditions exhibited lower percent nitrogen and higher C:N ratios in leaf tissues than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 5, Figure 14). Plants grown in treatments receiving N and N&P had slightly lower C:N ratios than those grown in pots with just P addition or no nutrient addition (main effect nutrients, $P = 0.02$, Table 5, Figure 14). Plants grown in dry conditions receiving N and N&P had the highest values for percent nitrogen in leaf tissues (2-way interaction - nutrients x moisture, $P = 0.004$, Table 5, Figure 14). The total amount of assimilated nitrogen (g), calculated by percent nitrogen multiplied by total dry mass of the plant organ, was found to be higher in plants grown in saturated conditions than those grown in dry conditions, while no difference was observed between nutrient treatments (main effect moisture, $P < 0.0001$, Table 5, Figure 14). Plants grown in saturated conditions exhibited higher NUE in leaf tissues than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 5, Figure 14).



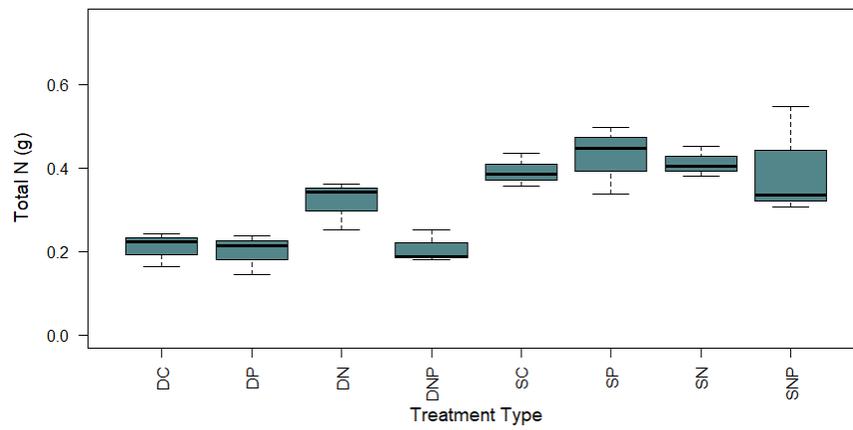
b)

Leaf - Full Sun



c)

Leaf - Full Sun



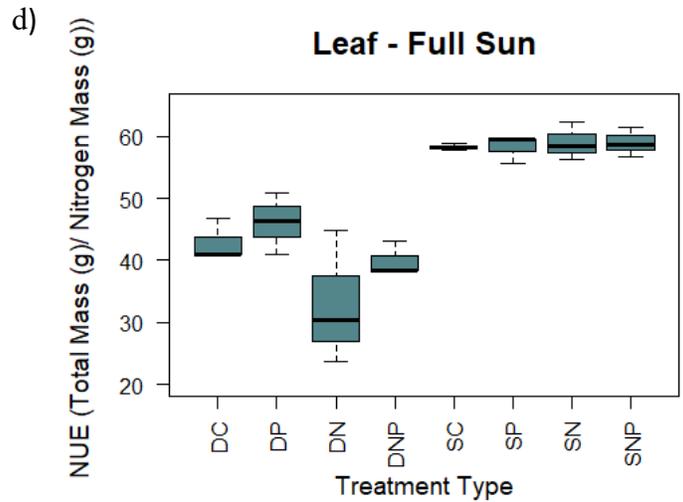


Figure 14

Box and whisker plots of a) C:N ratio of leaf tissues, b) Percent nitrogen of leaf tissues, c) total nitrogen in leaf tissues, d) NUE of leaf tissues. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=Phosphorus, N= Nitrogen, NP=nitrogen & phosphorus.

Table 5

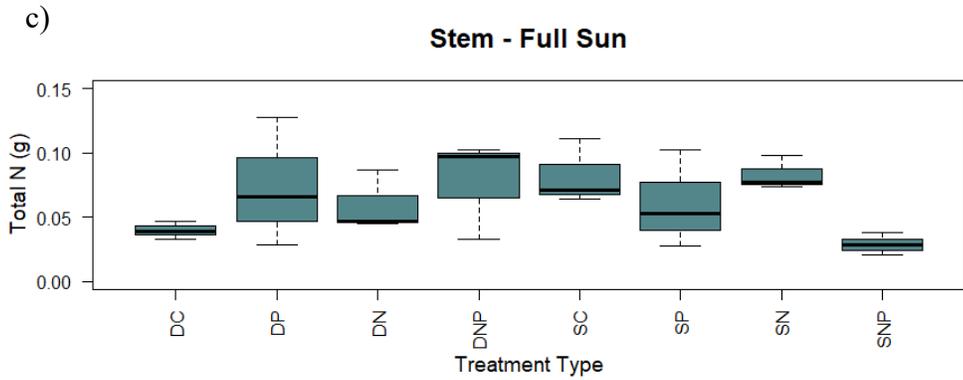
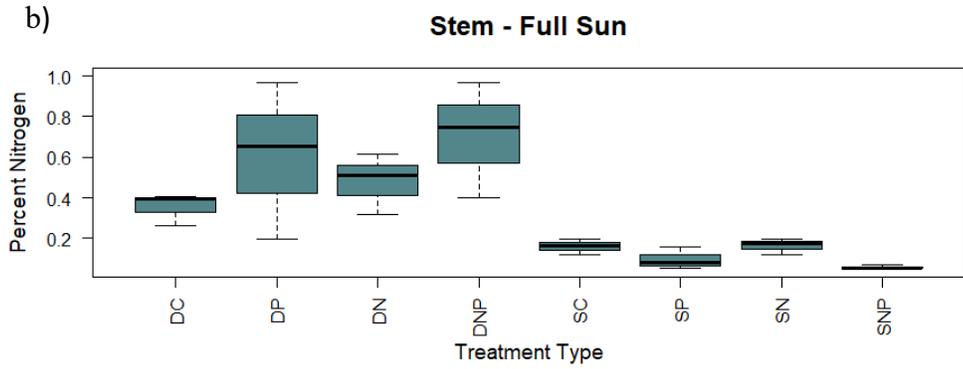
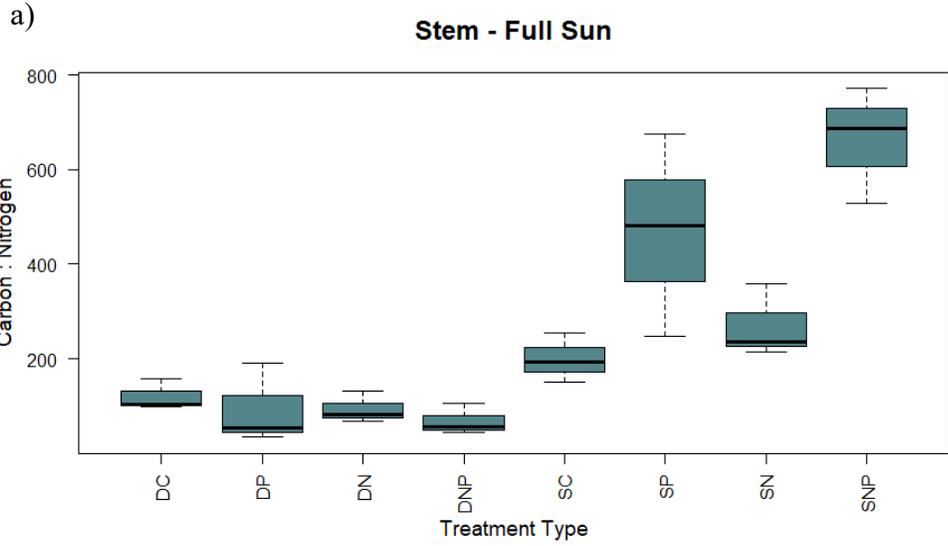
F values and significance levels for ART test, for the effect of nutrients and soil moisture on leaf carbon:nitrogen, leaf percent nitrogen, total g N in leaf tissues, and NUE in leaf tissues. * p<0.05, ** p<0.01, ***p≤0.001

Source	Carbon:Nitrogen	Percent Nitrogen	Total N (g)	NUE
Nutrients	4.21*	2.55	1.78	0.65
Moisture	23.09***	18.95***	49.61***	49.85***
N:M	4.55*	6.41**	1.16	0.18

Stems

Plants grown in saturated conditions with added phosphorous and nitrogen exhibited the highest C:N values while those grown in saturated conditions with only

phosphorus had slightly lower C:N ratios. Plants grown in saturated conditions with only N addition exhibited the second lowest values for C:N ratios in saturated treatments having C:N values that were only slightly higher than those of the control treatment (2-way interaction - nutrients x moisture, $P = 0.002$, Table 6, Figure 15). *Arundo* grown in saturated conditions exhibited lower percent nitrogen and higher C:N ratios in stem tissues than plants grown in dry conditions (main effect moisture, $P < 0.001$, Table 6, Figure 15). Plants grown in pots with added nitrogen and phosphorous exhibited different responses in C:N ratio though patterns were not consistent between dry and saturated treatments (main effect nutrients, $P = 0.004$, Table 6, Figure 15). The total amount of assimilated nitrogen (g) was not influenced by moisture or shade treatments. Plants grown in saturated conditions with added nitrogen and phosphorus exhibited the highest NUE while plants grown in dry conditions exhibited minimal response to the addition of nitrogen and/or phosphorus (2-way interaction - nutrients x moisture, $P < 0.001$, Table 6, Figure 15). Plants grown in saturated conditions exhibited higher NUE in stem tissues than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 6, Figure 15). Plants grown with added nutrients exhibited higher NUE in stem tissues than those grown without nutrient addition (main effect nutrients, $P = 0.005$, Table 6, Figure 15).



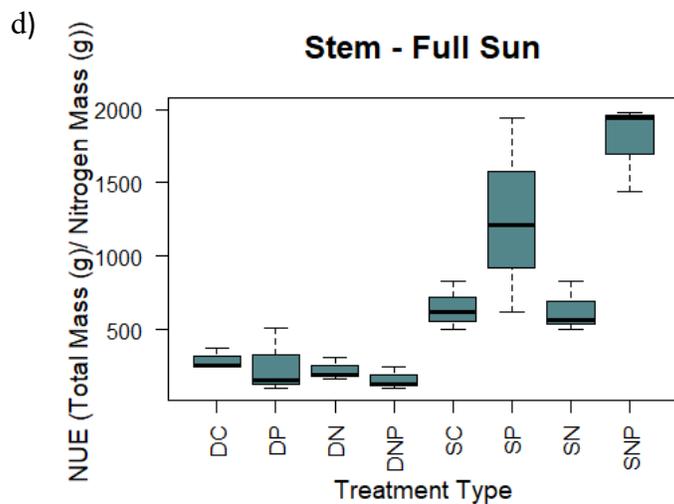


Figure 15

Box and whisker plots of a) C:N ratio of stem tissues, b) Percent nitrogen of stem tissues, c) total nitrogen in stem tissues, d) NUE of stem tissues.

Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=Phosphorus, N= Nitrogen, NP=nitrogen & phosphorus.

Table 6

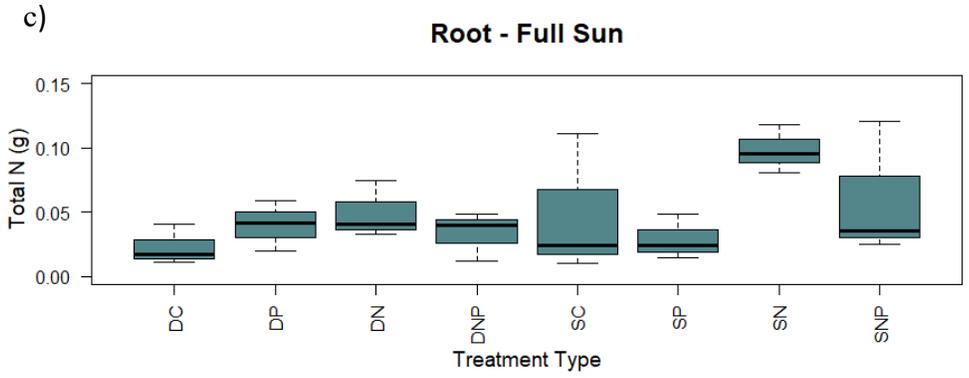
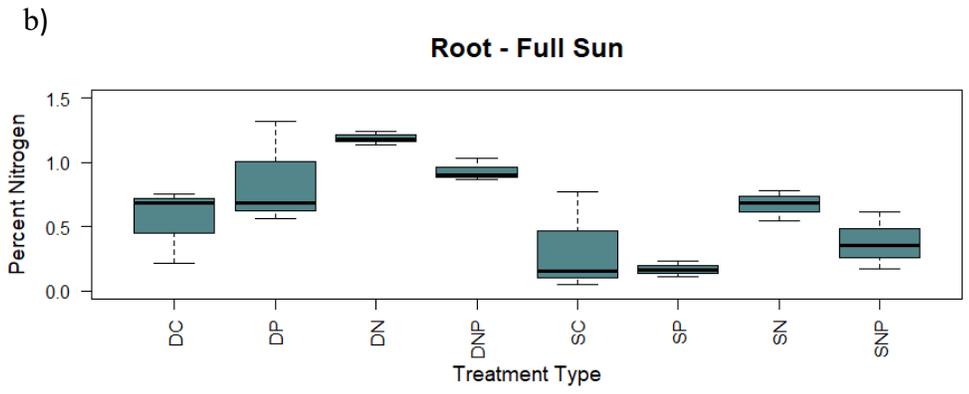
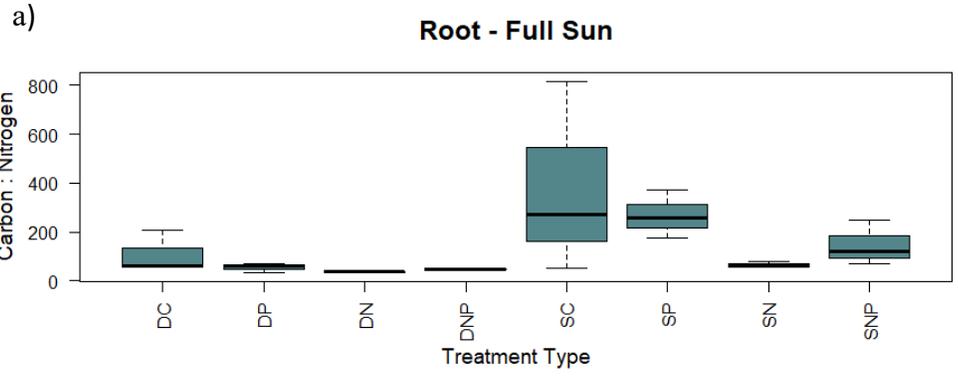
F values and significance levels for ART test, for the effect of nutrients and soil moisture on stem carbon:nitrogen, stem percent nitrogen, total g N in stem tissues, and NUE in stem tissues.

* p<0.05, ** p<0.01, ***p≤0.001

Source	Carbon:Nitrogen	Percent Nitrogen	Total N (g)	NUE
Nutrients	6.3692**	1.7090	0.3341	6.2414**
Moisture	44.5121***	30.2799***	0.0024	44.5121***
N:M	7.5745**	3.0344	2.9677	9.0998***

Roots

Plants grown in saturated conditions exhibited lower percent nitrogen and higher C:N ratios in roots than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 7, Figure 16). Plants grown in pots with added nitrogen were found to have lower C:N ratios than plants grown without nutrients or with just phosphorus or the addition of both nitrogen and phosphorus (main effect nutrients, $P = 0.015$, Table 7, Figure 16). Plants grown in pots with added nitrogen and a combination of nitrogen and phosphorus exhibited higher percent nitrogen in root tissues than those grown without added nutrients or with phosphorus alone (main effect nutrients, $P = 0.014$, Table 7, Figure 16). The total amount of assimilated nitrogen (g) was not found to change in varying moisture and nutrient treatments. Plants grown in saturated conditions exhibited higher NUE in root tissues than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 7, Figure 16). Plants grown in pots without added nitrogen exhibited the highest NUE in root tissues while those grown with additional nitrogen exhibited lower NUE (main effect nutrients, $P = 0.0111$, Table 7, Figure 16).



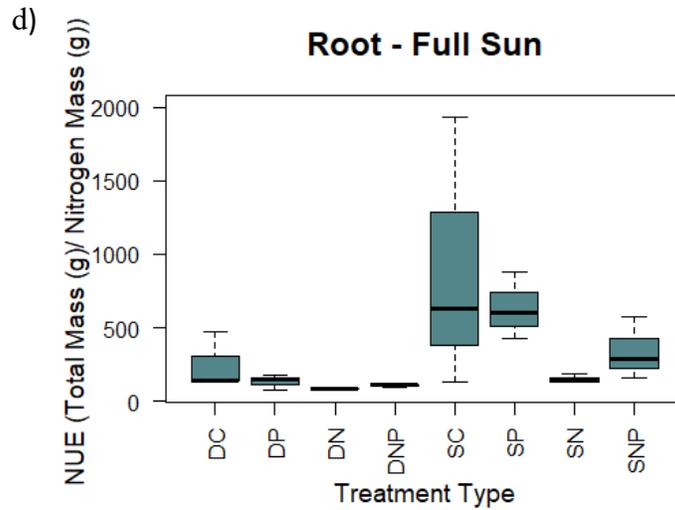


Figure 16

Box and whisker plots of a) C:N ratio of root tissues, b) Percent nitrogen of root tissues, c) total nitrogen in root tissues, d) NUE of root tissues. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C=control, P=Phosphorus, N= Nitrogen, NP=nitrogen & phosphorus.

Table 7

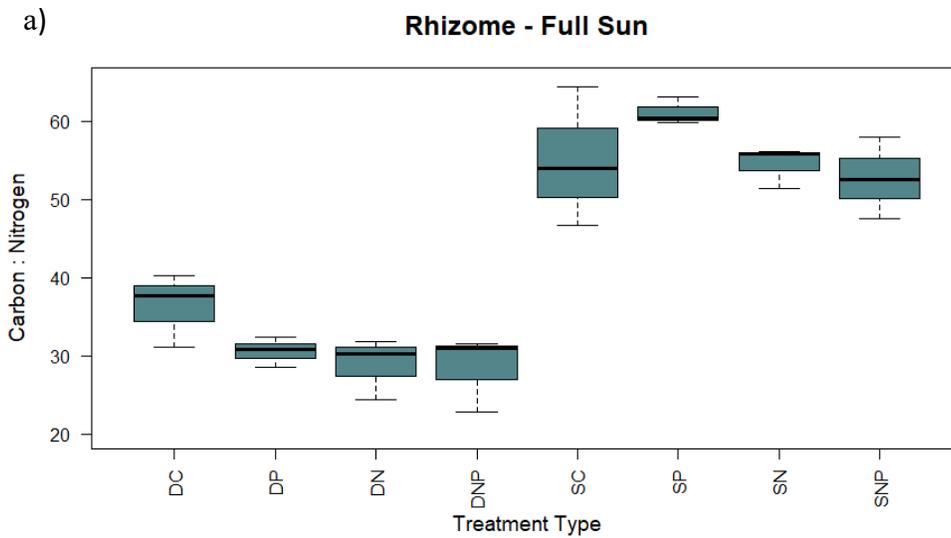
F values and significance levels for ART test, for the effect of nutrients and soil moisture on root carbon:nitrogen, root percent nitrogen, total g N in root tissues, and NUE in root tissues.

* $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$

Source	Carbon:Nitrogen	Percent Nitrogen	Total N (g)	NUE
Nutrients	4.6651*	4.7717*	2.8532	5.1433*
Moisture	17.0105***	27.9679***	2.5974	16.9661***
N:M	1.9152	0.1860	1.1867	1.8896

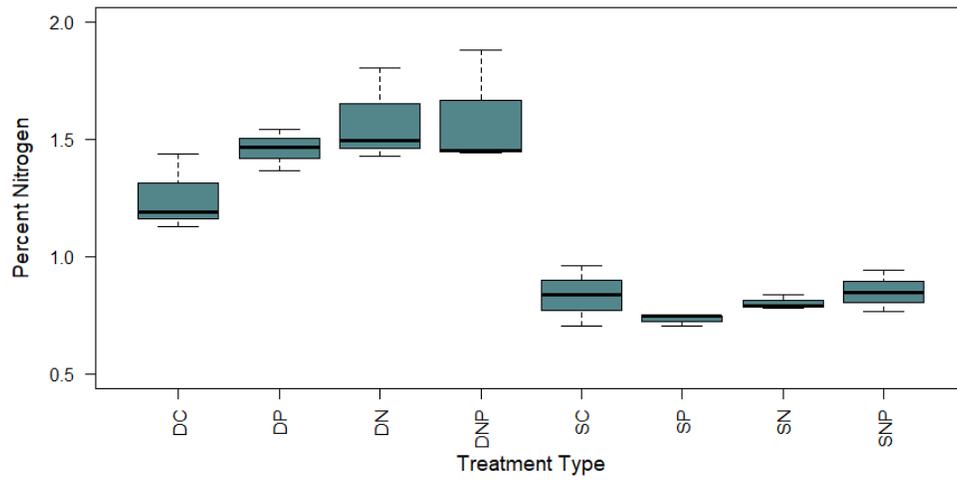
Rhizomes

Plants grown in saturated conditions exhibited lower percent nitrogen and higher C: N ratios in rhizome tissues than those grown in dry conditions, while no difference was observed between nutrient treatments (main effect moisture, $P < 0.001$, Table 8, Figure 17). The total amount of assimilated nitrogen (g) was not found to be influenced by nutrients or soil moisture. Plants grown in saturated conditions exhibited higher NUE in rhizome tissues than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 8, Figure 17).



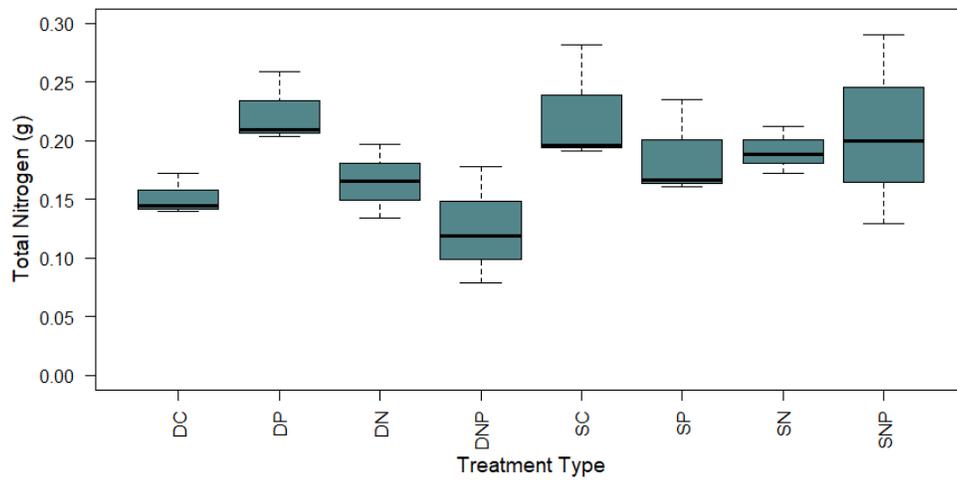
b)

Rhizome - Full Sun



c)

Rhizome - Full Sun



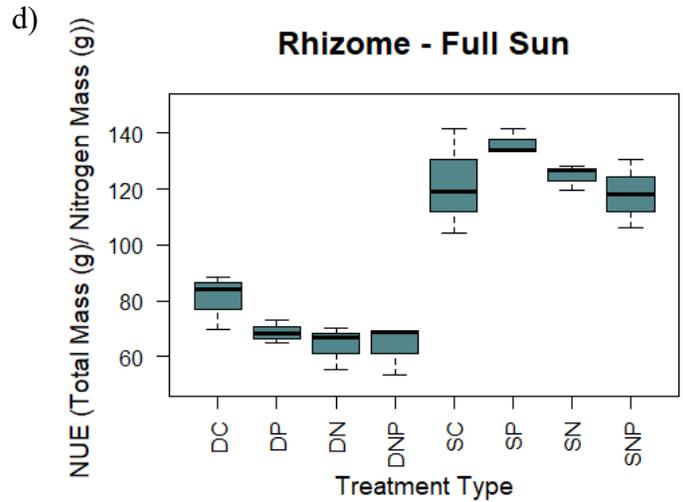


Figure 17

Box and whisker plots of a) C:N ratio of rhizome tissues, b) Percent nitrogen of rhizome tissues, c) total nitrogen in rhizome tissues, d) NUE of rhizome tissues. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=Phosphorus, N= Nitrogen, NP=nitrogen & phosphorus.

Table 8

F values and significance levels for ART test, for the effect of nutrients and soil moisture on rhizome carbon:nitrogen, rhizome percent nitrogen, total g N in rhizome tissues, and NUE in rhizome tissues.

* $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$

Source	Carbon:Nitrogen	Percent Nitrogen	Total N (g)	NUE
Nutrients	3.2135	1.5835	1.0035	2.5753
Moisture	49.0793***	49.3714***	3.7950	49.0213***
N:M	1.3827	1.6127	2.2467	1.4425

Whole Plant

Plants grown in saturated conditions exhibited higher NUE than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 9, Figure 18). Plants grown in treatments with added nitrogen exhibited lower NUE than those grown without added nutrients and those grown with the addition of phosphorus or the combination of nitrogen and phosphorus (main effect nutrients, $P = 0.016$, Table 9, Figure 18)

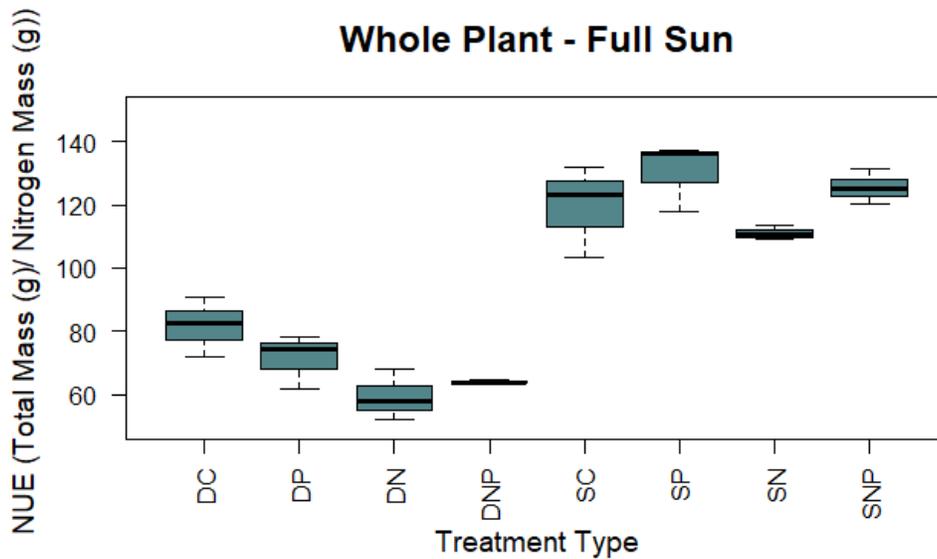


Figure 18

Box and whisker plot of NUE of whole plant. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=Phosphorus, N= Nitrogen, NP=nitrogen & phosphorus.

Table 9

F values and significance levels for ART test, for the effect of nutrients and soil moisture on whole plant NUE.

* p<0.05, ** p<0.01, ***p≤0.001

Source	NUE
Nutrients	4.6103*
Moisture	50.5756***
N:M	2.0345

Discussion

I made five main predictions for the response of *Arundo* to varying abiotic conditions, which were as follows: 1) *Arundo* will have higher values for performance-related traits, such as height and photosynthetic rate when grown under high nutrient, saturated soils without shading; 2) *Arundo* will have higher photosynthetic rate and lower NUE and WUE when grown in saturated, high nutrient soils; 3) *Arundo* will have lower biomass and number of stems when grown in the shade; 4) *Arundo* will exhibit growth-related responses indicating nutrient colimitation with N and P; 5) *Arundo* will allocate more biomass to stem and root tissue as opposed to leaf and rhizome tissue when grown in high nutrient, saturated soils without shading

Variation in light and soil moisture significantly influenced the performance-related traits of *Arundo*; however, nutrients were not found to significantly influence performance-related traits of the species in any of the treatment combinations. The lack of three-way interactions does not support prediction one; however, eight of the eleven response variables showed a significant interaction between soil moisture and shade. This

shows that tests of these resources independently may not fully explain how *Arundo* would respond to varying abiotic conditions. For example, across nutrient treatments, AGB increased in full sun and high soil moisture conditions, while AGB remained consistent across treatment types in low light conditions. These results show that soil moisture can have varying effects on AGB under different light conditions. This suggests that in disturbed sites where light competition has been eliminated and soil moisture is high (i.e., recently scoured riverbanks or riparian areas), *Arundo* can successfully establish and become dominant; otherwise, if the area remains shaded, *Arundo* will not maintain a competitive advantage regardless of other abiotic conditions. Studies of other invaders have suggested that height and or overall size may be a significant contributor to the overall invasive ability of a species (Van Kleunen 2010, Wang 2021). The invasiveness of both *Solidago canadensis* and *Conyza canadensis* were observed to be mainly influenced by overall plant height and, therefore, higher competition for light (Wang 2021). Previous studies of *Arundo* have shown that growth of the plant is closely related to soil moisture (Quinn 2006, Nackley 2014). Although capable of withstanding extreme drought and excessive soil moisture, *Arundo* seems to perform best in well-drained saturated soils (Perdue 1958); which was observed in this experiment *Arundo* has also been found to withstand the effects of intermittent shading for over two years (Spencer 2012). Though tolerant of shading, the effects have proven detrimental to the ability of *Arundo* to accumulate biomass (Lambert 2014); results of this study were consistent with these findings. While independent effects of soil moisture and shading have been reported, no studies prior to this study have reported a significant interaction between light availability and soil moisture. Studies of *Arundo*, and other invaders, have

found that these species perform best in high nitrogen conditions (Perdue 1958, Davis 2000, Maurer 2003); however, a significant effect due to nutrients was not observed in this experiment.

The highest WUE and photosynthetic rates occurred under full sun and saturated conditions. Nutrients were not found to play a significant role in the variation in these response variables. Organ specific nutrient use efficiency was consistently found to be highest in plants grown in saturated soils. Stems and roots exhibited changes in NUE in response to nutrient addition and interactions between soil moisture and nutrient addition. Stems were found to have the highest NUE in saturated soils with added nutrients, while roots had the highest NUE in saturated soils with no nitrogen addition. Further research into how *Arundo* utilizes nutrients is necessary to understand how environmental factors influence nutrient use efficiency. Due to the lack of a two-way interaction between soil moisture and nutrients, prediction two is unsupported. However, similar patterns to other response variables were observed in WUE and photosynthetic rate. WUE and photosynthetic rate exhibited the greatest response to a combination of high light and high soil moisture, suggesting that plants grown in full sunlight and saturated soil conditions can perform at higher efficiency than those in shaded environments. In agreement with my results, a study of *Capsicum annum* found that WUE increased with shading (Zhu 2012). A separate study found that *Actinidia deliciosa* var. *deliciosa* when under drought, had increased WUE when shaded (Montanaro 2009). However, the plants observed in the aforementioned study does not share growth habits, ecosystem types, or life-history strategies with *Arundo*. Drought stress is considered one of the most influential factors limiting photosynthetic rate—moderate leaf water deficits (relative

water content down 70%) can diminish photosynthesis in plants under drought stress (Giardi 1995). A study of perennial rhizome and bunchgrasses found that photosynthetic rate is highest in moderately saturated soils (Xu 2011).

On average, *Arundo* grown in shade tended to have lower AGB, BGB, and fewer tillers. This supports prediction three. As well as having a positive response to sunlight, both AGB and BGB exhibited an interaction between soil moisture and light availability. However, the total number of tillers was only influenced by shade and saw no effect due to the interaction between soil moisture and light availability. This suggests that *Arundo*, when colonizing areas with established canopy cover, may be at a disadvantage, especially if soils are dry. In a model of *Phalaris arundinacea* in restored sedge meadows, it was found that canopy cover may lead to the out competition of *Phalaris arundinacea* by native species if 1) the native species have lower light requirements than the invasive species and 2) the success of the invasive species is a result of quick establishment and competitive resource acquisition (Perry 2006). In a separate study, shading meant to represent riparian canopy cover suppressed the establishment of another invasive member of *Poaceae*, *Urochloa arrecta*. Results from this and other experiments are supported by the theory of native community resistance (Funk 2008). Given the negative response of *Arundo* to shading, it is likely that canopy cover may provide some defense against invasion.

The growth-related responses of *Arundo* to the addition of nitrogen and phosphorous did not support prediction four. Variables such as AGB, BGB, total tiller height, and number of tillers did not exhibit a response to nutrient addition, and therefore no evidence of nutrient colimitation was observed. These results conflict with current

understanding of how *Arundo* responds to nutrient addition. Some studies of *Arundo* to date have found that the species responds positively to nitrogen addition (Perdue 1958, Cano-Ruiz 2020). However, a lack of effect due to nitrogen addition has been observed in other experiments (Christou 2001, Quinn 2006). Quinn (2006) found that the number of new tillers, shoot, and rhizome biomass were not significantly affected by the addition of nitrogen. New rhizome length, however, was found to increase significantly in pots receiving nitrogen (Quinn 2006). Christou (2001) found that highly irrigated *Arundo* consistently yielded the highest biomass, but that application of nitrogen had no effect on biomass yields.

Although nutrients were not found to have significant interactions with other abiotic factors in the experiment for growth-related characteristics, they did influence the allocation of biomass to plant organs in *Arundo*. The linear mixed-effects model found that plants with added nutrients had higher shoot:root ratio and stem:leaf ratio suggesting that plants with higher nutrient availability allocated more resources to gaining height. This is further supported by MANOVA on the percent of total biomass allocated to stems, leaves, roots, and rhizomes. MANOVA found that plants grown in soils where nutrients were added had a higher proportion of biomass allocated to stem and root tissue than plants grown in control pots, specifically those with N & P added allocated the most biomass to stem and root tissue. MANOVA did not suggest any interactions between nutrient addition and other independent variables; however, a significant interaction between soil moisture and light availability was observed in biomass allocation to all plant organs. Plants grown in full sun and saturated conditions tended to allocate less biomass to leaf and rhizome tissue and more to stem and root tissue, which supports

prediction five. This tradeoff likely confers *Arundo* a competitive advantage over other plant species allowing it to obtain resources by gaining dominance both belowground and aboveground rapidly. These results are supported by Quinn (2006), who found that *Arundo* grown in pots treated with nitrogen allocated more biomass to aboveground biomass and root tissues. A study comparing two invasive and two native grass species found that the invaders tended to allocate more biomass to roots while natives allocated more biomass to the crown (Dong 2012). Xiangfeng (2012) found that invasive shrub *Rhus typhina* allocated more resources to increasing height compared to native and non-native non-invasive shrubs. Invasive species using high relative growth rates and increasing traits associated with resource acquisition is not uncommon and is often what gives invasive species a competitive edge over their native counterparts. This pattern, however, has not been observed in all invasive species. *Arundo* grown in CO₂ and N enriched environments was found to have 50% more biomass to rhizomes (Nackley 2017). Studies of invasive Hawaiian rainforest species showed no difference in biomass allocation under different light regimes (Pattison 1997). Understanding the life history strategies of individual invasive species can help develop an understanding of what ecosystems may be at the highest risk of invasion and under what conditions.

Nitrogen analysis of plant organs (leaves, stems, roots, and rhizomes) showed that *Arundo* grown in saturated conditions tended to have lower percent nitrogen and higher carbon: nitrogen values than those grown in dry soils across all organs. This effect may be present because plants grown in saturated treatments accumulated much more biomass and therefore assimilated more carbon than those grown in dry treatments. This would lead to the diffusion of nitrogen throughout the plant tissues leading to lower percent

nitrogen and higher carbon: nitrogen ratios. Leaf tissues were observed to have higher total assimilated nitrogen in leaves in saturated treatments than those grown in dry treatments. Higher nitrogen values in leaf tissues of saturated plants may indicate that more chlorophyll and Rubisco enzyme is present in the leaf (Fritschi 2007), leading to higher photosynthetic capability and better overall plant performance. A study of C:N ratios of *Arundo* leaf tissues found that leaf C:N ratios varied with season and that generally, C:N ratios were >17 after mid-May which is believed to fall outside of the range of C:N ratios preferred by aquatic herbivores (≤ 17) (Spencer 2005). Values for leaf C:N ratios in this experiment fell between ~ 0.5 and 25, with the highest C:N ratios occurring in plants grown in saturated soils receiving no additional nitrogen.

Arundo grown in saturated soils, especially plants grown in full sun, tended to have greater photochemical efficiency of PSII, suggesting that plants grown in saturated soils can photosynthesize more efficiently than those grown in dry soils. Long-term drought stress in *Pisum sativum* L. was shown to lower the photochemical efficiency of PSII (Giardi 1995). A study of *Gossypium hirsutum* L. grown in dry and irrigated conditions found that the plant had higher photochemical efficiency of PSII in dry treatments over irrigated treatments in the morning; however, as the day progressed, the photochemical efficiency of PSII decreased and was lower than irrigated plants (Pettigrew 2004). This suggests that the time at which measurements of PSII are taken may influence results. The operating efficiency of PSII (F_v/F_m), often used as a proxy for plant stress, was higher in plants grown in full sunlight than those grown in shade, indicating that plants grown in full sun were experiencing less stress than those grown in shade. A study of *Brassica oleracea* L. found that F_v/F_m in water-stressed and heat-stressed plants

decreased over a nine-day period of exposure to stressors; high light stress was not found to have a significant impact on values obtained for Fv/Fm (Ibaraki 2006). Observations of parameters associated with chlorophyll fluorescence are useful in determining stress responses of plants. Assessment of these variables in this experiment showed that light availability and sometimes soil moisture are the most influential factors in *Arundo*'s stress response.

Conclusions

More research into the abiotic factors that influence successful *Arundo* invasion and establishment is necessary to inform management strategies in Texas and other invaded states fully. This experiment began to elucidate some of the factors that contribute to the plant's success, as well as what strategies *Arundo* may use to gain a competitive advantage over other species. Interactions between soil moisture and light availability were found to have the most significant influence on the performance of *Arundo*. In addition, light availability was integral to the potential for dominance of the species. Though nutrients did not have as significant of an effect on the primary performance-related traits of *Arundo*, a more nuanced relationship was found in which increased nutrient availability may allow the plant to allocate more biomass to stem tissue, which would increase the plants' competitiveness for light.

Further investigation into the effects of nutrient addition on *Arundo* needs to be conducted to understand this relationship better. Overall, this experiment showed that *Arundo* responds most positively to conditions with ample soil moisture and light. We can use this information to continue to refine species management efforts.

II. THE EFFECTS OF FLOODING ON THE SPREAD OF *ARUNDO*

Introduction

To understand invasion and effectively manage ecosystems, it is imperative that all stages of the invasion process are studied. In addition, research on the invasion process needs to address how disturbance and establishment of new populations are linked (Hobbs 1995). One of the most widely accepted theories regarding the spread of *Arundo* in riparian habitats is the movement of plant fragments and clumps downstream as a result of flood events (Bell 1997, DiPietro 2002). This idea has partially informed management strategies for the species through the prioritization of management of upstream source populations. There is, however, dissent surrounding this theory. Boland (2008) argues that evidence for this mechanism of invasion is limited and anecdotal, suggesting that other anthropogenic activities such as construction and earth-moving activities are responsible for propagule dispersal and that inadequate research has been completed to support the mainstream framework of *Arundo* invasion. Dispersal of *Arundo* does not seem to be random; a study by Rieger et al. (1990) suggests that the highest concentration of *Arundo* colonies in San Diego County, California, occur closest to rivers. Rieger et al. (1990) cite flooding as a potential mechanism for the spread of *Arundo*; however, they acknowledge that earth-moving activity and equipment can contribute to introduction of the species to novel habitats. The fragmentation of *Arundo* by earth-moving equipment, mowing, and animal disturbance also has the potential to dislodge *Arundo* fragments allowing for them to be carried downstream by flood events, potentially linking these two processes in their contribution to the spread of *Arundo*. Anecdotal evidence acquired through personal communication with Sky Lewey of the

Nueces River Authority suggests that fill dirt used in construction (including dirt used at bridge construction sites along rivers) may also contribute to the introduction of *Arundo* to novel sites.

Riparian ecosystems are known to have a high diversity of species. The dynamic hydrological, geological, ecological, and biogeochemical processes in these habitats all contribute to a variety of life-history strategies (Naiman 1993). Natural rivers—those allowed to follow natural hydrogeographic patterns—will reset patterns of succession, leaving patches of bare ground following scouring by floods. The introduction of invasive species to these areas can disrupt habitat function to the point of producing novel successional sequences (Vitousek 1990). *Arundo* can disrupt natural successional patterns, and the stands can become climax communities in riparian ecosystems (Rieger 1990). *Arundo* has been shown to reduce native riparian diversity by forming dense monotypic stands that outcompete native species (McGaugh 2006, Yang 2011, Racelis, 2012).

Understanding large-scale population dynamics of plant species and their relation to disturbance events using traditional methods, such as hand-mapping or aerial photography, can be time-consuming and limited in scope (DiPietro 2002). These methods can be further complicated by private land ownership and difficulty accessing riparian habitats. There is a need for reliable techniques to monitor the spread of invasive species and the effects of control efforts (DiPietro 2002). Remote sensing offers an alternative to these methods allowing researchers to monitor aquatic and riparian species over relatively large spatial and temporal scales (Ackelson 1987, Hestir 2008). In addition, classification and mapping of vegetation provide insight for the management

and restoration of ecosystems by allowing researchers to quantify and visualize vegetation cover in large areas over continuous periods (Egbert 2002, Xie 2008). Remote sensing offers many advantages for monitoring and detecting invasive species, with perhaps the most important feature being the ability to detect and monitor changes in land cover (Joshi 2004). Remote sensing can also be used to evaluate factors contributing to invasion success; for example, Bren (1992) evaluated invasion of *Eucalyptus camaldulensis* using aerial photography over 45 years and found that hydroperiod played a significant role in the spread of this invasive species. In recent years, the number of publications using GIS and remote sensing to monitor and detect invasive species has significantly increased (Joshi 2004, Ahmed 2020).

Arundo donax in Remote Sensing Literature

There have been many attempts to map weedy or invasive plant species using remote sensing (Asner 2008, Somodi 2012, Bourgeau-Chavez 2013). Several of these studies utilize spectral response—unique color characteristics of the plant species of interest that help to distinguish it from surrounding vegetation (Lass 1996, O'Neill 2000). These studies rely on the reflectance characteristics of the plant in question to be detectable with remote sensing equipment.

Several studies to date have attempted to identify the spectral response of *Arundo* in both the vegetative and senescent periods. In Portugal, during the vegetative period, *Arundo* was found to be the most spectrally separable from surrounding vegetation in the red-edge and visible regions (Fernandes 2012). With the use of hyperspectral remote sensing imagery in California, *Arundo* could be identified remotely with 71-95% accuracy using bands of visible and infrared reflectance (DiPietro 2002). Oakins (2001)

was also able to identify the spectral response of *Arundo* with 94.96% accuracy and suggested the red, green, and near-infrared bands contained the most spectrally distinct information.

It is important to note that many of these findings used higher resolution imagery than will be used in this study. Spatial resolution is an important factor that must be considered when mapping vegetation at the species level. One study suggested that higher resolution imagery would be more successful at detecting *Arundo* and that a pixel size of >4 m would decrease the detectability of *Arundo* (Oakins 2001). Though high resolution imagery in most cases is preferable to low resolution imagery it is often not publicly available and can be costly to acquire. Sensors with coarser resolutions such as Landsat-8 which are publicly available can, however, be effective in mapping species if the species being studied occupies a large area and is relatively homogenous, both characteristics that frequently apply to *Arundo* infestations (Bradley 2004).

Hypothesis

This study aims first to identify the spectral response of *Arundo* in central Texas watersheds using supervised classification methods. Studies using remote sensing to identify *Arundo* rarely apply the data obtained from classification to monitor populations in occupied watersheds.

Through the use of remote sensing and records of major flood events in central Texas, the goal of this study is to determine to what extent flooding influences the spread of *Arundo* in riparian areas. Understanding how *Arundo* invades new habitats can inform management strategies, aiding in determining where to prioritize management efforts by

identifying high vulnerability areas or areas with the greatest current or potential impacts on habitat quality.

If *Arundo* is found to be spectrally distinct from other riparian vegetation, then the next phase of the study will seek to determine if the floods of May 2015 contributed significantly to the spread of *Arundo* in riparian areas in central Texas. While previous studies have successfully recognized the spectral response of *Arundo* as distinct from other riparian vegetation types, none have yet applied their findings to evaluate the widely accepted theory that the primary spread mechanism for *Arundo* is downstream spread during flood events and subsequent colonization of new areas.

Although there are field observations of flood-driven dispersal in Texas, and this has been hypothesized as a primary driver of *Arundo* dispersal (Bell 1997, DiPietro 2002, Rieger et al. 1990), given my firsthand field experience with the plant's robust and difficult to fragment rhizome network and hardened adult stems, as well as the dissenting opinions of Boland (2006, 2008), I anticipate that there will not be a significant increase in the number of *Arundo* populations following a major flood event.

1) If *Arundo* is spread via downstream colonization of fragments following flood events, then a noticeable increase in the number of populations of downstream riparian *Arundo* will be detected with remote sensing within three years after the 2015 flood event.

Methods

To understand how to best manage *Arundo*, a general framework for how the colonization of new areas occurs must be established. The current theory that flooding is the primary spread mechanism, though anecdotally confirmed, lacks the evidence necessary to consider transport of propagules downstream as the primary driver of

Arundo colonization. This study aims to evaluate the leading theory that *Arundo* colonizes new areas following the transport of propagules downstream by floods.

To identify the severity of flooding in May 2015, the United States Army Corps of Engineers (USACE) Antecedent Precipitation Tool and Palmer Drought Severity Index were used to determine if the climatological and precipitation conditions were typical for the time period. The USACE antecedent precipitation tool is an open-source tool that allows for the comparison of antecedent rainfall conditions in a given location relative to the “normal” rainfall conditions of the preceding thirty years. The tool also provides insight into drought conditions and assesses whether a specific time period was under wet or dry conditions. This information was used to support anecdotal evidence and USGS flood gage evidence of the major flood event that occurred in May of 2015. The tool also provided insight into the climatological conditions of the years preceding and following the May 2015 flood.

I attempted to identify the spectral response of *Arundo* in central Texas and determine if it was spectrally separable from other riparian species using moderate-resolution remote sensing data. To do this, a dataset of known populations of *Arundo* acquired from the Blanco River by Texas Parks and Wildlife via aerial surveys was obtained. Next, 2015 Landsat-8 imagery of selected locations were downloaded from the USGS Earth Explorer Database. Data were clipped to the 100-year floodplain based on the Federal Emergency Management Agency's (FEMA) National Flood Hazard Data. Using known sites of the species 30 m or larger, a training dataset composed of known *Arundo* populations and Texas Natural Resource Information System (TNRIS) orthoimagery to validate known populations of *Arundo*, water, bare ground, and "other"

vegetation classes were created. The classification model was trained using known locations from TPWD and TNRIS orthoimagery was used for validation. Additional data layers calculated from Landsat-8 imagery containing spectral indices such as the Normalized Difference Vegetation Index (NDVI) and the Red:Green ratio were added in an attempt to enhance spectral separability of *Arundo* (Rouse 1974, den Dulk 1989, Vescovo 2008). Classes were determined not to be spectrally separable from each other through the use of transformed divergence separability cell arrays and feature space plots. Separability cell arrays showed that the spectral response of *Arundo* was not significantly different from other vegetation with or without the use of spectral indices. Feature space plots revealed overlap between the *Arundo* class and the “other” vegetation class. Therefore, the supervised classification using maximum likelihood was unable to be performed.

Upon finding supervised classification to be unsuccessful, unsupervised classification methods using ISODATA were performed using the added NDVI and Red:Green ratio layers. Once completed, the computer-generated classes containing *Arundo* were reclassified using the cluster busting technique up to two times. Accuracy assessments using error matrices, accuracy totals, and kappa statistics were performed on unclassified imagery to determine the reliability of the classified pixels. Error matrices revealed that cluster busting techniques and the inclusion of alternative spectral indices did not enhance the spectral separability of *Arundo* from other vegetation. Kappa statistics for these clustering methods were found to be close to zero, indicating that the classification schema was not significantly better than if that data were grouped by chance.

Unsupervised classification was found to yield unreliable results; therefore, visual analysis and digitization of *Arundo* populations was performed using TNRIS orthoimagery. Google Earth imagery was used for visual confirmation of *Arundo* locations. One reach of both the Guadalupe and Medina Rivers, approximately 40 river kms each, were visually analyzed, and *Arundo* populations were digitized for the years 2010, 2012, 2014, 2016, and 2018. The total area and the total number of populations was determined, and the rate of spread between image acquisition dates was calculated. To analyze the accuracy of the digitization of *Arundo* by hand, a combination of ground-truthing and the use of high-quality drone imagery was used. Drone footage of a 4 km stretch of the Blanco River from the Blanco Shoals Natural Area where populations of *Arundo* had been confirmed by ground-truthing was collected in fall of 2021. Due to the lack of TNRIS imagery for the year, the 2021 expected number of patches in the area for that year was extrapolated from the rates of *Arundo* patch increase from the years 2014 to 2020 observed with available TNRIS imagery. Given the calculated rate of patch increase from 2014 to 2020, it was expected that six patches of *Arundo* would be identified within the 4 km stretch of the Blanco River in 2021. With 2021 drone imagery, 10 *Arundo* patches were identified. This indicates a 60% accuracy rate for patch identification using TNRIS imagery. In this accuracy assessment, *Arundo* was never incorrectly identified, meaning that the estimations provided by this experiment tend to underestimate the total patch number.

Z-values for total patch area and total patch size were calculated and the average of patch size and area was taken for the years before 2015 and the years after 2015. Paired t-Tests were performed on these values to determine significance. and the rate of

change in total area for time periods before and after the 2015 flood. R (version4.1.0) was used for all analyses.

Results

Over the course of the eight-year study period, USGS flood gages reported periods of high gage heights in the spring of each observed year on the Medina and Guadalupe rivers. The observed stretch of the Medina River experienced higher than average gage heights of 25 ft during the extreme rain events of 2015, while the observed stretch of the Guadalupe River experienced increased gage heights of 10 ft. (Figure 19). Increased gage heights were also observed in 2016 (Figure 19). The Palmer Drought Severity Index class for the Medina and Guadalupe Rivers in 2015 was “Severe Wetness” (Table 10). The Antecedent Precipitation Tool class for both the Medina and Guadalupe Rivers in 2015 was “Wetter than Normal.” Prior to 2015, both sites experienced extreme to moderate drought, followed by a year of severe wetness in 2016 and normal conditions in 2017 (Table 10).

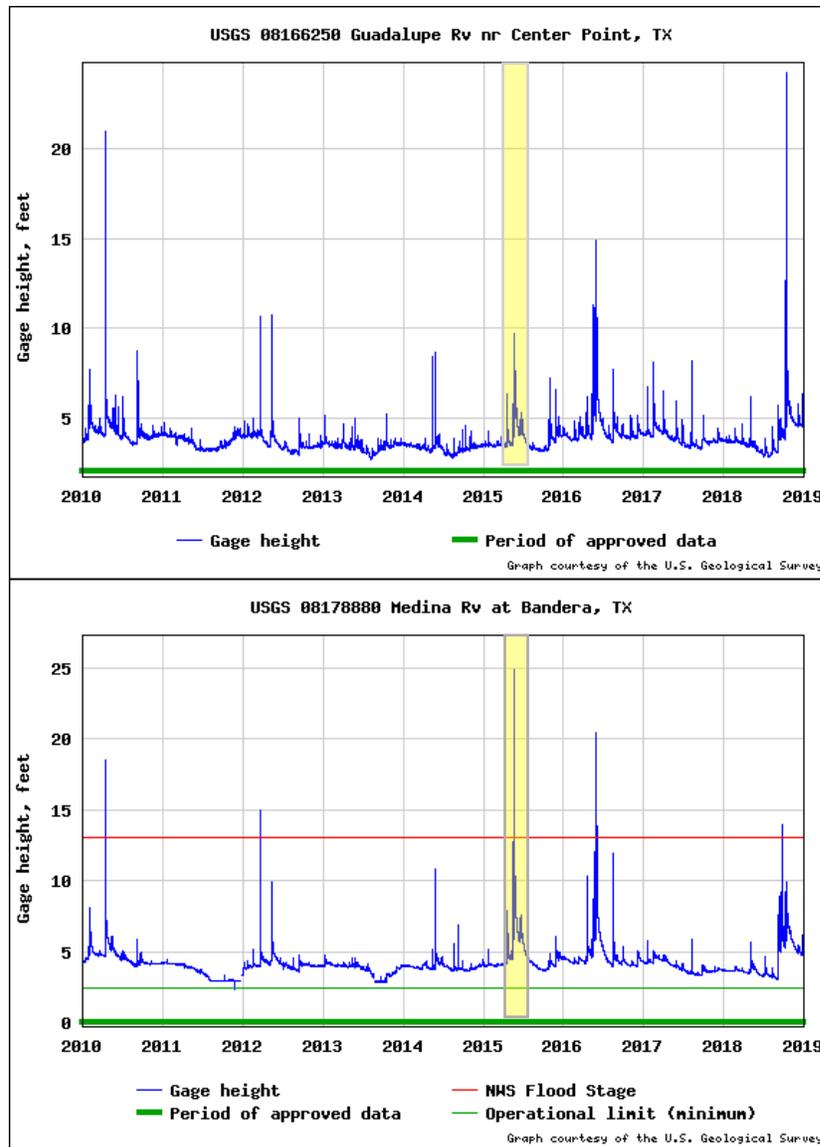


Figure 19

Graphs of USGS gage height for USGS stations along observed stretches of the Guadalupe and Medina rivers between 2010 and 2018. Highlighted portion shows the spring 2015 flood event.

Table 10
Palmer Drought Severity Index (PDSI) and USACE Antecedent Precipitation Tool class for observed stretches of river in May from 2010 to 2018.

River	Date	PDSI Class	Antecedent Precipitation Tool Class
Medina	May 2010	Moderate Wetness	Wetter than Normal
Medina	May 2011	Extreme Drought	Drier than Normal
Medina	May 2012	Moderate Drought	Wetter than Normal
Medina	May 2013	Severe Drought	Drier than Normal
Medina	May 2014	Moderate Drought	Normal Conditions
Medina	May 2015	Severe Wetness	Wetter than Normal
Medina	May 2016	Severe Wetness	Normal Conditions
Medina	May 2017	Normal	Normal conditions
Medina	May 2018	Moderate Drought	Normal Conditions
Guadalupe	May 2010	Moderate Wetness	Wetter than Normal
Guadalupe	May 2011	Extreme Drought	Drier than Normal
Guadalupe	May 2012	Moderate Drought	Wetter than Normal
Guadalupe	May 2013	Severe Drought	Normal Conditions
Guadalupe	May 2014	Moderate Drought	Normal conditions
Guadalupe	May 2015	Severe Wetness	Wetter than Normal
Guadalupe	May 2016	Severe Wetness	Wetter than Normal
Guadalupe	May 2017	Normal	Drier than Normal
Guadalupe	May 2018	Moderate Drought	Normal Conditions

Guadalupe River

In the observed stretch of the Guadalupe River, the total area of *Arundo* patches was found to increase by about 831% from 2010 to 2018 (Figure 20). The largest rate of increase in total area of *Arundo* was observed between 2014 and 2016, where the area of *Arundo* increased from 2,890 m² to 14,074 m², a 5,592 m² yr⁻¹ increase in total patch

area. During this period the average patch size of *Arundo* was found to increase significantly from $\sim 60 \text{ m}^2$ to $\sim 204 \text{ m}^2$. This increase coincided with periods when climatic conditions were found to be wetter than normal following a moderate drought and when flood gage peaks were observed. Total area was found to decrease between the years 2010 to 2012, in which total area of *Arundo* patches decreased by $171 \text{ m}^2 \text{ yr}^{-1}$. The decrease in total *Arundo* area corresponds with periods of drought and drier than normal conditions.

The total number of *Arundo* patches in the Guadalupe River from 2010 to 2018 was found to increase by about 177%. The largest increase in total patch number was observed from 2016 to 2018, where total number of patches increased by $19.55 \text{ patches yr}^{-1}$. During this time, the observed area was experiencing wetter than normal conditions, followed by normal-dry conditions. During this period, there were flood-gage peaks ranging from 15 to 25 ft. The total number of patches decreased by $5 \text{ patches yr}^{-1}$ from 2010 to 2012, which also corresponded with severe to extreme drought conditions.

Medina River

The total area of *Arundo* patches in the Medina River from 2010 to 2018 increased by 874%. The largest increase in total area, $552 \text{ m}^2 \text{ yr}^{-1}$, was observed between 2014 and 2016, in which the area experienced a moderate drought followed by extremely wet conditions. During this period the average patch size of *Arundo* was found to increase significantly from $\sim 13 \text{ m}^2$ to $\sim 102 \text{ m}^2$. Flood gage peaks were observed in 2014, 2015, and 2016 with the highest gage height occurring in 2015 at about 25 ft. Total *Arundo* area decreased from 2010 to 2012 and from 2012 to 2014. The most significant

decrease occurred from 2010 to 2012, in which total *Arundo* area decreased by 32 m² yr⁻¹, during which conditions were drier than normal.

In the observed stretch of the Medina River, the total number of *Arundo* patches was found to increase by 200% from 2010 to 2018. The largest percent increase in total patch number was by 2 patches yr⁻¹, which was observed between 2012 and 2014, during which the area was experiencing drought and drier than normal conditions preceded by wetter than normal conditions. Two moderate flood gage peaks occurred over the three-year period. There was no decrease in patch number observed in the Medina River; however, from 2010 to 2012, there was no increase in the total number of patches. During this period, the area was experiencing a drought, and two of the three years within the period experienced a flood gage peak.

Table 11

Tables of total calculated area and total number of patches identified along the observed stretches of the Medina & Guadalupe rivers from 2010 to 2018.

Guadalupe			
<i>Year</i>	<i>Total Arundo Area (m²)</i>	<i>Total Patch Number</i>	<i>Average Patch Size (m²)</i>
2010	1,918.804	39	49.201
2012	1,576.000	29	54.344
2014	2,890.852	48	60.226
2016	14,074.488	69	203.978
2018	18,012.182	108	166.779

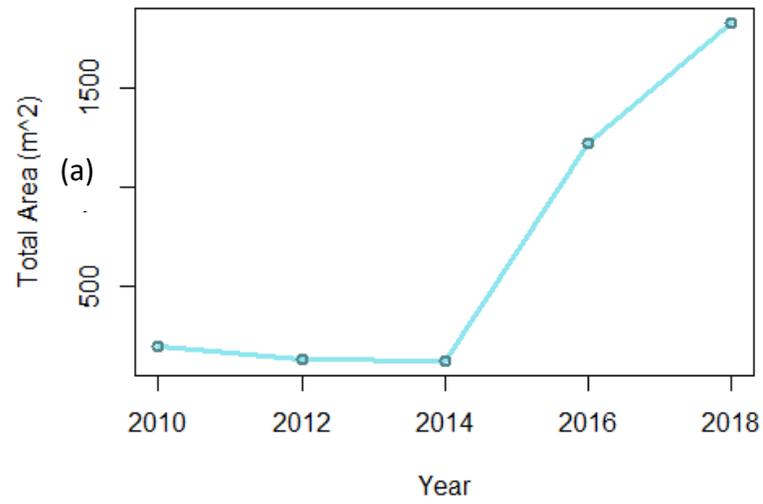
Medina			
<i>Year</i>	<i>Total Arundo Area (m²)</i>	<i>Total Patch Number</i>	<i>Average Patch Size (m²)</i>
2010	188.552	5	37.710
2012	123.470	5	24.694
2014	116.530	9	12.947
2016	1,221.091	12	101.757
2018	1,837.229	15	122.481

Table 12

P-value, test statistic, upper and lower confidence intervals for paired t-tests of total area, and total number of patches for the Guadalupe and Medina rivers.

	P-Value	Test Statistic	95% Confidence Interval - Lower	95% Confidence Interval - Upper
Total Patch Area	0.0069	92.5217	-2.0168	-1.5297
Total Patch Number	0.0088	572.5356	-1.8966	-1.3312
Rate of Change in Area	0.0245	25.9844	-2.4762	0.8498
Rate of Change in Patch Number	0.2898	2.0429	-6.7882	4.9077
Average Patch Size	0.0031	203.9524	-1.8957	-1.6734

a)



b)

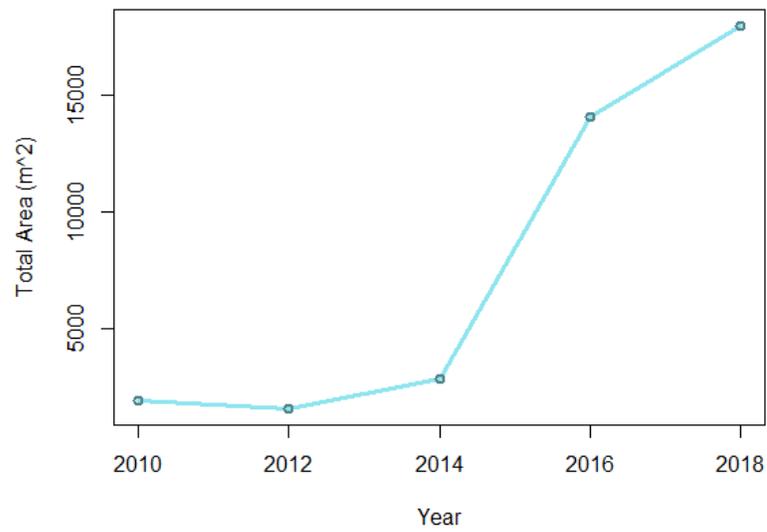
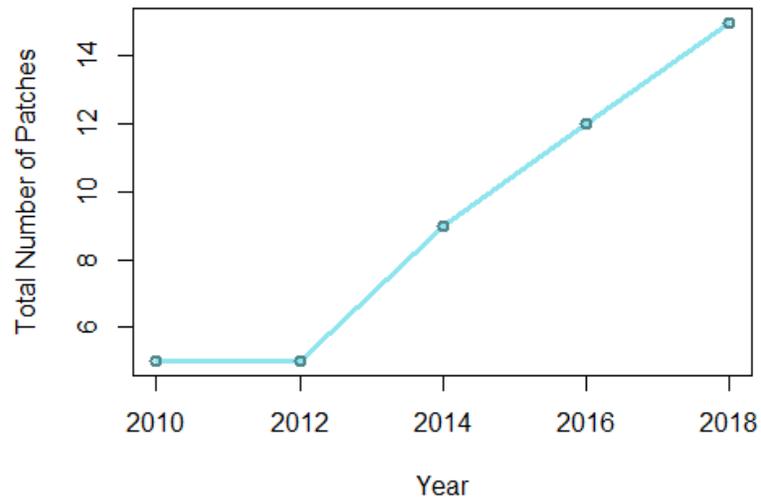


Figure 20

Figures of total calculated area of *Arundo* patches identified within the a) Medina & b) Guadalupe Rivers from 2010-2018.

a)



b)

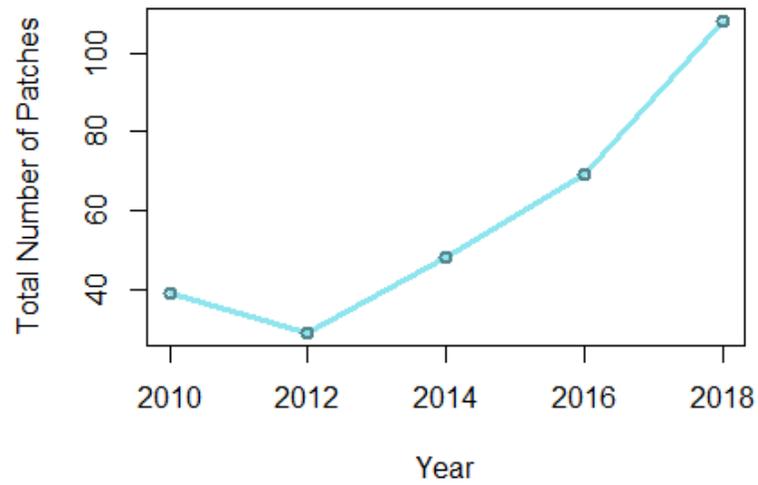
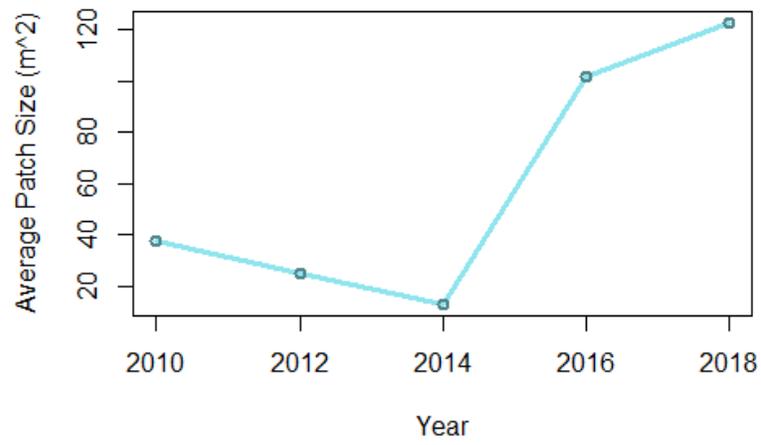


Figure 21

Figures of total number of *Arundo* patches identified within the a) Medina & b) Guadalupe Rivers from 2010-2018.

a)



b)

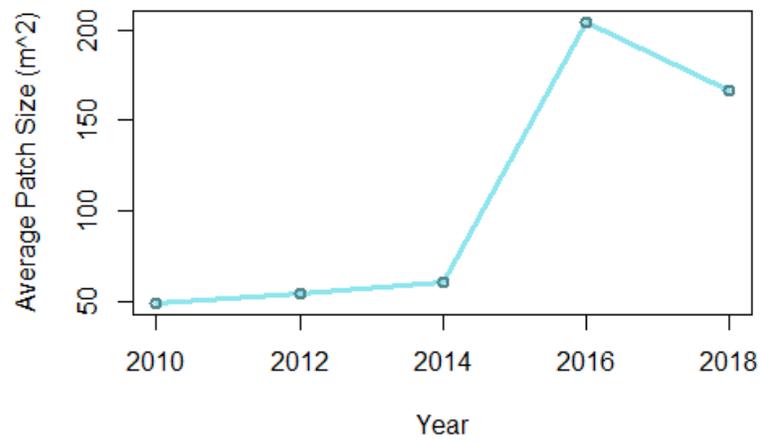


Figure 22

Figures of average *Arundo* patch size within the a) Medina & b) Guadalupe Rivers from 2010-2018.

Discussion

I predicted that if *Arundo* is spread via downstream colonization of fragments following flood events, then a noticeable increase in the number of populations of downstream riparian *Arundo* will be detected with remote sensing within three years after the 2015 flood event. The total number of populations of *Arundo* and total area of *Arundo* were found to increase significantly between 2014 and 2016. T-tests revealed that the total patch area of *Arundo* after 2015 was significantly larger than the total area of *Arundo* before 2015 ($P = 0.0069$, Table 12). Likewise, the total patch number of *Arundo* before 2015 was found to be significantly more than the total patch number after 2015 ($P = 0.0088$, Table 12). Average patch size before 2015 was also found to be larger than after 2015 ($P = 0.0031$, Table 12). May 2015 experienced higher than average precipitation along with flood gage peaks in the observed stretches of the Medina and Guadalupe Rivers. The largest observed increases in total *Arundo* area in both the Medina and Guadalupe Rivers occurred between 2014 and 2016, during which there was increased rainfall and a major flood event. The largest observed rate of increase in the number of *Arundo* patches occurred between 2012 and 2014 for the Medina years, in which there were severe droughts and precipitation was less than average to normal. The rate of increase in number of *Arundo* patches, however, stayed consistent after 2014. The largest observed rate of increase in the number of *Arundo* patches in the Guadalupe occurred between 2016 and 2018. During this time, the observed area was experiencing wetter than normal conditions, followed by normal-dry conditions.

The pattern of *Arundo* increasing patch size under wet conditions suggests that wetter conditions allow *Arundo* to expand existing populations. The growth and success

of *Arundo* has been closely tied to soil moisture; however, the species is understood to be highly drought-tolerant, often able to thrive in floodplain terraces where soil moisture is relatively low (Perdue 1958, Quinn 2006, Lambert 2010, Nackley 2014). More thorough investigation into the factors influencing the spatial dynamics of the spread of *Arundo* is required to fully understand how flooding and other climatic variables contribute to the spread of this species.

One of the most commonly accepted frameworks for understanding the spread of *Arundo* in riparian habitats is the movement of plant fragments and propagules downstream following flood events (Bell 1997, DiPietro 2002). Else (1996) recorded that *Arundo* populations tended to increase in number as distance from river headwaters increased, supporting the idea that *Arundo* propagules spread downstream. *Arundo* can typically be found along disturbed stream banks, stream beds, lakes, and other wet areas, further supporting the paradigm that the species colonizes new areas via water-mediated dispersal (Perdue 1958, Bell 1997). The idea that invaders colonize new areas via downstream dispersal of propagules can be seen in other experiments. Bren (1992) found that hydroperiod played a significant role in the spread of *Eucalyptus camaldulensis* over the course of 45 years using aerial photography. A study of *Impatiens grandiflora* found that flooding accounts for the spread and dominance of the species in river corridors as flooding facilitates seed dispersal, increases nutrient availability, and causes disturbance (Čuda 2007).

Results from this experiment indicate flood events do influence the spatial dynamics of *Arundo* populations. In years that experienced flooding and wetter than normal conditions, *Arundo* spread at a greater rate. Results from chapter one and other

studies of the plant indicate that the species thrives in high soil moisture (Perdue 1958, Quinn 2006). When major flood events scour riverbanks and high-water levels lead to prolonged inundation, *Arundo* may be better equipped to survive extended periods of flooding than other riparian species allowing it to persist and potentially colonize larger expanses of area surrounding existing stands. Excluding 2010 to 2012, *Arundo* patch number was observed to increase at a relatively constant rate over the course of the experiment. More investigation is required to understand the drivers of *Arundo* colonization in riparian corridors.

Conclusions

The goal of this thesis was to determine the environmental conditions under which *Arundo* was most likely to colonize and invade a new area. A two-step approach using a greenhouse experiment and remote sensing methodology was used to develop an understanding of where *Arundo* may be the most likely to become invasive and how it may colonize new areas. Chapter one addressed the conditions under which *Arundo* performed the best and how light, nutrient, and moisture availability contribute to the growth, biomass allocation, and stress responses of *Arundo*. Moisture and shade were found to have the largest effect on overall size and growth of the plant. This suggests that *Arundo* is likely to perform the best under conditions with high light availability and soil moisture in areas, such as recently scoured riverbanks where there is little to no canopy cover and high soil moisture. Nutrient availability had minimal effect on overall plant size, but biomass allocation patterns changed in response to the addition of nitrogen and phosphorus. Plants grown with additional nutrients tended to allocate more biomass to stem and root tissues, suggesting that when provided with additional resources, *Arundo*

will increase its below-ground and above-ground competitive ability. By allocating more biomass to stem tissue and increasing height, *Arundo* can maximize light capture by dominating the canopy of colonized areas and outcompeting shorter statured species. Similarly, by increasing the amount of biomass allocated to roots *Arundo* can dominate belowground spaces and maximize resource capture of water and nutrients, outcompeting slower growing species or species that allocate less biomass to belowground organs.

Chapter two found that the rate of increase in *Arundo* area and patch size is related to intense flood events and precipitation that is higher than average. Results from this experiment are supported by the results found in chapter one that suggested *Arundo* would respond positively to increased light and moisture availability which can be produced by the scouring of banks by extreme flood events. Findings from chapter two support the current paradigm of downstream colonization of *Arundo* propagules by flood events.

Overall, this experiment found that the success and invasive ability of *Arundo* is primarily influenced by soil moisture and light availability, both of which are abiotic factors created by extreme flood events. Although nutrient addition was not observed to have an impact on the performance related traits of the species it was found to influence the biomass allocation and potential competitive ability of the plant. Further investigation into how anthropogenic disturbances such as land moving equipment, mowing, runoff, and bank channelization influence the conditions necessary for *Arundo* to thrive is necessary to understand how this plant and other large-statured invasive grasses may invade ecosystems. This thesis has applications for informing management strategies of *Arundo* in central Texas. Having insight into the abiotic factors that influence the spread

of this species can help to develop management plans that prioritize high risk areas and can provide justification and support for state and federal agencies to implement management efforts that combat *Arundo* colonization. This thesis also has implications for the development of ecosystem modeling. Information on the response of *Arundo* to various abiotic conditions and the spatial and colonization dynamics of the species can help to develop comprehensive models that further our understanding of wetland invasion dynamics.

APPENDIX SECTION

Regressions

Initial rhizome weight x AGB

Initial rhizome weight was not found to be a significant predictor of aboveground biomass ($P>0.05$).

Initial rhizome weight x BGB

Initial rhizome weight was found to be a significant predictor of below-ground biomass ($P=0.026$, Figure 23). Initial rhizome weight explained about 4% of the variability in total BGB. This suggests that higher initial rhizome weight is associated with greater total belowground biomass.

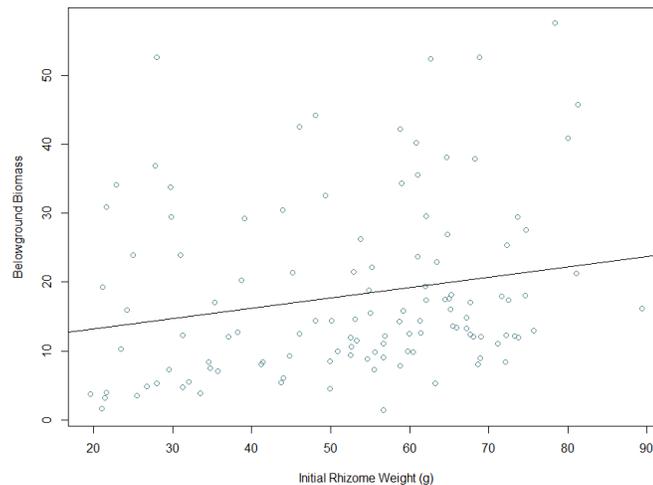


Figure 23
Plot of BGB as a function of Initial Rhizome Weight

Percent Phosphorus & Carbon:Phosphorus

Leaves

Arundo grown in saturated conditions exhibited higher percent phosphorus, and lower C:P ratios in leaf tissues than those grown in dry conditions no difference was observed between nutrient treatments ($P=0.003$, Figure 24).

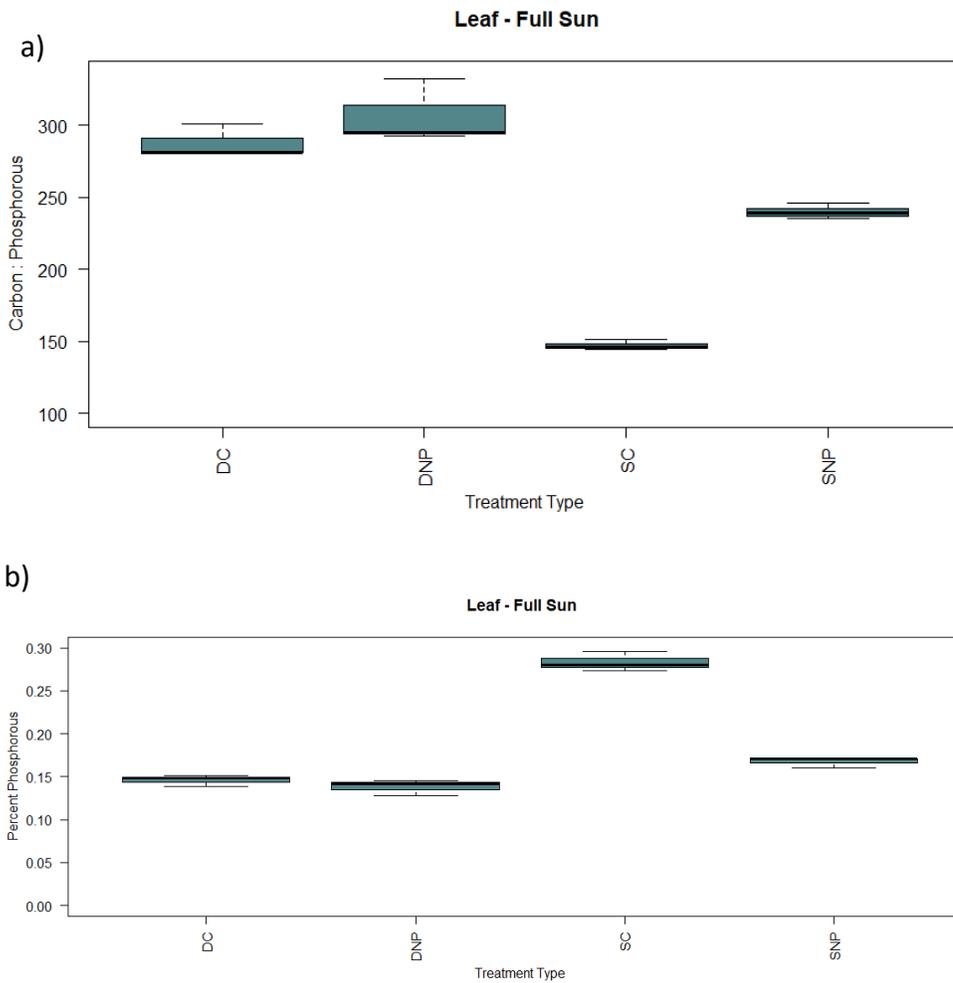


Figure 24
 Box and whisker plots of a) C:P ratio of leaf tissues, b) Percent phosphorus of leaf tissues, Treatment combinations along the X axis: D=dry,S=saturated, C= control, , NP=nitrogen & phosphorus.

Stems

Plants grown saturated conditions exhibited lower percent phosphorus, and higher C: P ratios in stems than those grown without added nitrogen and phosphorus no difference was observed between nutrient treatments ($P=0.016$, Figure 25).

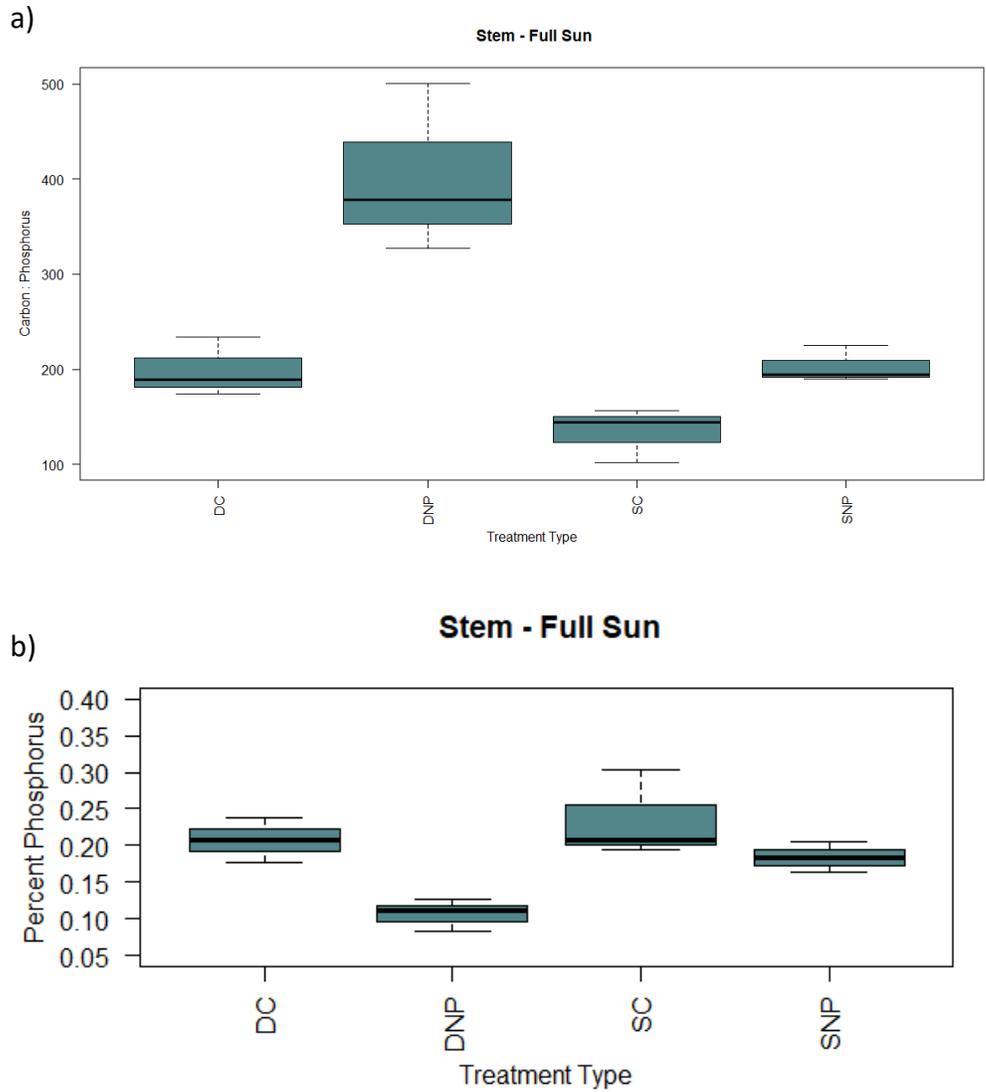


Figure 25
 Box and whisker plots of a) C:P ratio of stem tissues, b) Percent phosphorus of stem tissues, Treatment combinations along the X axis: D=dry, S=saturated, C= control, , NP=nitrogen & phosphorus.

Roots

No difference was observed in C:P ratios or percent phosphorus of root tissues between moisture or nutrient treatments in *Arundo* (Figure 26).

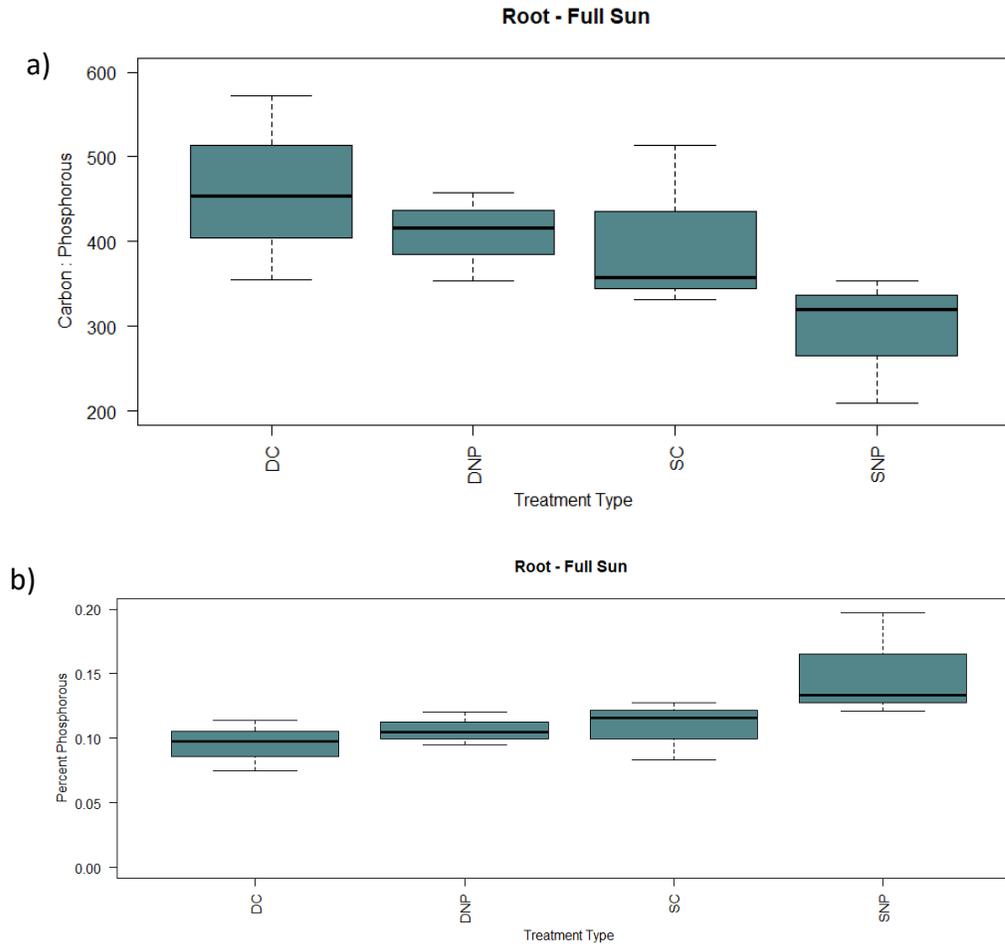


Figure 26

Box and whisker plots of a) C:P ratio of root tissues, b) Percent phosphorus of root tissues, Treatment combinations along the X axis: D=dry, S=saturated, C= control, , NP=nitrogen & phosphorus.

Rhizomes

Arundo rhizomes grown in saturated conditions exhibited higher percent phosphorus, and lower C:P ratios than those grown in dry conditions, while no difference was observed between nutrient treatments ($P=0.010$, Figure 27).

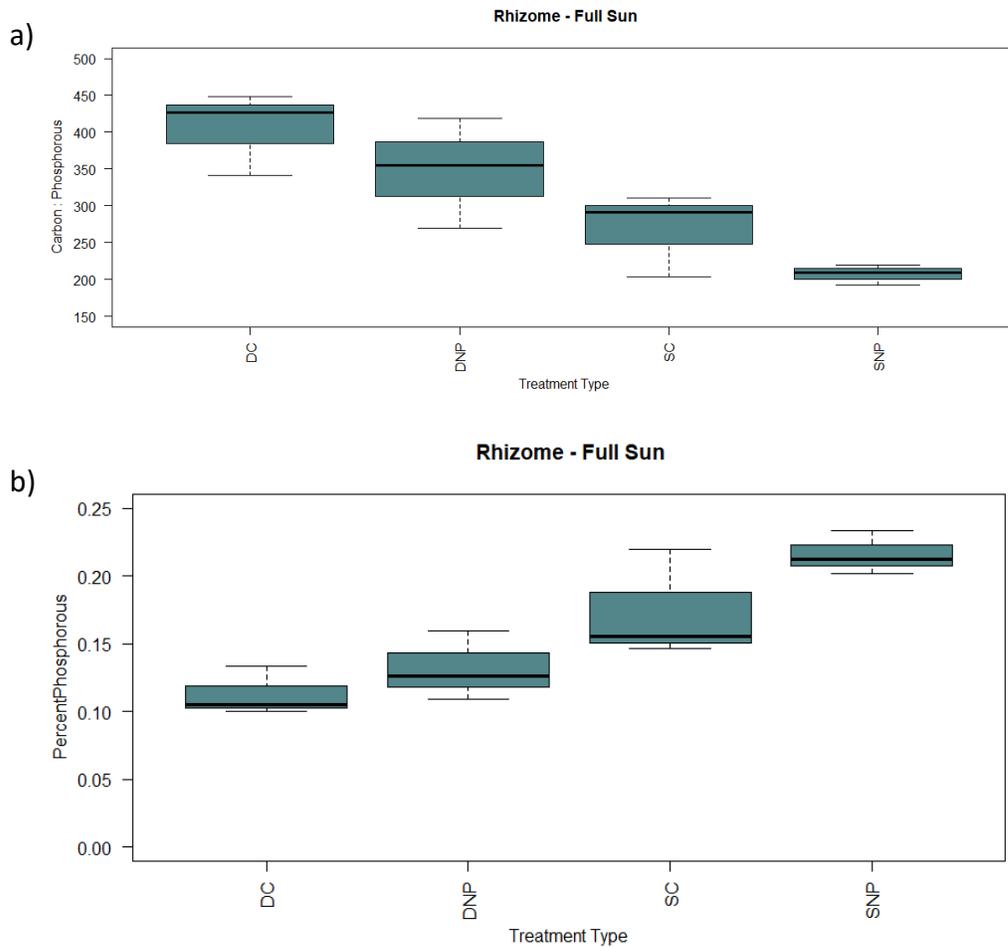


Figure 27

Box and whisker plots of a) C:P ratio of rhizome tissues, b) Percent phosphorus of rhizome tissues, Treatment combinations along the X axis: D=dry, S=saturated, C= control, , NP=nitrogen & phosphorus.

Non-Parametric Tests

Phosphorus Use Efficiency

Plants grown in saturated conditions exhibited lower PUE than those grown in dry conditions (main effect moisture, $P < 0.001$, Table 3, Figure 6). Plants grown in treatments with added nitrogen and phosphorous exhibited no difference in PUE than those grown without added nutrients (Table 13, Figure 28)

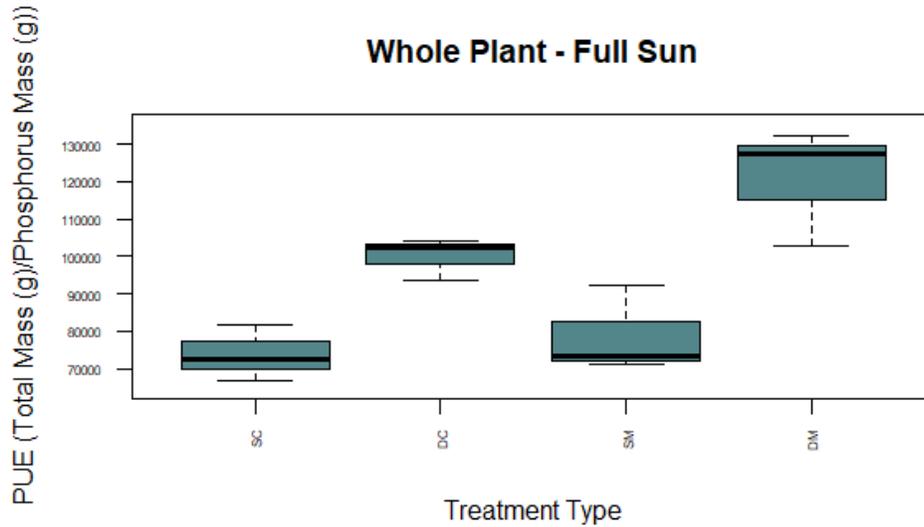


Figure 28
Box and whisker ploof Phosphorus Use Efficiency. Treatment combinations along the X axis: D=dry, W=wet, S=saturated, C= control, P=Phosphorus, N= Nitrogen, NP=nitrogen & phosphorus.

Table 13
F values and significance levels for ART test, for the effect of nutrients and soil moisture on whole plant PUE.
* $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$

Source	Phosphorus Use Efficiency
Nutrients	4.114
Moisture	25.920***
N:M	1.406

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