



Water-Use Dynamics of an Invasive Reed, *Arundo donax*, from Leaf to Stand

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Abstract We investigated water use of an invasive riparian reed species, *Arundo donax* (L.), along moisture gradients to determine how extensively this plant might affect water resources. On an approximately 250 m stretch of the Lower Rio Grande in South Texas, we measured the gas exchange of water vapor at the leaf scale and structural characteristics, such as leaf area and shoot density, at the stand scale. To assess the effect of water availability, we used transects perpendicular to the edge of the river along a potential moisture gradient. Stands of *A. donax* used approximately 8.8 ± 0.9 mm of water per day during the peak of the 2008 growing season; this rate of water use is at the high end of the spectrum for plants. Transpiration and leaf area index varied with water availability, which suggests this plant is sensitive to drought and declining water tables. This provides a baseline for future studies comparing water use between *A. donax* and other plant species, especially native species considered in riparian restoration efforts.

Keywords Ecohydrology · Ecophysiology · Giant reed · Invasive species · Riparian vegetation · Scaling

Introduction

Invasive species have altered the structure and function of numerous ecosystems (Vitousek 1990; Walker and Smith 1997; D'Antonio et al. 1999; Parker et al. 1999; Belnap et al. 2005; Lau 2008). In water-limited river systems, there are added pressures from riparian invasive species (Dukes and Mooney 2004), which can not only alter the dynamics between vegetation and geomorphology in riparian systems (Rowntree 1991), but negatively affect 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). Much recent attention has been paid to the role of invasive semiarid woody plants, such as saltcedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia* L.) (Devitt et al. 1998; Dahm et al. 2002; Katz and Shafroth 2003; Nagler et al. 2003; Cleverly et al. 2006; Nagler et al. 2008) in the water cycle because they may compete for water resources aggressively (Wilcox and Thurow 2006). However, the water regained by invasive plant removal is not easily predictable in semiarid and arid landscapes (Wilcox 2002; Huxman et al. 2005). Owens and Moore (2007) have pointed out that, in some cases, predictions for water savings from these efforts have been unrealistically high.

Although interactions between water sources and riparian forests have been studied (Clinton et al. 2002; Wagner and Bretschko 2003), little is known about the interactions between nonwoody vegetation and saturated or vadose zones of riparian corridors. Impacts of invasive grasses on water resources in particular have been understudied (Milton 2004), largely due to the focus on highly problematic woody invaders (Richardson and van Wilgen 2004).

Giant reed (*Arundo donax* L.) has been in the southwestern United States since at least the early 19th century

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(Dudley 2000) and is now found in the 25 southernmost states (Bell 1997). This species covers approximately 4,800 ha of riparian area in the Rio Grande basin of Mexico (Yang et al. 2009) and is targeted for control in parts of its introduced range (Milton 2004). Quantifying variation in the water use of *A. donax* is an important step in understanding how its invasion affects the water cycle, but as with many riparian plants (Tabacchi et al. 2000), this basic information is lacking. Iverson (1998) reported its water consumption at over 1,700 mm year⁻¹ by assuming that *A. donax* transpires the same quantity of water as rice. This figure exceeds evapotranspiration values measured in riparian woodland systems in the southwestern United States, including dense, multi-story canopies, by 18–40% (Devitt et al. 1998; Cleverly et al. 2002; Dahm et al. 2002).

Fluctuations in water supply 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). Some nonphreatophytic riparian vegetation responds largely to either recent rainfall or water from deeper in the soil profile without using much or even any groundwater (Dawson and Ehleringer 1991; Scott et al. 2000). Thus, as soil moisture in riparian zones varies interannually and seasonally due to precipitation fluctuations (Joris and Feyen 2003), transpiration rates of riparian vegetation can be accordingly dynamic (Williams et al. 2006).

This study represents a critical step (Baldocchi et al. 1996) in characterizing the dynamics of how *A. donax* impacts water resources. First, we examined spatiotemporal variability in transpiration by examining *A. donax* stand structure, leaf gas exchange, and water use efficiency along potential water supply gradients perpendicular to the Rio Grande. We tested the hypotheses that (a) leaf area and leaf level transpiration declined with distance away from the river; (b) any seasonality in the above spatial trends was driven by water availability gradients, i.e., a more pronounced trend with distance would occur during warm seasons with high evaporative demand; and (c) within-stand spatial variability was more pronounced during drought. Second, we used a bottom-up approach to scaling to estimate stand level transpiration (Baldocchi et al. 1991) based on observed spatial and temporal variance.

Methods

Study Site

This study was conducted adjacent to the Rio Grande (26° 01'53" N, 97°43'41" W, 15 m.a.s.l.) in Cameron County,

Texas. Mean annual precipitation was 715 mm and monthly average temperatures ranged from 9 to 21°C in January and 23 to 35°C in August and September (TAES 2007). 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).

Twelve transects were established immediately adjacent and perpendicular to the Rio Grande within a large monoculture of *A. donax*. Few other plant species were present at the site except a sparse ground cover layer consisting largely of buffel grass, *Pennisetum ciliare* (L.) Link. Transects were located perpendicular to the river in continuous stands whose slope was sufficient to allow for a potential gradient in plant available water from river edge to upper bank. *Arundo donax* extended at least 1 m beyond each transect, minimizing edge effects (Spencer et al. 2005). Four 1.0-m² plots were spaced evenly within each transect. 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 leaf gas exchange, stand structure, and water use efficiency.

Data Collection

In three transects, gas exchange measurements were taken on 23 separate days between the period of 27 June 2007 through 22 July 2008 using a LI-6400 portable infrared gas analyzer (LI-COR, Inc., Lincoln, NE, USA). Within each plot, four stems were selected from within the subset of all stems that both reached the top of the sunlit canopy and retained the apical meristem (Peterson and Chesson 2002), and the chosen stems did not appear to emerge from the same rhizome (Decruyenaere and Holt 2005). For 18 of the 23 sampling days, measurements were taken at midday (between 1000 and 1400 h CST) to capture peak rates of physiological processes. Leaf transpiration rates (E_l), were averaged for each stem for a single midday value. On the remaining 5 days, diurnal changes in gas exchange were measured on all stems within one of the three transects every 2 h between 0700 and 1900 CST. Gas exchange measurements were conducted on clear days whenever possible, although 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 h on days of diurnal samplings), and CO₂ concentration was set to maintain 370 μmol mol⁻¹ in the sample chamber.

To estimate seasonal leaf water use efficiency (Ehleringer et al. 1993; Dawson et al. 2002), the same leaf tissue used for diurnal measurements of gas exchange collected on 3 to 5 June 2008 was analyzed for total C, total N, and stable carbon isotope ratios ($\delta^{13}\text{C}$) using an elemental analyzer (Carlo Erba EA-1108, CE Elantech, Lakewood, NJ, USA) interfaced with a Delta-plus mass spectrometer (ThermoFinnigan, San Jose, CA, USA). Also within the three transects selected for leaf gas exchange, predawn and midday leaf water potentials (Ψ_{pd} and Ψ_{md} , respectively) were measured on 10 days using a pressure chamber (PMS Instrument Co., Albany, OR, USA). On each day, 12 to 16 Ψ_{pd} measurements ($n=3/\text{plot}$) were completed before astronomical sunrise, and at least an equivalent number of Ψ_{md} measurements were taken on the same day between 1100 and 1400.

We also looked for spatial trends in soil moisture by taking volumetric water content (VWC) measurements in the top 20 cm of soil in each of the four cardinal directions within 1.0 m from the center of each gas exchange plot on 4 June 2008. Soil samples were also collected from 0 to 10 and 10 to 20 cm at 1.0–2.0 m distance laterally from the plot's center, and analyzed for total C, N, and P, as well as pH, cation exchange capacity, and base saturation by the Forest Science Laboratory at Texas A&M University (Sparks et al. 1996). Daily weather data, including reference evapotranspiration (ET_0) and precipitation, were obtained from the nearest weather station, the Texas AgriLife Research Weslaco Center (26° 9'52" N, 97°57' 25" W).

Nine other transects ≥ 5 m away from (between or outside) the gas exchange transects were allocated for one-time destructive sampling and harvested at approximately two-month intervals from July 2007 through March 2008, and again in July 2008. Plots in these transects were divided into three vertical sections—the upper (LAI_U), middle (LAI_M), and lower (LAI_L) portions of the canopy—that were partitioned equally, relative to the height of the tallest stems near each transect. The stem density, and diameter and height of each stem, were recorded in each plot. Total leaf area within 0.25-m² subplots was quantified using a LI-3100 C leaf area meter (LI-COR, Inc., Lincoln, NE, USA) for five transects in order to develop Eq. 1. All stems were then cut at ground level and oven-dried at 60°C for biomass measurements. Leaf area index (LAI) for each 1.0-m² plot was then estimated by the relationship,

$$L_s = e^{(4.293 - 0.010D + 0.853 \ln M)} \quad (1)$$

between leaf area (L_s , cm²) and biomass (M , grams) of each stem and its distance from the river (D , m). Values of L_s for each stem harvested within the subplots were summed, converted to m², then multiplied by four to yield a value of LAI for a 1.0-m² plot. Equation 1 was derived from a

multiple regression model of leaf area ($R^2=0.912$, $N=90$, $P \leq 0.05$). For one transect from this site, specific leaf area (SLA) was determined by weighing dry leaf material separately from stem material for 5 random stems from each plot before measuring leaf area.

Analysis

To compare between growing seasons, data were combined into three groups: summer 2007 (June to July), winter 2007/2008 (November to February), and summer 2008 (May to July). We used a one-way analysis of variance (ANOVA), followed by Fisher's LSD pairwise comparisons of plot means for all transects and sampling dates, to test whether the following varied with distance from the river or among transects: $\delta^{13}\text{C}$, E_t , LAI, leaf Ψ_{pd} and Ψ_{md} , leaf C and N, and soil VWC, C, N, P, pH, cation exchange capacity, and base saturation. All statistical analyses were conducted using SPSS 14.0.2 (SPSS Inc., Chicago, IL, USA).

Season could not be included in the preceding analyses because the same stems were used for gas exchange in the winter and summer of 2008; inclusion would violate the assumption of independence in ANOVA. Instead of comparing all seasons, 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 stem. 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:

$$E_{\text{stand}} = (E_U \times \text{LAI}_U) + (E_M \times \text{LAI}_M) + (E_L \times \text{LAI}_L) \quad (2)$$

Diurnal estimates for each day were based on peak midday values and the shape of second-order polynomial curves fit to gas exchange measurements conducted for an entire diurnal cycle. To be conservative, we assumed that transpiration was zero at night, increased linearly from dawn until the first morning measurement at 0700, and declined linearly to zero from the last evening measurement at 1900 until twilight, which yielded curves similar to the diurnal pattern in the mature stage of *P. australis* (Zhou and Zhou 2009). The model partitioned 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

corresponding transpiration values from light response curves conducted on shaded leaves (Niinemets 2007). This is the most conservative method in this type of scaling (Dang et al. 1997). Instantaneous gas exchange values, in $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$, were integrated for each day and converted to mm day^{-1} . This was done for each plot and canopy layer, and using the LAI for each of the three vertical sections, total daily transpiration per unit ground area (E_{stand}), expressed in mm day^{-1} , was calculated (Eq. 2).

Results and Discussion

Within-Stand Dynamics

Stable carbon isotope ratios ($\delta^{13}\text{C}$) of leaves collected during the dry summer of 2008 provided a more time-integrated perspective of leaf level water use efficiency (or carbon gained per unit water lost) in stand moisture gradients than in situ soil moisture or leaf water status measurements. Results suggested that water use efficiency was higher at greater distances away from the river. The mean value of $\delta^{13}\text{C}$ for plots nearest the river (Plot 1) was the most negative; it was lower than those of Plots 3 and 4 by 0.54‰ and 0.76‰, respectively (Fig. 1). Plot 4, farthest from the river, had the least negative values. Given that these leaves varied in their water use efficiency, these results suggest that plant available water decreased with increasing distance from the river.

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 affect leaf nutrient status. At our site, however, both leaf N and several measures of soil fertility indicated no difference

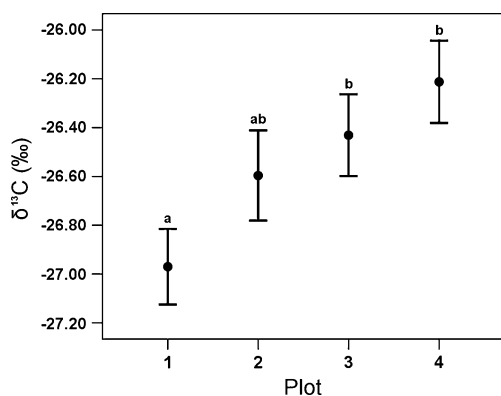


Fig. 1 The relative water use efficiency of young leaves of giant reed as measured by carbon isotope discrimination ($\delta^{13}\text{C}$) in parts per thousand ($N=3$). Plot 1 is closest to the river channel; plot 4 is at the greatest distance. Letters indicate significance of *post hoc* pairwise comparisons (Fisher's LSD) between plots' means ($P \leq 0.05$)

with distance to the river, supporting water limitation as the driver for differences in both LAI and E_t . 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 $\delta^{13}\text{C}$ (adjusted $R^2 < 0.001$, not shown), further indicating that the variation in $\delta^{13}\text{C}$ values likely reflected differences in stomatal conductance rather than leaf chemistry. Cation exchange, base saturation, pH, soil C, soil N, and soil P content did not vary with distance to the river in the top 20 cm of soil (Table 2). We would expect differences in plant available N to be reflected in *A. donax* growth or gas exchange because it is known to respond to N enrichment (Abissy and Mandi 1999).

The *A. donax* in this essentially monocultural stand was highly productive for a graminoid species (Perdue 1958; Sharma et al. 1998; Angelini et al. 2005; Papazoglou et al. 2005). Its mean LAI in our study site was 4.5 (Fig. 2). A similar mean LAI of 4.1 was observed at another site over 240 km upstream (data not shown). Stands of *Tamarix ramosissima* (Ledeb.), another common invasive species on the Rio Grande, have lower LAI than *A. donax*, ranging from 2.5 to 3.6 (Dahm et al. 2002). *Phragmites australis*, which has 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 an approximately 1-m wide band immediately adjacent to the river (Pers. obs.). Maximum values of leaf transpiration were approximately $8 \mu\text{mol m}^{-2} \text{s}^{-1}$ compared with *P. australis* that can reach nearly $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Weis et al. 2002).

The *P. australis* stand in Spain (Moro et al. 2004) exhibited a stronger seasonal trend than we observed for *A. donax*. LAI of *A. donax* increased steadily throughout the growing season and ranged from 3.3 in March 2008 to 5.5 in January 2008 (Fig. 2), with most leaf senescence and abscission occurring after the coldest period in late January. We did not observe the onset of leaf production due to infrequent sampling.

Areas very near to the river tend to support a higher LAI than those farther from the active channel and topographically upslope (Table 1). This pattern was observed in most individual transects measured and throughout most sampling periods. Greater light availability and reduced intraspecific competition occurs at the most laterally distant edge of stands, which allows for compensation in stem growth (Urbanc-Bercic and Gaberšcik 1997).

Mean E_t also varied with distance to the river in both summers, and followed the same trend as LAI, having the highest values near the channel (Fig. 3). The two summers differed greatly in precipitation, with 6.37 mm day^{-1} and

Table 1 Comparisons between plots in a stand of *A. donax*. Shown are characteristics of stand structure [leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$, $N=10$) and specific leaf area (SLA, $\text{m}^2 \text{kg}^{-1}$, $N=1$)], leaf water stress [pre-dawn (Ψ_{pd} , $N=3$) and midday (Ψ_{md} , $N=3$) water potential (kPa)],

and leaf chemistry [nitrogen and carbon (N and C, %, $N=3$)]. Of all the listed characteristics, only LAI differed between plots, as indicated by letters from *post hoc* pairwise comparisons (Fisher's LSD, $P \leq 0.05$)

Plot	Stand structure		Leaf water status		Leaf chemistry	
	LAI	SLA	Ψ_{pd}	Ψ_{md}	C	N
1	6.1±1.1 <i>a</i>	12.3±0.8	-0.6±0.1	-2.1±0.1	42.0±0.3	2.3±0.1
2	4.6±0.3 <i>ab</i>	9.5±1.9	-0.8±0.1	-2.3±0.1	42.0±0.4	2.2±0.1
3	3.4±0.4 <i>b</i>	13.5±0.6	-0.9±0.1	-2.5±0.2	42.4±0.3	2.3±0.1
4	4.0±0.7 <i>b</i>	12.5±1.7	-0.8±0.1	-2.2±0.1	43.1±0.3	2.4±0.1

2.42 mm day^{-1} in 2007 and 2008, respectively. E_1 was higher in the wetter summer of 2007 than the drier summer of 2008 (t -statistic=7.958, $P < .001$, d.f.=19.003), and E_1 was higher in the drier summer than in winter 2007/2008 (t -statistic=2.224, $P < 0.05$, d.f.=11). In summer 2007, the lowest E_1 rates were observed in plots farthest from the river. In summer 2008, E_1 in Plot 3 was 68% lower than Plot 1. During the cool winter season, E_1 did not differ within the stand likely because of reduced evaporative demand (Franks et al. 2007).

As mentioned above, water supply fluctuations within the stand were likely a driving factor for the observed spatial and temporal dynamics, and the most pronounced differences with distance to the river occurred during periods of high moisture stress. The magnitude of difference in E_1 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. Interestingly, the specific leaf area (SLA) of *A. donax* (Table 1) suggests that it is poorly adapted to frequent or prolonged submerged conditions (Mommer et al. 2006), which may indicate why this species has proliferated in areas with relatively stable water level (e.g., near dams).

Soil moisture content in the top 20 cm on 4 June 2008 did not differ with increasing distance to the river (Table 2).

Table 2 Comparisons between plots in a stand of *A. donax*. Shown are the soil properties volumetric water content (VWC, %), total nitrogen (N, ppt), total carbon (C, ppt), total phosphorus (P, ppm), total potassium (K, ppm), cation exchange capacity (CEC, meq

100 g^{-1}), and base saturation (Base Sat., %). All data are reported as mean \pm S.E.M. *Post hoc* pairwise comparisons yielded no differences between plots for any soil property ($N=6$ for all except VWC, where $N=12$)

Plot	Soil properties						
	VWC	C	N	P	pH	CEC	Base Sat.
1	24.5±2.4	36.3±5.2	1.5±0.4	17.9±7.0	7.24±0.04	18.2±2.2	92.3±1.6
2	25.2±1.5	33.6±3.0	1.3±0.2	12.6±5.5	7.34±0.03	16.9±1.2	94.5±1.3
3	26.0±0.9	33.9±1.8	1.3±0.2	11.6±4.4	7.29±0.04	16.6±0.4	93.9±0.6
4	25.4±1.5	38.4±4.6	1.6±0.3	11.4±4.5	7.25±0.04	17.5±1.2	90.7±1.4

Stand Transpiration

The observed spatial and temporal variation in LAI and E_1 described above were incorporated into a scaling model for stand transpiration (E_{stand}) which resulted in an overall estimate of $9.1 \pm 1.1 \text{ mm day}^{-1}$, averaged over all 23 sample dates (Fig. 4), although it should be noted that the vast majority of sampling dates were during the summer. An example of the measured and modeled diurnal patterns is given in Fig. 5. The derived diurnal trend in E_1 resembles that of the driving variables for transpiration: humidity, light, and temperature (Fig. 5). Large differences in E_{stand}

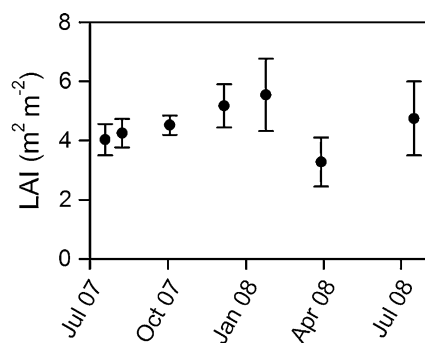


Fig. 2 Mean leaf area index (LAI) estimates in $\text{m}^2 \text{m}^{-2}$ throughout the study period. Standard error bars are indicated ($N=4$ in all cases except October 2007, where $N=8$)

were evident within short time periods (Fig. 4); e.g., in only a week (29 May–5 June, 2008), E_{stand} varied from 4.7 mm to 10.9 mm. This was likely a result of physiological responses to differences in weather conditions on those measurement days (Herbst and Kappen 1999; Lissner et al. 1999). Differences between the peak growing season and a much less active winter season are also clear (Fig. 4). The model estimated that mean daily E_{stand} was 17.8 mm in the summer of 2007, 4.8 mm during the following winter, and 8.8 mm during the summer of 2008.

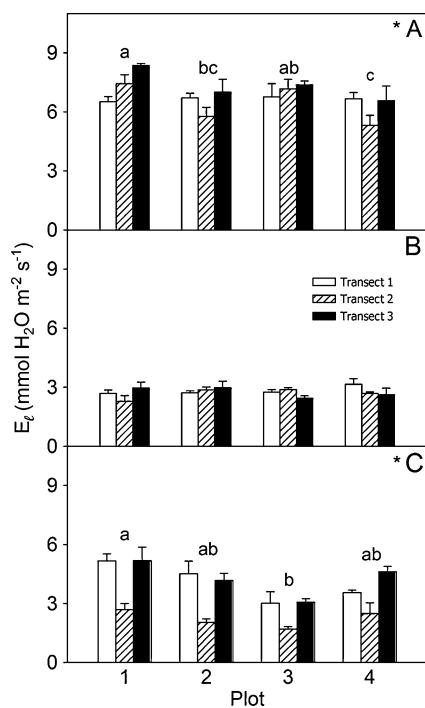


Fig. 3 Leaf scale transpiration (E_l) in $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ for each sampling period and standard error bars for: **a** summer 2007 ($N=4$ days); **b** winter 2007/2008 ($N=7$ days); and **c** summer 2008 ($N=12$ days). Plot 1 is closest to the river channel. Individual bars indicate the three randomly located transects. Asterisks denote differences between transects ($P \leq 0.05$) within a season. Letters denote differences between plots from *post hoc* pairwise comparisons (Fisher's LSD) ($P \leq 0.05$) within a season

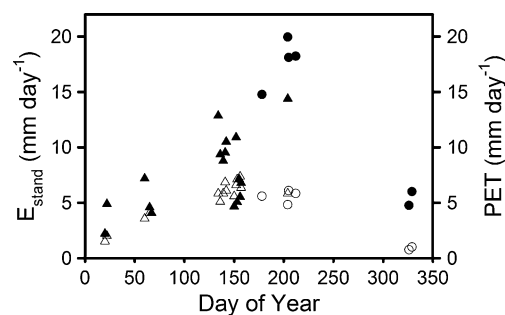


Fig. 4 Total daily stand scale transpiration (E_{stand} , closed symbols) and daily reference evapotranspiration (ET_0 , open symbols) in mm d^{-1} for all sampling days in 2007 (circles) and 2008 (triangles)

These E_{stand} values exceed most 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^{-1} (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^{-1} (Dahm et al. 2002). Reeds, such as *Phragmites australis*, are known to have higher transpiration than other vegetation types, particularly during the peak of the growing season (Batty et al. 2006). E_{stand} in a pond lined by *P. australis* (Cav.) Trin. ex Steud. in Nebraska, USA was estimated at 6.5 mm day^{-1} at the peak of the growing season in a stand that had a maximum LAI of 2.6 (Burba et al. 1999a, b). E_{stand} in *P. australis* in Germany is estimated at 10 to 16 mm day^{-1} in stands with summertime LAI of about 5 (Herbst and Kappen 1999). *P. australis* in semiarid Spain has been shown to have average midsummer E_{stand} values of about 23 mm day^{-1} in a stand with simultaneous LAI values of 8.9 (Moro et al. 2004). Keeping transpiration rates constant, this last value would equate to approximately 9.6 mm day^{-1} if LAI were equivalent to that of *A. donax* in this study, which is very similar to our modeled mean for the summer of 2008.

Additionally, the ratio of E_{stand} to reference evapotranspiration (ET_0) for reed systems can range from 0.75 to 3.4. Our data show that *A. donax* had $E_{\text{stand}}:ET_0$ ratios ranging from 1.4 in the summer of 2008 to 3.7 in the summer of 2007. One of the strongest controlling factors in these systems is the horizontal advective component that supplies additional energy to drive evaporative demand (Devitt et al. 1998; Burba et al. 1999b; Herbst and Kappen 1999; Fermor et al. 2001; Moro et al. 2004; Peacock and Hess 2004). 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 reasonable for similar *A. donax* stands throughout the Rio Grande Valley, but water

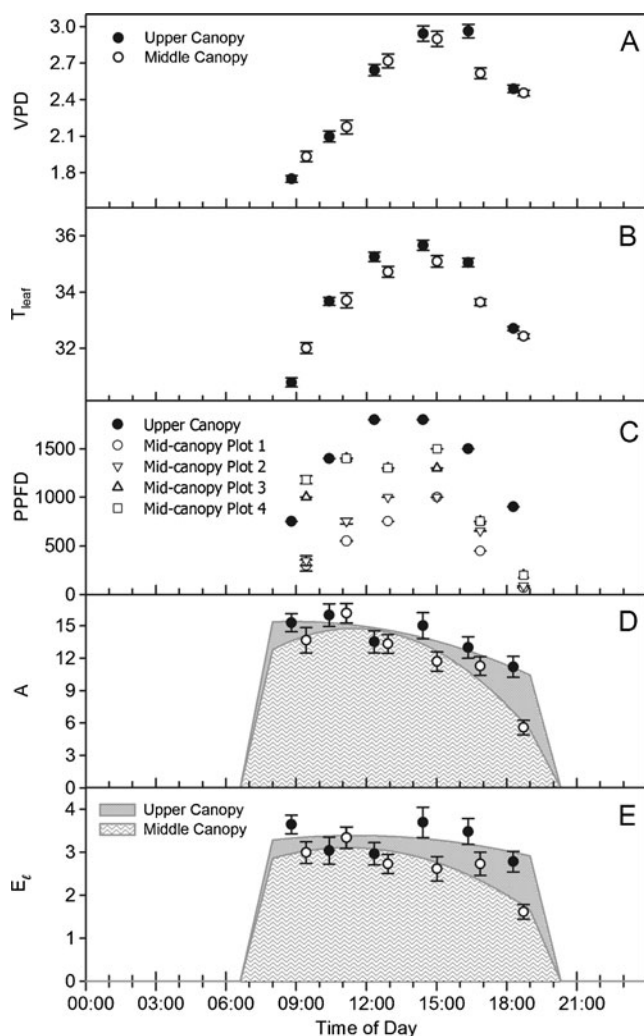


Fig. 5 Diurnal observations from 3 June, 2008. Shown are: **a** vapor pressure deficit (VPD, kPa); **b** leaf temperature (T_{leaf} , °C); **c** photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$); **d** carbon assimilation rate (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$); and **e** transpiration rate (E_t , $\text{mmol m}^{-2} \text{s}^{-1}$) collected at approximately 2 h intervals throughout the daylight hours. *Closed symbols* indicate leaves from the upper canopy layer; *open symbols* indicate leaves from the middle canopy layer. Means and standard error bars are given for each point ($N=16$ stems). For open symbols in panel C, circles represent *Plot 1*, downward-pointing triangles represent *Plot 2*, upward-pointing triangles represent *Plot 3*, and squares represent *Plot 4*. In panels **d** and **e**, shaded regions are time-integrated predicted values for the upper and middle canopy layers using the diurnal model described in “Methods”

use patterns across larger-scale moisture gradients cannot be determined from our results. The observed heterogeneity in stand structure and transpiration rate of *A. donax* further underlines the importance of recognizing spatial variation at the population scale (Levin 1992). On an annual basis, the estimation of approximately $1,700 \text{ mm year}^{-1}$ made by Iverson (1998) may be reasonable for *A. donax* stands in the Rio Grande watershed (Yang et al. 2009). However, Iverson’s (1998) discussion was of *A. donax* in California,

which experiences drier summer growing seasons than typical at our site.

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). It is possible for leaf gas exchange to overestimate E_{stand} , as is known to occur in *Stipa tenacissima* (L.) by 71% (Ramírez et al. 2006). Leaf age accounted for over a third of that difference (Ramírez et al. 2006), and the basal sprouting growth form of *S. tenacissima* creates a complex vertical light environment that was explicitly considered in their scaling model. Our model accounted for shading and carefully controlled the light environment during gas exchange measurements to best isolate effects of moisture gradients.

When the canopy is strongly decoupled from the bulk atmosphere, as is the case at low wind speeds, scaling transpiration from leaf to stand requires estimates of both leaf stomatal conductance and canopy boundary layer conductance (Meinzer et al. 1995). Typically, decoupling occurs in crops with large leaves such as sugarcane (Meinzer and Grantz 1989), or in large continuous stands because of high aerodynamic resistance (Tolk et al. 2006). This could lead to overestimates in transpiration based on leaf conductance alone. However, at high wind speeds, canopies are well coupled to the bulk air (Jarvis 1981). High wind speeds well in excess of 6 m s^{-1} (more than double what was observed in Meinzer’s sugarcane fields) were prevalent near our study site (WBAN Station 12919) on all measurement dates (<http://www.ncdc.noaa.gov/oa/ncdc.html>), and *A. donax* is commonly found in areas with high wind speeds (Speck 2003; Speck and Spatz 2004). Moreover, these *A. donax* stands had a high degree of edge relative to their total size, which would further increase the importance of wind turbulence and mixing (Tolk et al. 2006). While we cannot rule out potential for overestimated transpiration in this study, given the high winds this site experienced, we predict such overestimates are modest.

In conclusion, our evidence suggests that *A. donax* transpires at high rates similar to other riparian reeds (Weis et al. 2002), which combined with high leaf area results in high stand-level estimates of water use. *In situ* comparisons of water use between *A. donax* and other plant species, especially native species considered in restoration efforts, would be needed to determine how this invasive species may have impacted site water balance. We found that rates of transpiration varied with water availability, which suggests this plant is sensitive to water gradients across the floodplain and may not transpire as much during dry periods or with declining water tables. The higher leaf areas observed closer to the river further demonstrate that resources were constrained by distance to the river.

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