DYNAMICS OF WATER USE AND RESPONSES TO HERBIVORY IN THE INVASIVE REED, *Arundo donax* (L.)

A Thesis

by

DAVID AMI WATTS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2009

Major Subject: Rangeland Ecology and Management

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Approved by:

Chair of Committee,	Georgianne Moore
Committee Members,	David Briske
	Harry Cralle
Head of Department,	Steven Whisenant

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ABSTRACT

Dynamics of Water Use and Responses to Herbivory in the
Invasive Reed, *Arundo donax* (L.). (May 2009)
David Ami Watts, B.S., University of California, Los Angeles
Chair of Advisory Committee: Dr. Georgianne W. Moore

The first objective of this study was to investigate the role of an invasive grass species, *Arundo donax* (L.), on the hydrologic cycle. At a site on the Rio Grande in South Texas, we measured the gas exchange of carbon dioxide and water vapor at the leaf scale and structural characteristics, such as leaf area and shoot density, at the stand scale. In order to assess the effect of water availability, this study was conducted along transects perpendicular to the edge of the river along a potential moisture gradient. The second objective was to quantify the effect of two herbivores, an armored scale, *Rhizaspidiotus donacis* (Leonardi), and a stem-galling wasp, *Tetramesa romana* (Walker),on the photosynthetic and transpiration rates of *A. donax*. Leaf gas exchange measurements were made to determine the direction and magnitude of the effect on physiological processes and by what mechanisms any effects arose.

Stands of *A. donax* used approximately 9.1 ± 1.1 mm of water per day. This rate of water use was at the high end of the spectrum for plants. The major controls on stand scale transpiration were evaporative demand, leaf area index, and water availability. During two summer seasons, stand scale transpiration varied greatly, following the pattern of variability in precipitation, suggesting that recent rainfall constituted a significant proportion of the water taken up by this species.

Herbivory by a stem-galling wasp and a sap-feeding scale, both separately and together, reduced the rates of leaf scale physiological processes in *A. donax*. The efficacy of the wasp was density dependent, and this herbivore reduced the carboxylation rate of Rubisco. The effect of the scale took approximately five months to manifest, which coincided with generation time. Scale reduced photosynthesis by decreasing the maximum rate of electron transport. When the two insects were both present, the effect of their herbivory seemed to be additive. These results will assist the responsible management agencies in evaluating the propriety of using one or both of the insect herbivores as biological control agents.

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I also give thanks to my friends and colleagues at Texas A&M University, and in the Department of Ecosystem Science and Management in particular. Thanks, as well, go to the Texas Water Resources Institute, including the Rio Grande Basin Initiative, the United States Geological Survey, and the United States Department of Agriculture's Agricultural Research Service.

Finally, I must thank my family for always being wonderfully supportive.

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CHAPTER I

INTRODUCTION

Semi-arid regions are inherently water-limited. The importance of the relationships between the biological and hydrological constituents of these landscapes has recently been discussed (Wilcox and Newman 2005; Newman *et al.* 2006). The emerging field of ecohydrology has focused attention on two distinct but interacting components – the upland rangeland areas and the riparian corridors. Of special importance within semi-arid rangelands are causes and effects of the protracted expansion of woody plants (Archer 1989; Archer 1994; Archer *et al.* 2001; Ansley *et al.* 1995; Huxman *et al.* 2005; Potts *et al.* 2006; Schlesinger *et al.* 1990; Van Auken 2000), and management strategies beneficial to both the landscapes and the people who inhabit them (Wilcox 2002).

Ecohydrological research on the riparian zones of semi-arid regions has largely focused on the role of woody plants in the water cycle (Busch *et al.* 1992; Wagner and Bretschko 2003; Clinton *et al.* 2002; Tabacchi *et al.* 2000; Williams *et al.* 2006; Levine and Stromberg 2001; Scott *et al.* 2000; Stromberg 1998; Stromberg 2001). For example, invasion by saltcedar species, *Tamarix* spp., attracts particular interest in the quantity of water used by this invader and adjacent native species at multiple spatial and temporal

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This thesis follows the style of *Journal of Ecology*.

scales (Cleverly *et al.* 2002; Cleverly *et al.* 2006; Dahm *et al.* 2002; Glenn and Nagler 2005; Horton *et al.* 2001; Moore *et al.* 2008; Nagler *et al.* 2008; Nagler *et al.* 2003; Sala *et al.* 1996; Smith *et al.* 1996).

Non-woody vegetation, including grasses, can also play an important role in the dynamics of riparian ecosystems (Naiman and Decamps 1997). Grasses that invade ecosystems well outside their historical range damage these ecosystems measurably (D'Antonio and Vitousek 1992; Milton 2004). Such invaders are often labeled 'transformer species' (Pyšek *et al.* 2004). Because little is known about the interactions between non-woody vegetation and the water cycle in the riparian zones of semi-arid areas, the invasion by *Arundo donax* (L.) is worth studying. This species has already been labeled a 'transformer' (Spencer *et al.* 2005), exhibiting strong negative impacts on biodiversity (Guthrie 2007; Kisner 2004; Herrera and Dudley 2003) and ecosystem function (Quinn and Holt 2008; Quinn *et al.* 2007; Rieger and Kreager 1989; Scott 1994).

In the lower Rio Grande watershed in southern Texas, water resources are made scare by drought and human demand (Usborne 2001). Since this region supports large areas of irrigated agriculture and sizeable urban populations, water resources are decidedly important. *A. donax* is thought to cover approximately 40,000 hectares along the Rio Grande and its tributaries, irrigation canals, ditches, and resacas (oxbow lakes) (Yang, pers. comm.), and efforts are currently underway to use recently established remote-sensing methods to quantify the distribution and total areal coverage of this species throughout the lower portion of the Rio Grande/Rio Bravo watershed (Everitt *et al.* 2004; Everitt *et al.* 2008; Everitt *et al.* 2005).

Basic data on the rates and quantities of water used by *A. donax* are necessary but completely lacking at any spatial or temporal scale. One of the few estimates of water use rates of *A. donax*, at over 1700 mm year^{-1}, was not peer-reviewed and was based on the assumption that this species transpires the same quantity of water as rice (Iverson 1998). This figure exceeds reported values evapotranspiration measured in riparian woodland systems in the southwestern United States by 18-40% (Cleverly *et al.* 2002; Devitt *et al.* 1998). Therefore, the first step in this study was to understand how *A. donax* uses water resources at different spatial and temporal scales under highly variable field conditions. Leaf scale transpiration and leaf area index were measured at three different canopy heights across four plots that increase with lateral distance from the river's edge. Because a potential management method for this invader is biological control, the second step of this study was to quantify the effect of insect herbivores (which are potential biological control agents) on the rates of physiological processes in the host plant. The two selected agents were a stem-galling wasp, *Tetramesa romana* (Walker) and an armored scale, *Rhizaspidiotus donacis* (Leonardi). I examined their effects on transpiration and photosynthetic rates as well as the mechanism behind these effects. This research was conducted to provide critical feedback to the agencies responsible for their approval and eventual release.

CHAPTER II

WATER USE DYNAMICS OF *Arundo donax* FROM LEAF TO STAND

INTRODUCTION

The conservative use of water resources from both rivers and aquifers is vital for the maintenance of natural, agricultural, and municipal systems, and as these latter two sectors consume large shares of these resources, natural systems can be left in deficit. This is especially evident in drier periods, as exemplified by dramatic events such as when Rio Grande flows do not reach the Gulf of Mexico (Usborne 2001). Water-limited river systems, common in the western United States , are particularly susceptible to drought pressures (Cleverly *et al.* 1997), and have added biotic pressures from riparian invasive species (Dukes and Mooney 2004) that may be capable of significantly altering the structure and function of ecosystems (D'Antonio and Vitousek 1992; Hobbs and Mooney 1998; D'Antonio *et al.* 1999).

Much recent attention has been paid to the role of invasive semiarid woody plants in the water cycle, as exemplified by focus of research on saltcedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia* L.) (Cleverly *et al.* 2006; Dahm *et al.* 2002; Nagler *et al.* 2003), because some invasive species compete for water resources aggressively (Wilcox and Thurow 2006). To many restorationists and land stewards, the removal of invasive species will increase streamflow, and this notion is epitomized by flagship efforts like South Africa’s Working for Water Programme (Marais and Wannenburgh 2008; Cullis *et al.* 2007; Gorgens and van Wilgen 2004). However, the water regained by these types of projects are not easily predictable in semiarid and arid landscapes (Wilcox 2002; Huxman *et al.* 2005). Predicted differences do not always live up to expectations. For example, evapotranspiration (ET) in *Tamarix* stands on the Lower Colorado River was estimated to be only 1% of mean yearly streamflow (Nagler *et al.* 2008). Also, reducing water loss through one pathway, such as transpiration, does not necessarily equate to increases in streamflow if there are offsets through other pathways, such as increased soil evaporation (Wilcox and Thurow 2006). Moreover, depending on the rates of water use employed in economic models, expectations of potential water gain through the removal of invasive species can be unrealistically high (Owens and Moore 2007).

The hydrology, geomorphology, and ecology of riparian ecosystems are interdependent. For example, riparian vegetation can provide channel stability at small spatiotemporal scales but lead to instability at larger, longer-term spatiotemporal scales (Rowntree and Dollar 1999). Additionally, woody debris in streams can trap sediment, dissipate energy, and create habitats (Naiman and Decamps 1997). Tabacchi et al. (2000) reviewed the ways in which vegetation influences runoff and hydraulic processes, water cycling, and water quality. From the opposite perspective, plant species and diversity are partly a result of the distribution of hydrological and geomorphological processes and forms (Bendix and Hupp 2000; Amoros and Bornette 2002). These complex feedbacks can be altered by changes in community structure brought about as a result of invasions (Tickner *et al.* 2001). Invasive plant species can not only alter the dynamics between vegetation and geomorphology in riparian systems (Rowntree 1991), but they can also have negative effects on hydrology if increases in leaf transpiration rate, leaf area, and/or access to previously unused sources of moisture lead to reductions in soil moisture content (Walker and Smith 1997). Although interactions between various water sources and riparian forests have been studied (Clinton *et al.* 2002; Wagner and Bretschko 2003), little is known about the interactions between non-woody vegetation and the saturated or vadose zones of riparian corridors. The impacts of invasive grasses on water resources in particular have been understudied (Milton 2004), in large part due to highly problematic woody invaders (Richardson and van Wilgen 2004).

Giant reed (*Arundo donax* (L.)) is found in the 25 southernmost states (Bell 1997), and is known to have been in the southwestern United States since at least the early 19th century (Hoshovsky 1993; Dudley 2000). As with many riparian plants (Tabacchi *et al.* 2000), basic information on the rates and quantities of water used by *A. donax* is lacking. One of the few reports of water use rates in *A. donax* comes from non-peer-reviewed literature, where it reportedly consumes over 1700 mm/yr (5.62 ft/yr) based on the assumption that this species transpires the same quantity of water as rice (Iverson 1998). This figure exceeds reported evapotranspiration values measured in riparian woodland systems in the southwestern United States by 18 to 40%, including dense, multi-story canopies (Cleverly *et al.* 2002; Dahm *et al.* 2002; Devitt *et al.* 1998).

A. donax is currently targeted for control in some of its introduced range (Milton 2004). *A. donax* covers approximately 40,000 hectares in the Rio Grande basin (Yang, pers. comm.), and efforts are currently underway to use recently established remote-sensing methods (Everitt *et al.* 2004; Everitt *et al.* 2005) to quantify the distribution and total areal coverage of this species throughout the lower portion of the watershed. A necessary first step in understanding how this invasion affects the water cycle is quantifying variation in the water use of *A. donax* stands.

Water supply fluctuations increase variability in transpiration, even in riparian ecosystems (Williams *et al.* 2006). For example, soil moisture in a temperate riparian zone was spatially heterogeneous in both lateral gradients away from the edge of open water and vertical gradients away from the saturated zone (Dall'O' *et al.* 2001). The first objective of this study was to examine transpiration variance, both spatially and temporally, by examining stand structure, leaf gas exchange, and water use efficiency along potential gradients perpendicular to the Rio Grande. We predicted that leaf area and leaf level transpiration were highest near the active river channel and declines with distance away from the river, although soil fertility may also be a factor. We also anticipated some seasonality in the above spatial trends driven by water availability gradients. We expected that a more pronounced lateral trend with distance would occur during warm seasons with high evaporative demand. For the same reason, within-stand spatial variance was expected to be more pronounced during drought. Non-phreatophytic riparian vegetation responded largely to either recent rainfall or water from deeper in the soil profile without using much or even any groundwater, depending on the type of vegetation (Scott *et al.* 2000; Dawson and Ehleringer 1991). Thus, as soil moisture in riparian zones varied interannually and seasonally due to fluctuation in precipitation (Joris and Feyen 2003; Scott *et al.* 2004), transpiration rates of riparian vegetation were accordingly dynamic (Williams *et al.* 2006). Our second objective was to use a bottom-up approach to scaling to estimate stand level transpiration (Baldocchi *et al.* 1991) based on observed spatial and temporal variance. Thus, this study represents a critical first step (Baldocchi *et al.* 1996) in characterizing the dynamics of how *A. donax* impacts water resources.

MATERIALS AND METHODS

This study was conducted along the Rio Grande river (26°01′53″ N, 97°43′41″ W, 15 m a.s.l.) in Cameron County, Texas. Mean annual precipitation is 715 mm and monthly average temperatures range from 9 to 21 °C in January and 23 to 35 °C in September and August (Anonymous 2008). Soils at the site are characterized as loam or clay loam, which are a part of the Rio Grande-Matamoros association (Williams *et al.* 1977). This area consists of a historic gently sloping floodplain 4.0 to 6.0 km wide, where flooding still occasionally occurs as a result of rainfall, although dams and levees have altered the historic flood regime (Lonard and Judd 2002). Common native trees of the Lower Rio Grande include honey mesquite (*Prosopis glandulosa* Torr.), sugar hackberry (*Celtis laevigata* Willd.), cedar elm (*Ulmus crassifolia* Nutt.), and anacua (*Ehretia anacua* (Terán & Berl.) I.M. Johnst.), while the dominant shrub was granjeno (*Celtis pallida* (Klotzsch) Liebm.) (Lonard and Judd 2002). The most common ground cover species are the exotic Guinea grass (*Panicum maximum* (Jacq.) R. Webster) and buffel grass (*Pennisetum ciliare* (L.) Link) (Lonard and Judd 2002). During the 20th century, 91 to 99% of native woodland and riparian vegetation was cleared due to the expansion of agriculture and urban development (Jahrsdoerfer and Lesie 1988; Tremblay *et al.* 2005).

Three transects were established perpendicular to and immediately adjacent to the Rio Grande within a large monoculture of *A. donax* in order to investigate within-stand dynamics. Very few other plant species were present at the site except a sparse ground cover layer consisting largely of *P. ciliare*. The following conditions were used to locate transects: maximal lateral stand width perpendicular to the river, sufficient slope to allow for a potential gradient in plant available water from river edge to upper bank, and uniform connectedness of the stand of *A. donax*. Transects were set up with a minimum of 15 m separation, and were between 12 and 20 m in length. At least 1 m of *A. donax* extended beyond the ends of the each transect in all directions to minimize edge effects that might reduce competition for resources (Spencer *et al.* 2005).

Four 1 m by 1 m plots were spaced evenly within each transect according to total transect length. The relative proximity of these four plots to the active channel (hereafter referred to as ‘distance from the river’) was used to investigate differences in stand structure, leaf gas exchange, and water use efficiency. Within each plot, four ramets (individual stems within a single clonal stand) were selected from within the subset of all ramets that both reached the top of the sunlit canopy and retained the apical meristem (Peterson and Chesson 2002). Moreover, ramets were chosen that did not appear to emerge from the same rhizome, whenever possible (Decruyenaere and Holt 2005). Leaf gas exchange of the four chosen ramets per plot was measured throughout the study.

In order to assess stand structure and document phenological trends in allometric properties, ten additional transects were allocated for one-time destructive sampling as follows. These transects were located parallel to those previously discussed and harvested at approximately two month intervals from July 2007 through March 2008, and again in July 2008. As before, transects were divided into four 1.0 m^2 plots spaced at even intervals. They were then further divided into three vertical sections: the upper (L_U), middle (L_M), and lower (L_L) portions of the canopy. These vertical sections were partitioned equally, relative to the height of the tallest ramets in and around each transect. In the plots, the density of all ramets was recorded, as were the diameter and height of each ramet. Total leaf area within 0.25 m^2 subplots was quantified using a leaf area meter for five of the transects. All ramets were then oven-dried at 60° C for a minimum of 24 hours and continued drying until they were a constant mass. Leaf area index (LAI) for each 1.0 m^2 plot was then estimated by the relationship between ramet leaf area (L_r, cm^2) and biomass (BM, grams) and distance from the river (D, m) in the 0.25 m^2 subplots ($L_r = \exp(4.293+0.853\ \ln(BM) - 0.010D)$, $R^2 = 0.912$, $N = 90$, $P \leq 0.05$) derived from a multiple regression model of leaf area. For one transect from this site, specific leaf area (SLA) was determined by weighing leaf material separately from stem material for 5 random ramets from each plot.

Leaf based gas exchange measurements were taken on 23 days from 27 June, 2007 through 22 July, 2008 using a leaf gas exchange system with a red and blue light source and CO_2 injector. All but five sampling days entailed midday measurements to capture peak rates of physiological processes. On the remaining five days, diurnal changes in gas exchange were measured on all ramets within a single transect every 2 h between 07:00 and 19:00 CST. Measurement dates from 2007 were 27 June, 23, 24, and 31 July, and 22 and 25 November. Measurement dates from 2008 were 20 and 22

January, 29 February, 5 and 7 March, 13, 15, 18, 20, 21, 25, 29, and 31 May, 1, 3, 4, and 5 June, and 22 July. Gas exchange measurements were conducted on clear days whenever possible, though the prevailing weather conditions were partly cloudy, and small isolated showers were common. Light level was always set to match ambient conditions measured at the beginning of each measurement cycle (adjusted every 2 hours on days of diurnal samplings), and CO_2 concentration was set to maintain 370 µmol/mol in the sample chamber. Only the second fully-emerged leaf from each ramet was sampled in order to control for leaf age.

To further document spatial variation in soil and plant water status with distance to the river, predawn and midday leaf water potentials (Ψ_{pd} and Ψ_{md}, respectively) were measured on a total of 10 days throughout the sampling period using a pressure chamber. On each day, 12 to 16 Ψ_{pd} measurements were completed before astronomic sunrise, and an equivalent number of Ψ_{md} measurements (or more) were taken on the same day between 11:00 and 14:00 h. To corroborate soil water status trends with distance to the river, we also looked for spatial trends in soil moisture at a single point in time. On two days in the middle of the growing season (4 and 5 June, 2008), volumetric water content of the top 20 cm of soil was measured for each plot in each of the four cardinal directions within 1.0 m from the center point of the plot using a soil moisture probe. Soil samples were collected on these same dates from 0 to 10 and 10 to 20 cm between 1.0 and 2.0 m distance laterally from the center point of each plot to reduce the likelihood that rhizomes within the plot would sustain damage (Dong and Alaten 1999). These samples were analyzed for soil texture, pH, electrical conductivity, cation exchange, base saturation, and total C and N content by the Forest Science Laboratory at Texas A&M University. Such soil descriptors and fertility measures were used to verify that any observed physiological trends within the stand were unlikely caused by factors other than gradients of soil water access.

In order to have a longer, time-integrated view of leaf water use efficiency, which is the ratio of photosynthetic carbon gain per unit water transpired, the same leaf tissues from the second fully-emerged leaf from each ramet that was used for diurnal measurements of gas exchange were collected on 3 to 5 June to analyze stable carbon isotope ratios ($\delta^{13}C$) (Farquhar *et al.* 1989; Dawson *et al.* 2002; Ehleringer *et al.* 1993). Concurrent examinations of leaf C and N content were conducted to ensure that leaf nutrient status did not covary with $\delta^{13}C$ (Handley and Raven 1992). Samples were dried at 60° C for at least 24 hours until they were a constant mass and were then finely ground to an even texture by a combination of a custom-made roller grinder and a ball mill. Homogeneous 2 mg aliquots were analyzed by the Stable Isotope Biogeochemistry Laboratory in the Department of Ecosystem Science and Management at Texas A&M University.

Leaf transpiration rates (E_ℓ), were averaged for each ramet for a single set of midday measurements. To elucidate temporal differences in stand structure and leaf gas exchange with season and drought, data were divided into three temporal groups: summer 2007 (June to July), winter 2007/2008 (November to February), and summer 2008 (May to July). Daily weather data, including potential evapotranspiration (PET) and precipitation, were obtained from the nearest weather station, the Texas AgriLife

Research Weslaco Center (26° 9'52" N, 97°57'25" W). To compare between growing seasons, mean daily precipitation was calculated from one week prior to the first sampling date of each summer through the final measurement date. In order to look for the effect of distance from the river on LAI, a one-way ANOVA with Fisher's LSD as pairwise comparisons was used on plot means of LAI for all transects. Seasonal ramet means of E_ℓ were used in a separate two-way ANOVA, along with Fisher's LSD as pairwise comparisons to evaluate plot-level effects of distance to river as well as differences between transects. In order to test for effects of distance to river on the other leaf based data, one-way ANOVA was also used for ramet based averages of %C, %N, and δ^{13}C. To assess whether soil and plant water status differed within the distance treatment, a one-way ANOVA was run on each of Ψ_{pd} and Ψ_{md}. In order to determine whether the distance treatment also affected soil fertility properties, one-way ANOVAs were conducted on each of gravimetric water content (GWC), % N, % C, P, and cation exchange capacity. All statistical analyses were conducted using SPSS. Note, the original experimental design was set up to use repeated measures analysis of variance (ANOVA), but because the site was unexpectedly mowed in late July or early August by the Texas Commission on Environmental Quality after several days worth of leaf gas exchange measurements, this was no longer possible.

Because the same ramets were used for gas exchange in the winter season and the following summer (2008), including season in the preceding analyses was not possible because it would violate the assumption of independence in ANOVA. Instead, Student's t-tests were used to compare the gas exchange and precipitation data from summer 2007 and summer 2008. Gas exchange data for this comparison consisted of summer-long mean values for each ramet. Separately, a paired t-test was used to compare gas exchange data from winter 2007/2008 to summer 2008.

Bottom-Up Approach to Estimate Stand Transpiration

An empirical model was constructed to estimate total daily stand level transpiration as follows:

$$\mathrm{E_{stand}} = (\mathrm{E_U} \times \mathrm{L_U}) + (\mathrm{E_M} \times \mathrm{L_M}) + (\mathrm{E_L} \times \mathrm{L_L}) \qquad [1]$$

Diurnal estimates for each day were based on peak midday values and the shape of the curves from days in which gas exchange was conducted for an entire diurnal cycle. Second order polynomial curves provided a good fit to the diurnal measurements. It was assumed that transpiration was zero at night and increased linearly from dawn until the first morning measurement at 07:00 h and that it declined linearly to zero from the last evening measurement at 19:00 h until twilight. The model partitioned the measured transpiration into the three vertical canopy layers using measured data in the upper canopy (E_U) and estimated data in the middle (E_M) and lower (E_L) canopy layers based on the measured light penetration in those sections of the canopy and the corresponding transpiration values taken from light response curves conducted on shaded leaves (Niinemets *et al.* 1999; Niinemets 2007). This method is the most conservative method in this type of scaling (Dang *et al.* 1997). Instantaneous gas exchange values, in mmol $H_20/m^2/s^1$, were integrated for each day then multiplied by the molar mass of water and divided by density of water at 25 °C to convert to mm/day. This was done for each plot and canopy layer, and the three transpiration values were then multiplied by the LAI of each of the three vertical sections, L_U, L_M, and L_L. In order to derive total daily transpiration per unit ground area (E_{stand}), expressed in mm/day, the three stratified layers were summed (Equation 1).

RESULTS AND DISCUSSION

Within-Stand Dynamics

The *A. donax* stand we studied is notably productive for a graminoid (Sharma *et al.* 1998; Papazoglou *et al.* 2005; Perdue 1958; Angelini *et al.* 2005). The mean LAI of *A. donax* in our study site was 4.1, and this is corroborated by measurements of LAI in a stand at another site 300 km upstream, where mean LAI was 4.5 (data not shown). These values of LAI are higher than those found in stands of *Tamarix ramosissima* (Ledeb.), another common invasive species on the Rio Grande, that range from 2.5 to 3.6 (Dahm *et al.* 2002). LAI values from 2007 were used in the scaling model to determine E_{stand} in both 2007 and 2008, but an independent measure of LAI in July 2008 verifies that LAI equaled or exceeded that of July 2007 (data not shown). *P. australis*, with very similar ecological and morphological characteristics to *A. donax*, has been reported to have LAI values of up to 8.9 in the peak of the growing season in wetlands of semi-arid southeastern Spain (Moro *et al.* 2004); however, *P. australis* growing at our study location was very sparse and limited to a band 1 m wide nearest the river (Pers. obs.).

The *P. australis* stand in Spain (Moro *et al.* 2004) exhibited a stronger seasonal trend than we observed at our site, wherein LAI increased gradually throughout the growing season and ranged from 3.3 in March 2008 to 5.5 in January 2008. Most *A. donax* leaves apparently do not senesce and abscise until late winter. The winter's coldest period occurred from January 2 to January 26, 2008, after which there was a strong reduction in leaf area (Figure 1). We did not observe the onset of leaf production due to lack of frequent sampling during early spring and summer. The rate of growth in *A. donax* should vary yearly in a similar fashion.

Ramets of *A. donax* growing very near to the river are capable of supporting a higher LAI than those at a greater distance from the active channel and topographically upslope. This pattern was observed in the majority of individual transects measured. Mean LAI for all sample dates varied with distance to the river channel (Table 1). Replicated plots nearest the channel (1 and 2) had the highest LAI and were 79% and 53% greater than plots farther away from the channel (3 and 4), respectively. Interestingly, the section of the stand of *A. donax* with the lowest LAI was not the plots furthest from the river's edge (Plot 4), but rather one plot closer (Plot 3).

An apparent edge effect in LAI further strengthens the argument that some combination of greater light availability and reduced intraspecific competition occurs in stands of *A. donax* at the most laterally distant edge allows for compensation in ramet growth despite the potential limitation of water resources (Urbanc-Bercic and Gaberšcik 1997). The edges of stands are also likely subject to greater advection (Speck 2003; Speck and Spatz 2004). Moreover, it has been shown that increased dispersal of offspring leads to greater competitive ability in clonal plants (Lenssen *et al.* 2005). For *A. donax*, the ramets that are the greatest lateral distance from the river channel may experience a reduction in intraspecific competition, and thus have a slight increase in metrics of yield like LAI.

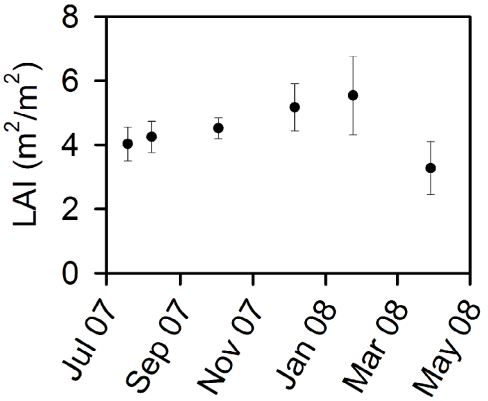

Figure 1. Mean leaf area index (LAI) estimates in m^2/m^2 throughout the study period. Standard error bars are indicated (N = 4 in all cases except October 2007, where N = 8).

Table 1. Comparisons between plots in a stand of *A. donax*. Shown are characteristics of stand structure [leaf area index (LAI, m^2/m^2) and specific leaf area (SLA, m^2/kg)], leaf water stress [pre-dawn (Ψ_{pd}) and midday (Ψ_{md}) water potential (kPa)], leaf chemistry [nitrogen (N, %), and carbon (C, %)], and soil properties [gravimetric water content (GWC, %), nitrogen (N, %), carbon (C, %), phosphorus (P, ppm), and cation exchange capacity (CEC, meq/100 g)]. All data are reported as mean (SE). Of all the listed variables, only LAI differed between plots, as indicated by letters from pairwise comparisons (Fisher's LSD) ($P \leq 0.05$).

	Stand structure		Leaf water status		Leaf chemistry		Soil properties				
Plot	LAI	SLA	Ψ_{pd}	Ψ_{md}	[N]	[C]	GWC	[N]	[C]	[P]	CEC
1	6.06 (1.13) a	12.25 (0.83)	-0.63 (.06)	-2.05 (.11)	2.32 (.05)	42.02 (.34)	24.50 (2.38)	0.15 (.04)	3.63 (.52)	17.90 (6.99)	18.23 (2.15)
2	4.63 (0.32) ab	9.45 (1.86)	-0.78 (.09)	-2.27 (.09)	2.24 (.06)	42.02 (.37)	25.24 (1.52)	0.13 (.02)	3.36 (.30)	12.57 (5.52)	16.91 (1.16)
3	3.38 (0.36) b	13.47 (0.62)	-0.90 (.10)	-2.50 (.16)	2.34 (.11)	42.44 (.28)	25.96 (0.87)	0.13 (.02)	3.39 (.18)	11.64 (4.39)	16.55 (0.39)
4	3.95 (0.68) b	12.45 (1.69)	-0.79 (.10)	-2.24 (.12)	2.37 (.12)	43.06 (.30)	25.44 (1.48)	0.16 (.03)	3.84 (.46)	11.40 (4.47)	17.48 (1.15)

Populations of *A. donax* frequently extend almost to the water's edge, but these areas were not sampled because of a drop-off extending approximately 3 m from the river to our first plots on top of the terrace (≈ 2 m vertically above the water level during normal flow). Both LAI and E_l would very likely be even higher in ramets below the terrace. Because *A. donax* appears to prefer habitats with mild slopes (≤ 2%) (Dudley 2000), the low floodplain slopes of many reaches along the Rio Grande are well suited for its survival.

Mean E_l also varied with distance to the river in summer 2007 and summer 2008, and followed the same trend as with LAI, having the highest values near the channel. The lowest values were in the plots farthest from the river in summer 2007, while in summer 2008, the lowest values of E_l were in the third, rather than fourth plots (Figure 2). During the cool winter season, E_l did not differ between parts of the stand either laterally or longitudinally (Figure 2). In the summer of 2007, mean E_l in Plot 1 was 15% and 20% greater than in Plots 2 and 4, respectively. Mean E_l in Plot 3 exceeded Plot 4 by 15%. In the summer of 2008, E_l was 68% higher in Plot 1 than in Plot 3. In the summer of 2008, E_l was highest in the plot closest to the river; however, the pattern that emerged during this growing season was different from the previous year in that the plot furthest from the river did not have the lowest E_l. Instead, the pattern here mirrored that of LAI, where Plot 3 had the lowest E_l. In both summer seasons, but not in the winter, the transects also differed from each other. For example, in summer 2008, transect 5 consistently had the lowest E_l (Figure 2). There was no interaction between plot and transect in either summer season, indicating that plots responded to distance from the

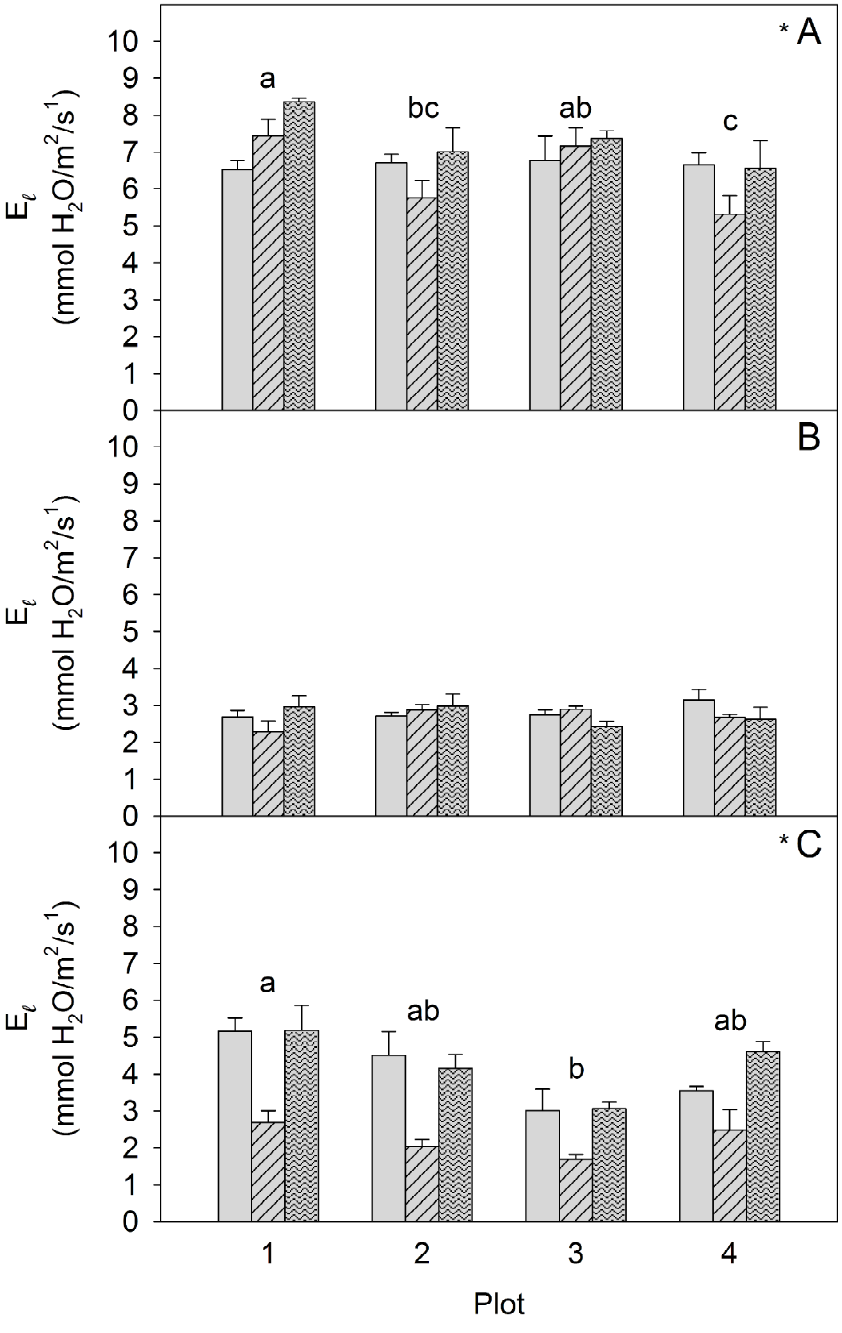

Figure 2. Leaf scale transpiration for each sampling period. Shown are mean leaf scale transpiration (E_l) and standard error bars (N = 4) for: (A) summer 2007 (N = 4 days); (B) winter 2007/2008 (N = 7 days); and (C) summer 2008 (N = 12 days). Bar patterns indicate the three randomly selected transects. Asterisks denote differences between transects ($P \leq 0.05$) within a season. Letters denote differences between plots from pairwise comparisons (Fisher's LSD) ($P \leq 0.05$) within a season.

river consistently in all transects. The two summers differed greatly in precipitation with 6.37 mm/day and 2.42 mm/day from 2007 and 2008, respectively.E_l was higher in the wetter summer of 2007 than the drier summer of 2008 (*t*-statistic = 7.958, $P < 0.000001$, d.f. = 19.003), and E_l was higher in the drier summer than in winter 2007/2008 (*t*-statistic = 2.224, $P < 0.05$, d.f. = 11).

The lack of spatial heterogeneity in E_ℓ during the winter season was likely due to reduced evaporative demand (Franks *et al.* 2007). Furthermore, the magnitude of the difference in E_ℓ between the highest and lowest plots was greater during the relatively dry summer of 2008 than the very wet summer of 2007, signifying that proximity to the river is even more important when there is less precipitation during the growing season. This likely means that *A. donax* does not use groundwater as its sole water source, but rather uses soil moisture from the vadose zone, and this lends credence to the conclusion that *A. donax* is not actually an obligate wetland plant. *A. donax* lacks adaptations for gas transfer to the root zone to tolerate the anoxic conditions found in frequently saturated soils (Brix *et al.* 1992). Also, the SLA of *A. donax* was 11.93 m^2/kg and did not differ between plots. This SLA estimate is roughly equivalent to the lowest values reported by Mommer et al (2006), who demonstrated that higher SLA correlates with plants that occur in wetter habitats. Thus, *A. donax* does not appear to have specialized adaptations to the wettest parts of riparian zones, and its occasional classification as a freshwater macrophyte warrants further scrutiny.

Water supply fluctuations within the stand were likely a driving factor for the observed spatial and temporal dynamics. Our results provide evidence of moisture gradients within the stand, depending on the measurement method. We found the most pronounced differences with distance to the river during periods of high moisture stress. Stable carbon isotope ratios ($\delta^{13}C$) of leaves collected during the dry summer of 2008 provide a more time-integrated perspective of plant-water relations and water use efficiency (or carbon gained per unit water lost). Results indicated that these leaves experienced a gradient of water availability over their lifespan until they were removed from the shoots. The values of $\delta^{13}C$ became less negative with increasing relative distance from the river channel's edge (Table 1, Figure 3), which suggests that water use efficiency was higher at greater distances away from the river. Plot 1 had the most negative $\delta^{13}C$ values and was lower than Plots 3 and 4 by 0.54‰ and 0.76‰, respectively (Figure 3). Plot 4 had the least negative values. Although every effort was made to select leaves of the same age, the wide scatter of $\delta^{13}C$ values within each plot is likely the result of a combination of varying leaf age and light environment (Sandquist *et al.* 1993). Small differences in leaf age in such a rapidly growing species may alter leaf carbon assimilation rates and thus affect isotope ratios.

Integrated water use efficiency, as measured by $\delta^{13}C$, varied with distance to the river. Instantaneous assessments of leaf water status were not affected by distance to the river in either predawn or midday measurements (Table 1). Soil moisture content in the top 20 cm also was unaffected by distance (Table 1). Although our data on both plant water status and soil moisture content showed no lateral distance trends, Ψ_{pd} did differ on 29 February, 1 June, and 22 July 2008, each amidst a dry down period (at least 14 days with < 4 mm precipitation). The unique circumstances of conducting research on

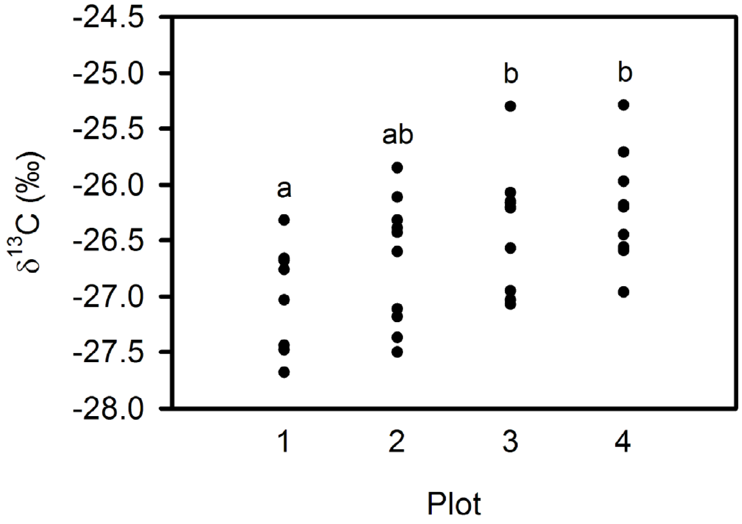

Figure 3. The relative water use efficiency of young leaves of giant reed as measured by carbon isotope discrimination, δ^{13}C. Plot 1 is closest to the river channel; plot 4 is at the greatest distance. Letters indicate significance of pairwise comparisons (Fisher's LSD) between plot means ($P \leq 0.05$).

an international boundary prevented more frequent collection of Ψ_{pd} data. Moreover, the trends in both Ψ_{pd} and Ψ_{md}, mirrored the pattern in E_ℓ from summer 2008, in that plants were least water stressed (i.e. least negative Ψ_{pd} and Ψ_{md}) adjacent to the channel, while in most cases plants in plot 3 were most stressed (i.e. most negative Ψ_{pd} and Ψ_{md}). Also, Ψ_{pd} may not be highly indicative of soil Ψ in wet environments (Donovan *et al.* 2001). Drought conditions, at least in the top 20 cm, were not apparent during the narrow timeframe when soil moisture was quantified, but soil moisture can vary greatly over small spatial scales (Peterson and Chesson 2002). *A. donax* has functional rhizomes at depths as great as 1 m (Boose and Holt 1999), so fine roots may extend even lower in the soil profile, giving this species access to soil moisture at depth (Kemp *et al.* 1997) in systems where doing so provides a benefit (Kleinhenz and Midmore 2001).

Soil fertility, and plant responses to it, can vary over small spatial (Robertson *et al.* 1988; Jackson and Caldwell 1993) and temporal (Jackson *et al.* 1990) scales, and inherently affects leaf nutrient status. Our results for both leaf N and several measures of soil fertility indicate no difference with distance to the river channel, further emphasizing that the differences in both LAI and E_ℓ may indicate that water was the limiting resource. There was no significant relationship between relative distance from the river and either % C or % N in leaves (Table 1). There was no relationship between leaf N content and δ^{13}C (adjusted $R^2 < 0.001$, not shown), indicating that the variation in δ^{13}C values is reflective of differences in water use efficiency rather than leaf chemistry. In determining measures of fertility for the top 20 cm of soil, none of cation exchange or soil N, C, or P content varied with distance to the river (Table 1). Moreover, *A. donax* is known to be quite effective at taking up nutrients (Abissy and Mandi 1999; Mavrogianopoulos *et al.* 2002; Cosentino *et al.* 2006; Manios *et al.* 2002; Srivastava *et al.* 2008) but does not appear to be nutrient limited at this site. If there were differences in plant available N, a reflection in *A. donax* growth or gas exchange would be evident because it is known to respond to N enrichment (Abissy and Mandi 1999).

Stand Transpiration

The observed spatial and temporal variation in LAI and E_ℓ described above were incorporated into a scaling model for stand transpiration (E_{stand}) which resulted in an overall estimate of 9.1 ± 1.1 mm/day, averaged over all 23 sample dates (Figure 4). An example of the measured and modeled diurnal transpiration patterns is given in Figure 5. The derived diurnal trend in E_ℓ resembles that of the driving variables for transpiration: humidity, and temperature, and light (Figure 5). Large differences in E_{stand} were evident within short time periods (Figure 4), and were likely a result of physiological responses to varying weather conditions (Herbst and Kappen 1999; Lissner *et al.* 1999). For example, in six sampling days between 29 May and 5 June, 2008, E_{stand} varied from 4.7 mm to 10.9 mm. Differences between the peak growing season and a much less active winter season are also clear (Figure 4). The model estimated that mean daily E_{stand} was 17.8 mm in the summer of 2007, 4.8 mm during following winter, and 8.8 mm during the summer of 2008.

These E_{stand} values are on the high end of the range of reported values in the literature on evapotranspiration in riparian ecosystems. For example, E_{stand} based on eddy-covariance from a site dominated by *T. ramosissima* reached up to 7 mm/day

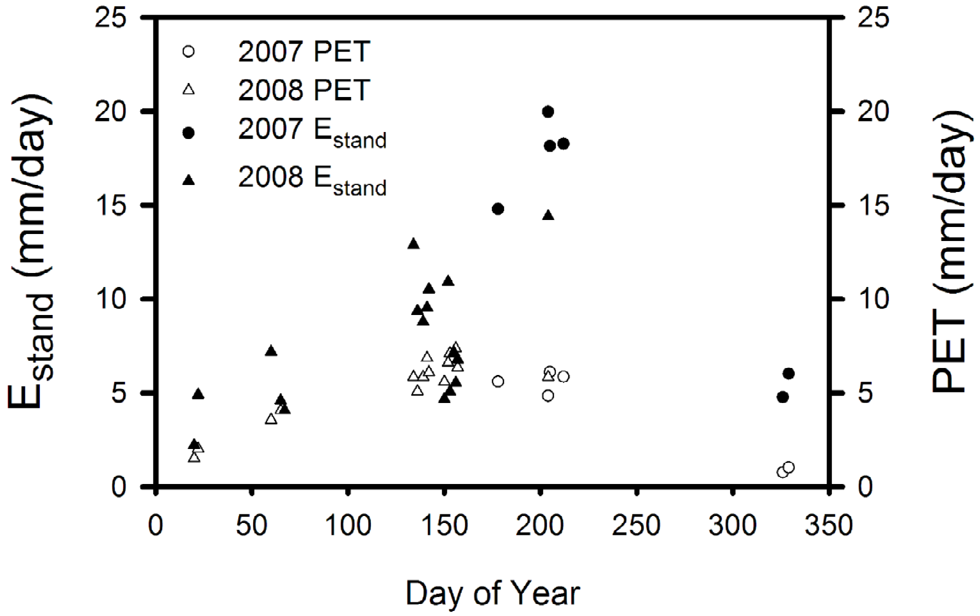

Figure 4. Total daily stand scale transpiration (E_{stand}) and daily potential evapotranspiration (PET) for all modeled sampling days in 2007 and 2008.

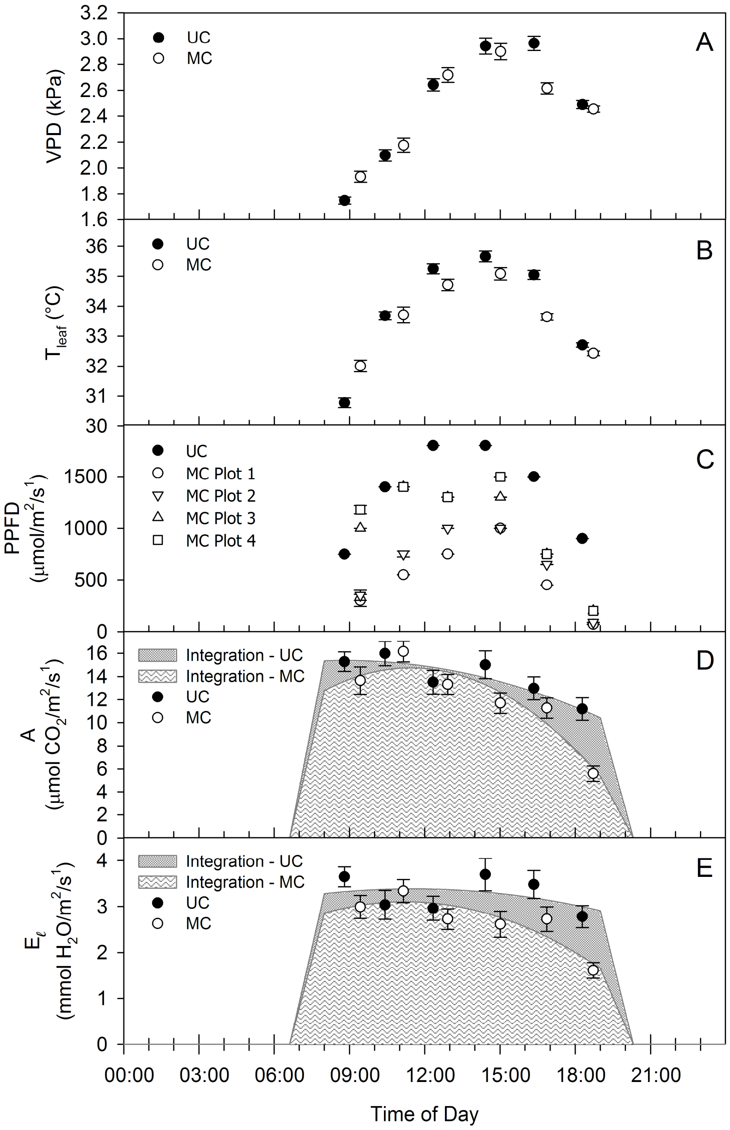

Figure 5. Diurnal observations from 3 June, 2008. Shown are: (A) Vapor pressure deficit (VPD); (B) Leaf temperature (T_{leaf}); (C) Photosynthetic photon flux density (PPFD); (D) Carbon assimilation rate (A); and (E) Transpiration rate (E) collected at approximately two hour intervals throughout the daylight hours. Closed symbols indicate leaves from the upper canopy (UC) layer; open symbols indicate leaves from the middle canopy (MC) layer. Means and standard error bars are given for each point (N = 16 ramets). For open symbols in graph (C), circles, downward-pointing triangles, upward-pointing triangles, and squares represent Plots 1, 2, 3, and 4, respectively. In graphs (D) and (E), shaded and lined regions are the integrated predicted values on this day for the upper and middle canopy layers, respectively, using the diurnal model described in the Materials and Methods section.

(Cleverly *et al.* 2002). In a similar study, E_{stand} from sites dominated by mixtures of native and invasive woody species reached peak values of approximately 9 mm/day (Dahm *et al.* 2002). E_{stand} in a pond lined by *Phragmites australis* (Cav.) Trin. ex Steud. in Nebraska, USA was estimated at 4 mm/day in a stand that had a maximum LAI of 2.6 (Burba *et al.* 1999). E_{stand} in *P. australis* in Germany is estimated at 10 to 16 mm/day in stands with summertime LAI of about 5 (Herbst and Kappen 1999). *P. australis* in semi-arid Spain has been shown to have average midsummer E_{stand} values of about 23 mm/day in a stand with simultaneous LAI values of 8.9 (Moro *et al.* 2004). Keeping transpiration rates constant, this would equate to approximately 9.6 mm/day if LAI were equivalent to that of *A. donax* in this study. Additionally, the ratio of E_{stand} to potential evapotranspiration (PET) for reed systems can range from 0.75 to 3.4, and one of the strongest controlling factors in these systems is the horizontal advective component that supplies additional energy to drive evaporative demand (Burba *et al.* 1999; Devitt *et al.* 1998; Moro *et al.* 2004; Herbst and Kappen 1999; Peacock and Hess 2004; Fermor *et al.* 2001). Our data show that *A. donax* had E_{stand}/PET ratios ranging from 1.4 in the summer of 2008 to 3.7 in the summer of 2007. Soil evaporation is unlikely a significant contributor to total evapotranspiration (Goulden *et al.* 2007), largely because of the substantial mulch layer and the general lack of exposed soil (Pers. obs.).

Our E_{stand} estimates may be representative of *A. donax* stands throughout the Rio Grande Valley, but a regional study is needed to determine larger-scale water use patterns. The climate of our study region is subtropical with evaporative demand that is very high in the summer and winters that are quite mild. *A. donax* is also well established and highly invasive in more temperate regions. Different reaches along the banks of waterways experience differing moisture conditions which exerts strong controls on E_{stand}. The observed heterogeneity of the stand structure and transpiration rate of *A. donax* further underlines the importance of recognizing spatial variation at the population scale (Levin 1992). Furthermore, riparian vegetation water use varies with stand size. Consequently, our results may not be representative of all stands of *A. donax*, particularly because stands vary in density, height, and extent. Advection may have elevated transpiration at our site because of its high edge-to-interior ratio. Nevertheless, the estimation of approximately 1700 mm/year made by Iverson (1998) may be a reasonable value for stand scale water use in stands of *A. donax* similar in structure to the stand in this study.

To have precise scaling from leaf to stand, our model utilizes detailed horizontal and vertical measurements and replicated on-site measures of LAI (Spencer *et al.* 2006) that are reliable for highly diverse locations (Spencer *et al.* 2008). Leaf age, however, was not taken into consideration in this study, although it has been shown to have little to no effect on leaf physiology in a tussock grass, *Stipa tenacissima* (L.) (Haase *et al.* 1999). It is possible for leaf gas exchange to overestimate E_{stand}, as is known to occur in *S. tenacissima* by 71% (Ramirez *et al.* 2006). Leaf age accounted for over a third of that difference (Ramirez *et al.* 2006), but the basal sprouting growth form of *S. tenacissima* creates a complex vertical light environment that was not considered in their scaling model. Our model proportionately reduced E_{ℓ} in middle and lower canopy layers according to observed reductions in light.

We accounted for shading and carefully controlled the light environment during gas exchange measurements to best isolate effects of moisture gradients. Ambient light was recorded in full sun and the cuvette set at this constant value at the start of a measurement cycle, which possibly exposed leaves to higher than ambient light conditions on partly or mostly cloudy days. This could only cause overestimation of E_{stand} if it stimulated artificial stomatal opening, which is unlikely since carbon assimilation in *A. donax* peaks at light levels well below the range of values observed under cloudy conditions (Pers. obs.).

We can better understand impacts of exotic species such as *A. donax* on ecosystems by examining the underlying mechanisms of invasion (Levine *et al.* 2003). *A. donax* is a clonal species that can maintain functionality and survive when resources are scarce; however, it actively spreads, through both rhizomes and stems, when and where resources are plentiful (Decruyenaere and Holt 2005; Boland 2006; Decruyenaere and Holt 2001). Because of the mechanism of spread, *A. donax* may maintain connections between parent and offspring rhizomes, through which resources could be shared in order to increase fitness of the overall stand (Peterson and Chesson 2002). This mechanism could allow portions of *A. donax* stands that are in low quality habitats to maintain a competitive advantage over native species. Resources could be translocated from resource rich sections of the stand to low quality areas without having a detrimental effect on the stand's overall fitness (Jónsdóttir and Watson 1997). Future research is needed to better understand how the clonal growth form of *A. donax* influences its ability to utilize resources and how this may contrast with non-clonal native species.

Additionally, the partitioning of the water sources used by *A. donax* into soil water from recent precipitation, groundwater, and streamflow through the use of hydrogen and oxygen isotope analyses (Busch *et al.* 1992; Lamontagne *et al.* 2005; Yakir *et al.* 1990) would further elucidate the impact of this species on water resources. Finally, *in situ* comparisons of water use between *A. donax* and potential replacement vegetation, especially native species that would be considered in restoration efforts, would provide knowledge that would allow for regionally-based management decisions.

CHAPTER III

ECOPHYSIOLOGICAL RESPONSES OF *Arundo donax* TO HERBIVORY

INTRODUCTION

Invasive species are frequently capable of significantly altering the structure and function of ecosystems (Vitousek 1990; D'Antonio and Vitousek 1992), and these invaders can sometimes be characterized as ‘transformer’ species, which substantially modify their environments (Pyšek *et al.* 2004). Such modification can come in several forms. Invasive species alter the historic patterns of disturbance, such as fire regime or erosional processes. Invasive species excessively use critical resources, like light or water, in competition with native species. Furthermore, invasive species modify or redistribute important resources, such as nutrients or halides (Pyšek *et al.* 2004; Richardson *et al.* 2000).

Arundo donax (L.) (Giant reed) has been present in parts of the southwestern United States since at least the early 19th century (Dudley 2000; Hoshovsky 1993), and is currently found throughout the southern half of the continental United States from California to Maryland as well as on the Hawai’ian archipelago (Bell 1997). *A. donax* is already considered a strong example of a transforming invader (Spencer *et al.* 2005). This species has modified ecosystem processes to such an extent that some riparian zones in California’s watersheds are now regulated largely by fire, rather than the historic control process of flooding (Scott 1994). *A. donax* burns easily at nearly all times of the year (Scott 1994), yet generally occupies a location in the landscape, the riparian zone, that would ordinarily be relatively sheltered from wildfires. Its presence increases both fire frequency and intensity (Bell 1997), which in turn favors its regeneration (Frandsen 1997). Other forms of disturbance, such as mechanical clearing or large flood events, can similarly lead to further expansion of this species (Rieger and Kreager 1989). Research examining the integrity of watersheds considers abundant occurrences of *A. donax* to be associated with disturbed and degraded systems, even in its naturalized range (Ferreira *et al.* 2005).

Because of its rapid growth rate (Dudley 2000; Perdue 1958) and ready ability to resprout (Else 1996), *A. donax* is capable of forming dense, monotypic stands within a relatively short time period (Coffman 2007; Perdue 1958; Rieger and Kreager 1989; Bell 1997), thus reducing the biodiversity of the riparian zone. Losses in the abundance and richness of both the avian (Kisner 2004) and aerial invertebrate (Herrera and Dudley 2003) communities have been positively correlated with *A. donax* coverage. One possible reason for this may be the reduction in structural complexity as riparian ecosystems shift from multi-story communities to systems dominated by a largely uniform canopy of *A. donax*, resulting in a reduction in the overall nesting habitat available to birds (Frandsen 1997).

Mechanisms for this reduction in the biodiversity of communities in riparian zones invaded by *A. donax*, other than the simplification of habitat structure, are not yet clearly understood. It has been suggested that *A. donax* tissue is not easily digested by generalist herbivores (MilesTunsuwanChittawongKokpol *et al.* 1993; MilesTunsuwanChittawongHedin *et al.* 1993; Spencer *et al.* 2005). As a result of the reduced biodiversity of the arthropod community in areas of the riparian zone dominated by *A. donax*, there is a lesser likelihood that generalist herbivores will have a significant impact on the growth and spread of *A. donax*. Mature *A. donax* has a mean carbon to nitrogen (C:N) ratio of 22.1, which is considered to be too high to be particularly favorable to generalist herbivores (Spencer *et al.* 2007). Young shoots may be the most favorable to many herbivores, but the rapid growth rate of this species presents only a small window of palatability. Also, there are no closely related native species that may put at risk by exotic herbivores (Lambert *et al.* 2007). Given the low incidence of generalist herbivores and the nearly complete absence of co-evolved specialist herbivores, *A. donax* seem like a good candidate for biological control, since introduced specialists would have access to a large resource with little pre-existing competition.

However, Peterson et al. (2005) note that assessment of the efficacy of biological control agents, in terms of having a injurious effect on the target plant species, is an important aspect in the decision making process, and that evaluation of the change in plant physiology in response to herbivory is an effective tool in determining the value of introducing additional species to a given ecosystem. Moreover, it is important to understand the mechanism by which different potential biological control agents affect plant physiology, since simply removing photosynthetic material does not ensure that the photosynthetic rate (A) of active leaf tissue decreases. Studies have shown, however, stem-boring arthropods can cause a reduction in A in *Linaria dalmatica* (L.) Mill. (Peterson *et al.* 2005). One potential mechanism for this may be the disruption of the flow of carbohydrates belowground (Jeanneret and Schroeder 1992). The stress of weevil herbivory seems to mimic water stress in *L. dalmatica* because it elicits a similar response (Saner *et al.* 1994). It is logical that root-mining and water stress have similar effects on plants because they both reduce the amount of water that a plant can take up, albeit through different mechanisms (Gange and Brown 1989).

Studies on a wide variety of other plant species also demonstrate the efficacy of herbivores in negatively impacting the physiology of their hosts. Cherry (*Prunus serotina* (Ehrh.)) and sumac (*Rhus glabra* (L.)) leaves galled by a mite had rates of A reduced by 24-52%, and even undamaged, neighboring cherry leaves experienced 24% reductions in A (Larson 1998). Galls in an aster, *Parthenium hysterophorus* (L.), induced by a moth used as a biological control agent showed declines in A, transpiration (E_l), stomatal conductance (g_s), and xylem water potential (Ψ) (Florentine *et al.* 2005). The mechanism is thought to be reduced water movement due to the disruptions in conductive tissue through a combination of damage and blockage of the phloem and associated components of the parenchyma by gall tissue (Raman and Dhileepan 1999). Both fungal infection and wasp galls in leaves of a suite of understory hardwood species have been shown to reduce the efficiency of photosystem II (Φ_{PSII}), a fundamental component process of photosynthesis, by over 25% (Aldea *et al.* 2006). Interestingly, this same study found that fungal infection raised leaf temperatures in areas surrounding damage, which was thought to be a result of reduced g_s, while wasp galls depressed leaf temperatures near sites of damage, which was thought to be due to an increase in g_s (Aldea *et al.* 2006). Another invasive species, *Hydrilla verticillata* (L. f.) Royle suffered 30-40% reductions in A with light (10-30%) damage and up to a 60% reduction in A with heavy (70-90%) damage by the leaf-mining fly *Hydrellia pakistanae* (Deonier.) (Doyle *et al.* 2002).

Interestingly, similar research has also uncovered the opposite phenomenon, whereby the physiological processes within leaf tissues remain unchanged or even increase. A and E_l remained unchanged in both apple (*Pyrus malus* (L.) Mill.) and crabapple (*Pyrus coronaria* (L.) Mill.) leaves subjected to herbivory by the moth *Hyalophora cecropia* (L.) (Peterson *et al.* 1996). These plants simply had reduced leaf areas rather than adjusting rates of physiological processes, either upward or downward (Peterson *et al.* 1996). Fay et al. (1993) found that in well-watered rosinweed species, leaf gas exchange was unaffected by wasp galls, but galled drought-stressed individuals increased leaf A, g_s, and Ψ. In a later study, galled rosinweed (*Silphium integrifolium* (Michx.)) in a common garden experiment suffered initial reductions in leaf area and plant height, but the production of axillary meristems led to a recovery in the number of inflorescences and an even greater leaf area (Fay *et al.* 1996). However, rosinweed was incapable of reproducing this herbivory tolerant axillary growth under competitive field conditions (Fay *et al.* 1996). The willow, *Salix eriocarpa* (Fr. & Sav.) showed similar compensatory axillary growth when subjected to herbivory by a stem-galling midge (Nakamura *et al.* 2003). This same willow species also increased basal diameter in response to galls, which increased shoot survival rates and ultimately led to increased bud production (Nakamura and Ohgushi 2007).

Transpiration has also been shown to remain constant or even increase, on a unit leaf area basis, in plants subjected to herbivory. Damage to major veins by leaf perforation significantly increased g_s and E_l in birch (*Betula pendula* Roth) and alder (*Alnus* spp.) (Oleksyn *et al.* 1998), and such damage is noteworthy because of the fundamental role major veins play in the transport of water through leaves (Sack *et al.* 2003). Interestingly, in soybean, *Glysine max* (L.) Merr., leaf-mass consumption as well as simulated herbivory temporarily increased water loss as a linear function of the amount of cut edge per unit leaf but did not simultaneously affect leaf A (Macedo *et al.* 2003; Peterson and Higley 1996). Rates of leaf E_l remained at normal levels in the intact parts of the leaves (Peterson and Higley 1996), and in some cases leaf E_l was reduced below rates in unaffected leaves within a period of approximately 16 h (Macedo *et al.* 2003). In another study, soybean leaves experienced an approximately 40% reduction in E_l in the first week after herbivory compared to undamaged leaves, although A and g_s remained unchanged, and the suggested cause is water lost through the edges of damaged areas as well as through small breaks in the cuticle (Aldea *et al.* 2005). It is important that research on the physiological response of plants consider the possibility of compensation through an increase in A or, of greater concern in this study, potential increases in E_l. This is especially true for research that will help understand how various modes of herbivory elicit different physiological and morphological responses by plants (Peterson *et al.* 2005; Karban and Myers 1989; Spence *et al.* 2007; Aldea *et al.* 2005).

One of the foremost methods for managing *A. donax* is likely to be biological control. This study is unique in quantifying the effect of insect herbivores that are potential biological control agents on the rates of physiological processes in the host plant in advance of their approval and release in order to further inform the decision-making process. The main objective was to elucidate what effect these potential biological control agents may have on the leaf scale physiology of *A. donax*. A stem-galling wasp, *Tetramesa romana* (Walker) and an armored scale, *Rhizaspidiotus donacis* (Leonardi), were examined in terms of their efficacy in reducing leaf scale rates of A and E_l. The feeding method of *T. romana* is to form a gall within the meristem, generally near the apex, that acts as a sink for photosynthates, while that of *R. donacis* is to congregate at the base of leaf sheaths and at nodes along the stem and drink sap directly from the phloem (Gullan and Cranston 1994). The effect of the wasps was examined at two different population densities, while the effect of the scale was investigated at two different times in their developmental cycle. We expected that the wasp population density would play a strong role in the magnitude of any potential reduction in A and E_l, and we also anticipated that the greatest effect of the scale population on leaf physiological processes would come as adult females were nearing a reproductive cycle that would demand greater resource consumption. A final experiment examined the effect of the herbivores on leaf scale physiology when *T. romana* and *R. donacis* were used in combination. We expected that the combination of two herbivores with very different consumption strategies would lead to the highest magnitude reductions in A and E_l of *A. donax* leaves.

This study was completed during the biological control assessment process in order to provide feedback about physiological impacts of these particular exotic herbivores. This study also documents to the agencies responsible the degree of damage to fundamental physiological processes in *A. donax* that may be expected from the use of biological control in management of this invasive plant. Our secondary objective was to further understand the mechanisms by which these insects impact *A. donax* through investigation of their effects on g_s and intercellular CO_2 concentration (C_i) and through the examination of photosynthesis CO_2 (A/C_i) response curves. The shapes of these curves reveals potential decreases in carboxylation capacity or electron transport rate (Lambers *et al.* 1998; Larcher 2003), and thus illuminate impairment in the basic components of the photosynthetic machinery by the two herbivores (Ni *et al.* 2008; Schroder *et al.* 2005).

MATERIALS AND METHODS

This study was conducted as a series of greenhouse experiments set up in a quarantined facility located within Moore Air Base, operated by USDA-APHIS (Animal and Plant Health Inspection Service) in Hidalgo County, TX (26° 23' 39"N/98° 20' 7"W). Because of the quarantined nature of this effort, the initial experiments were established using the wasp, *T. romana*, and the scale, *R. donacis*, alone and in separate greenhouses. Within each of these two greenhouses, pots containing shoots of *A. donax* were allocated to separate cages for this experiment. Because of the mobility of *T. romana*, two identical cages, one each for the control and herbivory treatments, were established and lined with mesh that prevented individual wasps from either entering or leaving the cages. By contrast, mobility was not a concern for *R. donacis*, so rhizomes for each of the treatments were established in large pots that were not segregated from the rest of the greenhouse. To ensure that no individuals of *A. donax* were resource limited, all pots were filled with a fertilized, uniform potting soil and were watered twice daily. Furthermore, both greenhouses were supplied with artificial lighting (≥500 µmol m^{-2} s^{-1}) to provide at least 12 hours of light per day when day length was short. With the use of climate control, the greenhouse with *T. romana* was kept between 22 and 33 °C, and the *R. donacis* greenhouse was kept between 18 and 35 °C.

There were a total of two trials for *R. donacis*, one long-term (24 weeks) and one short-term (14 weeks). The long-term trial held 7 control shoots and 7 treatment shoots with an exposure level of approximately 500-700 first-instar crawler scale released onto each shoot, and the trial was conducted from 26 February to 16 August, 2007. The short-term trial consisted of 3 control shoots and 3 treatment shoots with an exposure level of a known minimum of 500 first-instar crawler scale released onto each shoot, and the trial was run from 24 November, 2007 to 3 March, 2008. Before the second trial was completed, one of the control shoots was broken during handling and was therefore not used. Leaf gas exchange survey data and CO_2 response curves were collected, and the parameters of interest were primarily carbon assimilation (A) and leaf transpiration (E_l), and secondarily stomatal conductance (g_s) and intercellular CO_2 concentration (C_i). Further details on sampling methodology and instrumentation used are provided below.

There were also a total of two experiments conducted to test the effect of *T. romana* on leaf physiology an initial low herbivore density experiment followed by a high herbivore density experiment. Within the greenhouse containing *T. romana*, during the low density treatment experiment, two identical cages, one per treatment, housed 6 potted plants each. The control and treatment cages each experienced similar environmental conditions. Three 6-week low density trials were run from May to June,

June to August, and October to November, 2007, consisting of a total of 12 shoots of *A. donax*, each at least 1 m tall, that were grown from rhizomes of a standardized weight in a uniform mixture of potting soil. The shoots were paired by size, with each pair being randomly divided between the two treatments, using height as a proxy for biomass (Spencer *et al.* 2006).

Approximately 20-25 adult female *T. romana* were released into the treatment cage at the start of each low density trial. This density level mimiced the densities of adventive *T. romana* populations in stands of *A. donax* in its invasive range (Moran, pers. comm.). This density was well below the minimum release rate that is the goal of the biological control program and does not reflect population densities in the wasp's native range. Because the generation time of *T. romana* is approximately 4 weeks (~25 days as larvae, 7 days as pupae) (Moran and Goolsby 2009), leaf gas exchange survey data as well as CO_2 response curves were collected as near to 4 weeks from the onset of each trial as possible using the methodology and instrumentation described below. During the final low density trial, two ramets from the control group were broken at the main stem before gas exchange measurements could be conducted and were therefore excluded from the study.

The high density experiment was conducted as a part of a single long-term trial that maintained a *T. romana* only treatment. Roughly one third of the *T. romana* greenhouse was blocked off with the same fine black mesh used in cage construction, and this space was further divided to separate treatment and control sections. Seven potted plants of *A. donax* were added to each section. *T. romana* were released in high density into the treatment section, with an initial minimum of 60 wasps. Seven wasps per ramet per week were added, including additional wasps for ramets that appeared in the course of the trial. This treatment was considered high density because it approximates the level of the intended future mass releases of *T. romana* at established sites of *A. donax*, and it is assumed that the target *T. romana* population densities exceed the density of natural populations anywhere in the native and naturalized range of *A. donax* (Goolsby, pers. comm.). In addition to the high density *T. romana* only trial, a simultaneous trial added another treatment – combined herbivory by *R. donacis* in addition to the high densities of *T. romana*. This trial consisted of 7 additional pots, each starting out with a single shoot, and was also located within the same *T. romana* treatment section of the greenhouse. These pots were not separated from the wasp only high density treatment because of the negligible mobility of *R. donacis*, even in the first-instar crawling stage. A minimum of 500 first-instar *R. donacis* crawlers were released on the internodes of each of these ramets at the onset of the trial. Leaf gas exchange survey data and CO_2 response curves were recorded after 10 weeks and 26 weeks of exposure to herbivory to give the trial enough time to experience at least two generations of *T. romana* and one generation of *R. donacis*, respectively.

All leaf gas exchange data were collected using a LI-6400 open-pathway system with 6400-02B LED Light Source and 6400-01 CO_2 Injector. For each shoot, only the second fully expanded leaf was used for measurements in order to control for the effect of leaf age (Hikosaka 2005). All measurements were conducted between 10:30 and 14:30 CST, with photosynthetic photon flux density (PPFD) fixed at 1500 μmol m^{-2} s^{-1}

and CO_2 concentration at 370 μmol mol^{-1}. Leaves were given a minimum of 5 minutes to adjust to the conditions in the cuvette. Leaf gas exchange measurements were repeated on at least two, and usually three, consecutive days in order to obtain an average value per shoot. Calculations of the physiological parameters A, E_l, g_s, and C_i were as described by von Caemmerer and Farquhar (1981) and adjusted for sampled leaf area.

In order to understand through what mechanism the two herbivores, separately and in combination, impacted leaf scale physiology, we examined the shapes of A/C_i response curves for any changes in the Rubisco-limited carboxylation capacity or electron transport rate (Lambers *et al.* 1998). These measurements were taken once per leaf for each plant in each treatment. A/C_i response curves were generated at intervals of 50 μmol mol^{-1} from 50 to 400 μmol mol^{-1} and intervals of 100 μmol mol^{-1} from 400 to 800 μmol mol^{-1}. In order to model maximum carboxylation rate of Rubisco (V_{cmax}) and maximum rate of electron transport (J_{max}), values for necessary parameters were taken from Sharkey et al. (2007). The activation energy (E_a) of *A. donax* was assumed to be 60 kJ mol^{-1}, a value expected for a C-3 plant from a warm environment (Sage 2002).

SPSS 14.0 was used to analyze the data established as a randomized block design in which data were blocked by initial plant height. In order to compare between treatments, data were screened for outliers and checked for normality, then one-tailed Student's t-tests were used at a significance level of $\alpha = 0.05$. When the Levene's test for equality of variances failed ($P < 0.05$), data were compared assuming unequal variances. One-tailed tests were deemed appropriate due to the hypothesis that in all cases physiological processes will be reduced due to the method of herbivory by each of the two insects (Larson 1998; Meyer and Whitlow 1992; Peterson 2001; Peterson *et al.* 2005; Raghu and Dhileepan 2005; Raghu *et al.* 2006), and doing so enabled us to minimize Type II errors. Separate Student's t-tests were conducted for the *R. donacis* experiment (pooled for both trials due to low sample size), the low and high density *T. romana* trials, and the 10-week and 26-week combined *R. donacis*/ *T. romana* trials. Additionally, component slopes of the A/Ci response curves corresponding to Rubisco-limited carboxylation capacity or electron transport rate were compared to elucidate the mechanistic differences between the way different injury guilds elicit responses in *A. donax* (Macedo *et al.* 2005; Peterson *et al.* 2005).

RESULTS AND DISCUSSION

R. donacis effectively reduced leaf gas exchange rates in *A. donax*. Mean E_l was 40% lower in leaves of plants with *R. donacis* than in control plants after several months of exposure to the herbivore (Table 2). Furthermore, mean g_s was 46% lower in plants subject to herbivory (Table 2). These strong reductions in water use were anticipated because of the nature of the method of feeding by *R. donacis*. As plants lose sap to scale herbivory, leaves are more likely to wilt or distort (Gullan and Cranston 1994), which may explain reductions in E_l and g_s . Since scale insects feed directly on nutrients in fluids from the phloem, they can act as a sink for photosynthates that would otherwise be directed towards plant growth, maintenance, or storage (Risebrow and Dixon 1987), but contrary to our expectation, we found only weak evidence of a reduction in A_l (Table 2).

Mean A_l in leaves of plants with *R. donacis* was over 32% lower than mean A_l in control leaves (Table 2); however, this reduction in treated plants was only marginally

Table 2. The efficacy of two herbivores, separately and in combination, in reducing crucial parameters of leaf scale physiology. Shown are: photosynthesis (A), transpiration (E_l), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i). Mean ± standard error shown. Asterisks represent significance values of one-tailed Student's t-tests: * denotes $P < 0.05$; ** denotes $P < 0.01$; *** denotes $P < 0.001$. Single dash denotes not significant.

Agent	Experiment	A					E_l					g_s					C_i				
		C		T		Sig.	C		T		Sig.	C		T		Sig.	C		T		Sig.
		Mean	S.E.	Mean	S.E.		Mean	S.E.	Mean	S.E.		Mean	S.E.	Mean	S.E.		Mean	S.E.	Mean	S.E.	
R. donacis	——	10.21	1.58	6.92	1.12	—	3.44	0.41	2.08	0.21	**	0.22	0.03	0.12	0.01	**	278.1	9.1	267.0	7.9	—
T. romana	Low density	12.21	1.34	11.66	1.38	—	3.47	0.29	3.24	0.26	—	0.22	0.03	0.16	0.02	*	253.4	8.3	230.9	7.4	*
	High density	10.39	0.91	8.39	0.51	*	3.94	0.46	2.87	0.22	*	0.17	0.03	0.12	0.01	*	246.3	8.0	231.1	6.1	—
T. romana /	10 weeks	10.39	0.91	8.52	0.61	—	3.94	0.46	4.22	0.43	—	0.17	0.03	0.18	0.02	—	246.3	8.0	261.0	8.9	—
R. donacis	26 weeks	9.71	0.80	3.19	0.39	***	3.11	0.37	1.80	0.49	*	0.14	0.02	0.09	0.03	—	243.8	5.7	303.9	11.3	***

significant (*t* = 1.719, *d.f.* = 17, *P* < 0.052). This is likely a result of the large variance between leaves in the same treatment. The standard error was 15.5% and 16.2% of the mean for the control and scale treatments, respectively. Meyer and Whitlow (1992) also reported no effect of a phloem-feeding insect on rates of A_l in goldenrod, *Solidago altissima* (L.), normalized by leaf weight. The aphid used in Meyer and Whitlow's study actually had no measurable effect on any investigated parameter, including E_l, g_s, and C_i, though it should be noted the duration for which plants were exposed to herbivory was limited to 12 days (1992).

Because *R. donacis* had not yet reproduced at the time of the measurement in the short-term trial (Moran and Goolsby 2009), we investigated whether this affected our results. When those short-term data were excluded from the analysis, A_l differed between treatments (*t* = 2.279 , *d.f.* = 12, *P* < 0.025). *A. donax* leaf responses to herbivory by *R. donacis* were apparently sensitive to time of exposure, which is consistent with previously reported results for a tropical scale (Schaffer and Mason 1990). *R. donacis* may not be capable of negatively impacting physiological processes until after they produce offspring, which occurred between the 14-week and 24-week trials. It has already been shown elsewhere that as scale reach sexual maturity or some other significant stage in their life history, their demand for resources increases (Rees and Crawley 1989; Boggs 1992). *R. donacis* females do not produce offspring until at least 120 days when they are removed from the plant artificially and the next generation is not found on the plant until over 160 days when females are allowed to remain on the shoots (Moran and Goolsby 2009). The earlier instars may not take up many resources, and only when later life stages are reached does the collective herbivory of many individuals begin to adversely affect physiological processes in 'downstream' leaves that would otherwise have utilized the consumed resources.

The A_l/C_i response curve yields further evidence for the negative effects of 24 weeks of herbivory by *R. donacis* on leaf scale physiological processes. J_{max} was drastically reduced by *R. donacis* (Table 3, Figure 6), so the presence of this herbivore clearly lowered the overall maximum rate of photosynthesis when CO_2 availability was not a limiting factor. V_{cmax} was also reduced, but the magnitude of the decrease was much smaller, indicating that there may be some limited effect of *R. donacis* on the efficacy of Rubisco in *A. donax*. *R. donacis* may have been a sink for photosynthates that otherwise would have been directed toward root growth, leading to a potential reduction in nutrient uptake (Li *et al.* 2006). Because J_{max} is an estimate of the maximal rate of electron transport by proteins in the photosynthetic apparatus (von Caemmerer and Farquhar 1981), a reduction in J_{max} could indicate that less nitrogen was being allocated to those crucial proteins (Hikosaka and Terashima 1996; Hikosaka 2004).

Herbivory by low densities of the galling wasp *T. romana* did not reduce the rates of either of the basic physiological processes of A_l or E_l in leaves of *A. donax* (Table 2). C_i and g_s were reduced by 9% and 26%, respectively (Table 2). The decrease in C_i without a significant reduction A_l may be due to some compensation on the part of *A. donax* if leaves were able to more effectively utilize the available CO_2 in the intercellular airspaces. This situation would only plausibly arise if stomata were closed more in leaves of plants with galls, which the reduction in g_s suggests. It was unexpected

Table 3. The efficacy of two insect herbivores, separately and in combination, in reducing the carboxylation rate of Rubisco (V_{cmax}) and the rate of electron transport (J_{max}). Mean and percent difference shown. C and T represent Control and Treatment, respectively.

Agent	V_{cmax}			J_{max}		
	C	T	% diff.	C	T	% diff.
R. donacis	59.9	49.1	-18.0	78.7	30.9	-60.7
T. romana	63.3	67.7	7.0	90.7	97.0	6.9
T. romana/R. donacis	38.7	12.6	-67.5	48.5	24.5	-49.4

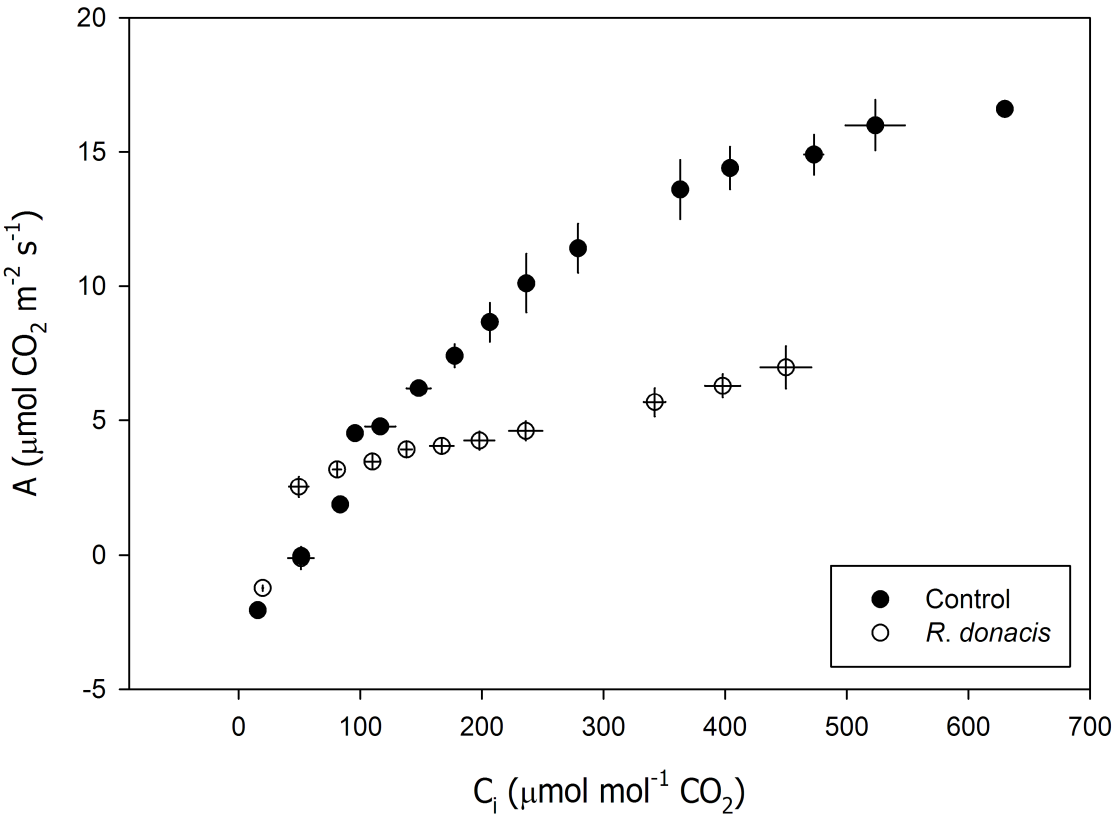

Figure 6. CO_2 response of leaves of *A*. *donax* to 24 weeks of exposure to herbivory from the armored scale, *R*. *donacis*. Mean values ± standard error are given. Photosynthetic photon flux density was 1500 μmol m^{-2} s^{-1}.

though, that such a strong reduction in g_s would not lead to a similar reduction in E_l. It may be the case that changes occurred below the detectable limit, especially since g_s is largely derived from E_l (von Caemmerer and Farquhar 1981). Leaf temperature and atmospheric pressure also factor into the calculation of g_s, so these variables were also compared between treatments, but no differences were found (data not shown). This is likely an indication that the E_l data had large enough variances to preclude statistical differentiation between treatments. Nonetheless, the ability of *A. donax* to balance the fundamental physiological processes of A_l and E_l did not seem to be perturbed by herbivory by *T. romana* at low density. Additionally, the A_l/C_i response curves for the low density treatment of *T. romana* demonstrated that there was little effect on *A. donax* physiology. Neither V_{cmax} nor J_{max} were much different in the plants experiencing herbivory (Table 3, Figure 7).

By contrast, when *T. romana* was present in high density, the response of *A. donax* to herbivory was quite distinct. A_l, E_l, and g_s were all lower in shoots that experienced herbivory, while C_i was not different between the two treatments (Table 2). In the high density treatment, A_l, E_l, and g_s were 19%, 27%, and 32% lower compared with control plants. The observation that both A_l and E_l are markedly lower in galled shoots in the high density treatment, in contrast with the low density experiment, clearly indicates that the effect of herbivory on *A. donax* by *T. romana* is density dependent. This phenomenon has been documented for galls by cynipid wasps on leaves (Bagatto *et al.* 1996; Dorchin *et al.* 2006), but to our knowledge, this is this first time this type of relationship has been documented for stem-galling wasps.

After 10 weeks of exposure to both *R. donacis* and high density *T. romana*, only A_l was marginally affected by this treatment ($t = 1.751$, $d.f. = 13$, $P < 0.052$). A_l in leaves from plants with herbivores was 18% lower than control leaves (Table 2), while none of E_l, C_i, or g_s were different between the two treatments. This is in contrast with the experiment of herbivory by *T. romana* alone while still in high density, in which, within 10 weeks, clear differences in these physiological parameters were evident (Table 2). Because these trials occurred simultaneously and within the same enclosure space, both the *T. romana* high density trials (with and without *R. donacis*) experienced similar levels of herbivory, which implies that leaves of *A. donax* exhibit a compensatory response when the shoot experiences multiple forms of herbivory. Another plausible explanation is that adult *T. romana* avoided shoots with *R. donacis* present in order to reduce interspecific competition, and that as time passed, there was a cumulative effect on leaf physiology that led to the difference between these treatments in leaf scale physiology after 10 weeks.

Apparently, compensation, if any, only lasts for a limited time, because 26 weeks after the two herbivores were released onto *A. donax*, very strong differences between the treatments had become manifest. A_l and E_l were lower in leaves of attacked shoots than in leaves of shoots without herbivores by 67% and 42%, respectively (Table 2). Conversely, C_i was greater in the herbivory treatment by approximately 25%, but g_s was not different between treatments (Table 2). This may be an indication that leaves of galled shoots are susceptible to increased water loss through parts of the leaf other than the stomata. Such strong reductions in A_l suggests that, as has been previously discussed

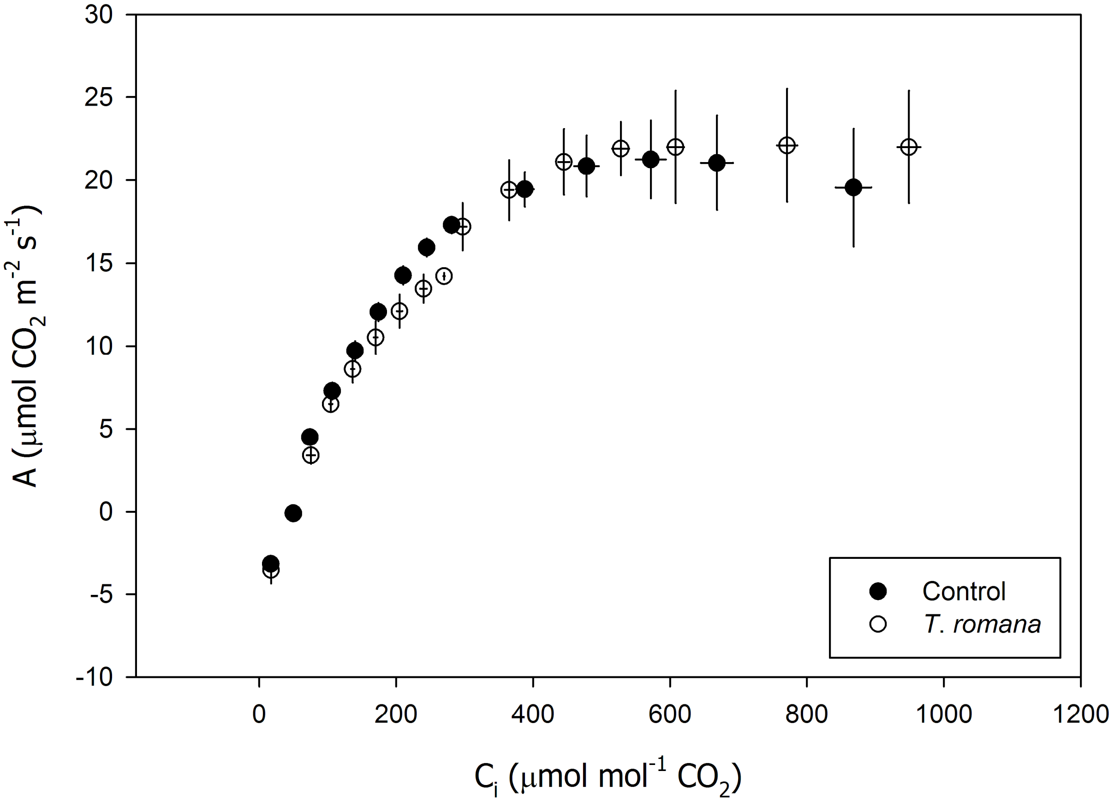

Figure 7. CO_2 response of leaves of *A. donax* to herbivory from low densities of the stem-galling wasp, *T. romana*. Mean values ± standard error are given. Photosynthetic photon flux density was 1500 μmol m^{-2} s^{-1}.

in the *R. donacis* only trials, as the scale reach the later stages of development and into the second generation, demand for photosynthates increased. These leaves do not appear to have lost stomatal control, as g_s remained unchanged, but the reduction in carbon assimilation is corroborated by the much higher CO_2 concentration in intercellular air spaces. This likely indicates that the photosynthetic machinery in the leaves subjected to prolonged herbivory by both insects is less capable of utilizing available carbon (Meyer and Whitlow 1992).

The A_l/C_i response of *A. donax* after 26 weeks of exposure to the two herbivores also points to a large cumulative impact, each likely acting in a different capacity. For example, a similar reduction in J_{max} to the presence of *R. donacis* alone was observed, suggesting this species negatively affects the process of electron transport (Table 3, Figure 8). Conversely, the much greater reduction in V_{cmax} with the additional presence of high densities of *T. romana* suggests that the carboxylation capacity of Rubisco was reduced largely as a result of the presence of a large number of galls (Table 3, Figure 8). Plants are already known to reduce both V_{cmax} and J_{max} in the presence of herbivores (Schroder *et al.* 2005), so this outcome was anticipated. The presence of two herbivores in large numbers may also induce *A. donax* into the production of plant secondary metabolites that would act as a further sink for energy gained from photosynthesis (Karban and Myers 1989), although their study did not explicitly address this question. However, this study is among the first to document that two insect herbivores differentially affect the physiology of their host species (Peterson *et al.* 2005). Because neither of these two insects feed by leaf consumption, understanding of the mechanisms

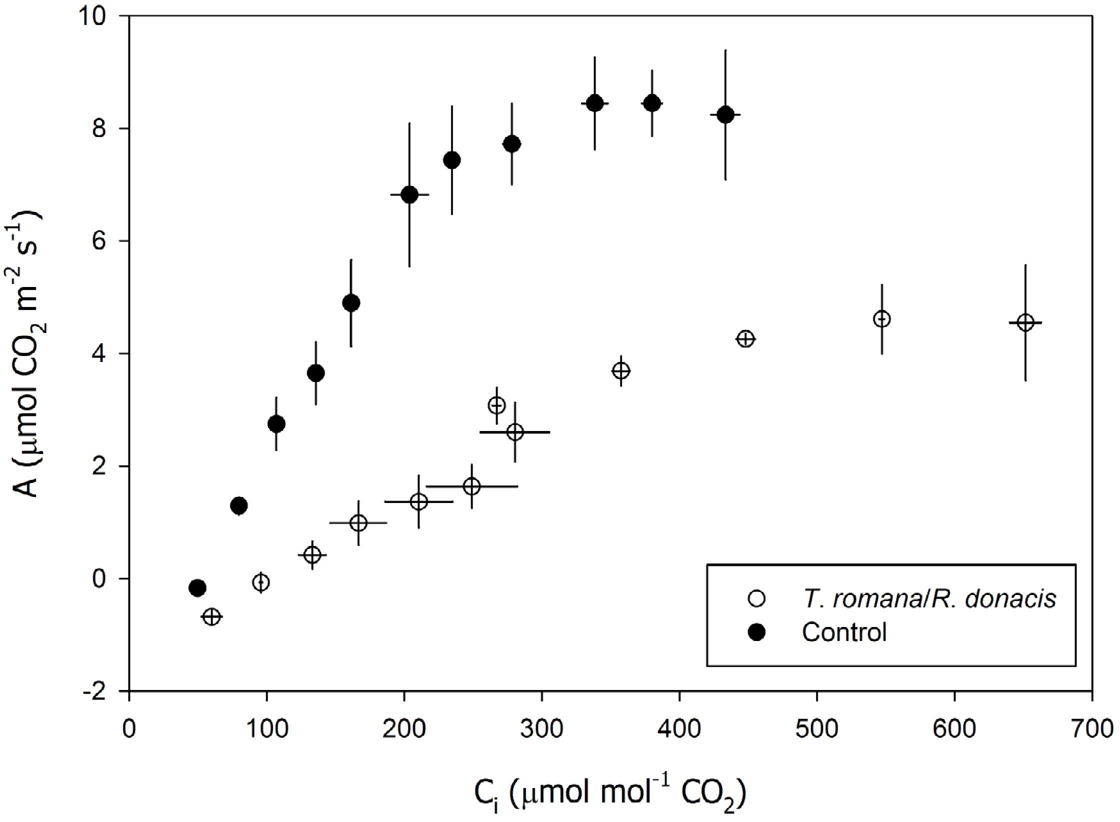

Figure 8. CO_2 response of leaves of *A. donax* to 26 weeks of herbivory from *R. donacis* and high densities of *T. romana*. Mean values ± standard error are given. Photosynthetic photon flux density was 1500 μmol m^{-2} s^{-1}.

by which they impact leaf scale processes is particularly lacking (Karban and Baldwin 1997).

From what little research has been done on combined herbivory by two or more phytophagous insects with differing foraging methods, we have learned that effects are not always directly additive (Meyer and Whitlow 1992). Results led to the evolution of the concept of the injury guild, which is simply the grouping of herbivores by the type of damage inflicted on plants rather than by taxonomic association, and examples include leaf mining, leaf mass consumption, and stem boring (Peterson 2001). It is well established that plants respond differently to these various forms of herbivory (Gavloski and Lamb 2000; Trumble *et al.* 1993). The data from these trials suggests that stem-galling negatively impacts the ability of *A. donax* to optimize the relationship between carbon gain and water loss, but that the addition of a sap-feeding insect may stimulate some temporary compensation by the plant. The trials of *R. donacis*, alone and combined with *T. romana*, have shown that it takes a comparatively long time for sap-feeding insects to impact physiological processes. However, once this temporal threshold is crossed, there do seem to be additive effects from both injury guild representatives on characteristics of leaf gas exchange, as the trial with the most deleterious impacts on *A. donax* was with both herbivores present. One possible explanation for this time lag may be that *A. donax* resorts to using stored carbon resources in its attempts to continue to produce young tissue (Boose and Holt 1999; Decruyenaere and Holt 2001), but once these resources become exhausted, the vigor of individual plants then begins to decline strongly.

In conclusion, the results of our greenhouse study clearly demonstrate that the stem-galling wasp *T. romana* is effective at inhibiting leaf-scale physiological processes of *A. donax* when present in high densities and that the armored scale *R. donacis* is also effective in reducing the rates of A_l and E_l given enough time. Moreover, these two insect herbivores seem to impact *A. donax* leaf physiology differentially, as *T. romana* appears to reduce the carboxylation capacity of Rubisco, while *R. donacis* measurably lowers the rate of electron transport.

CHAPTER IV

CONCLUSIONS

A model was developed to estimate stand scale water use in the invasive species *Arundo donax* (L.) in the lower Rio Grande basin. This study was the first attempt at quantifying water use in this species at any spatial or temporal scale. This model was based on using directly measured rates of transpiration to yield stand scale rates of transpiration by incorporating within-stand variability. Spatial heterogeneity was incorporated into the model through the measurement of vertical variation in parameters like leaf area index and light availability over four plots of increasing lateral distance from the edge of the water source. This model showed that mean stand scale transpiration for *A. donax* is approximately 9.1 mm per day, indicating that this species is at the high end of water use. By comparison, the highest values stand scale transpiration in the genus *Carex* is 8.8 mm per day (Busch 2001), while peak stand scale transpiration in *P. australis* was approximately 23 mm per day (Moro *et al.* 2004). *A. donax* is estimated to produce about 20 Mg per hectare per year on natural stands in sites in India and the United States (Sharma *et al.* 1998; Spencer *et al.* 2006), which is roughly 50% lower than yields of cropped C-3 plants (Nobel 1991).

The magnitude to which *A. donax* affects in-stream water resources remains somewhat unclear. Stand scale water use was much greater following periods of appreciable rainfall, suggesting that this species is not a true phreatophyte. Future work on tracing the source of the water used through the use of isotope analyses may elucidate to what degree *A. donax* uses water derived from streamflow or from soil moisture resources maintained by precipitation (Dawson 1993; Dawson and Ehleringer 1991; Lamontagne *et al.* 2005; Yakir *et al.* 1990). Furthermore, additional investigations into the potential for physiological integration, whereby connected ramets could simultaneously share resources like water, photosynthates, and nutrients (de Kroon *et al.* 1998), using tracers, such as isotopes or dyes (de Kroon *et al.* 1996; Liu *et al.* 2007; Zhang *et al.* 2003) in common garden experiments or field studies, could elucidate the mechanism by which *A. donax* is capable of such high rates of stand scale transpiration.

Additionally, this study quantified the efficacy of two potential biological control agents, a stem-galling wasp, *Tetramesa romana* (Walker), and an armored scale, *Rhizaspidiotus donacis* (Leonardi), in negatively impacting the leaf scale physiological processes of *A. donax*. *T. romana* was shown to be effective in reducing rates of key characteristics, such as photosynthesis and transpiration, when present in high density. *R. donacis* was effective at reducing these aspects of leaf physiology given enough time (24 weeks), and this coincided with the time necessary for a full reproduction cycle. The result of having the two herbivores feeding on *A. donax* concurrently was a seemingly additive effect on leaf scale physiology, but only after 26 weeks. CO_2 response curves indicated that *R. donacis* affected the rate of electron transport while *T. romana* impacted the carboxylation rate of Rubisco.

Theoretically, these physiological data could potentially be used in economic models, in conjunction with morphometric data, to estimate the value of potential water savings based on scenarios of reductions in water use by *A. donax*. There is, however, much uncertainty about the degree to which the magnitude of the effects of these herbivores holds at larger spatial and longer temporal scales. Moreover, further work on any mediation of the negative impact of one herbivore through the addition of a second herbivore may provide greater insight into the mechanisms behind plant responses to herbivory and whether this is partly a cause of the injury guild of the herbivores. Based on the results from this study, if the insect populations are maintained at a high enough density and given sufficient time to impact crucial physiological properties, the biological control of *A. donax* will likely enervate established stands of this highly invasive species.

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