

# Non-native tree in a dry coastal area in Hawai'i has high transpiration but restricts water use despite phreatophytic trait

Yoshiyuki Miyazawa,<sup>1,2\*</sup> Bruce D. Dudley,<sup>3,4,5</sup> R. Flint Hughes,<sup>3</sup> Joshua Vandemark,<sup>3,4</sup> Susan Cordell,<sup>3</sup> Michael A. Nullet,<sup>1</sup> Rebecca Ostertag<sup>4</sup> and Thomas W. Giambelluca<sup>1</sup>

<sup>1</sup> Department of Geography, University of Hawai'i at Mānoa, Honolulu, HI, 96822, USA

<sup>2</sup> Research Institute for East Asia Environments, Kyushu University, 744 Motoooka, Fukuoka 819-0395, Japan

<sup>3</sup> Institute of Pacific Islands Forestry, USDA Forest Service, 60 Nowelo Street, Hilo, HI, 96720, USA

<sup>4</sup> Department of Biology, University of Hawai'i at Hilo, 200 W. Kawili Street, Hilo, HI, 96720, USA

<sup>5</sup> National Institute of Water and Atmospheric Research, 10 Kyle Street, Riccarton, Christchurch, New Zealand

## ABSTRACT

In arid systems, phreatophytes are often among the most effective invaders because of their capacity to access and exploit groundwater resources otherwise unavailable to native vegetation. On Hawai'i Island, a non-native phreatophyte, *Prosopis pallida* (kiawe), has invaded extensive dry lowland areas following its introduction in the 19th century. To better understand the influence of this invader on the host ecosystem, and vice versa, we determined transpiration characteristics of *P. pallida* by monitoring sap flux of mature individuals over an 18-month period on the arid leeward coast of Hawai'i Island. Daily sap flux increased with increasing atmospheric vapour pressure deficit ( $D$ ) and exhibited no clear response related to rainfall events or prolonged drought. Annual transpiration (i.e. 308 mm) was 80% higher than rainfall. Stomatal conductance decreased with increasing vapour pressure deficits more slowly than the theoretical stomatal conductance– $D$  relationship that assumes stomatal regulation of leaf water potential above a critical level. While daily peak stomatal conductance was relatively high, it nonetheless appeared limited by high intrinsic water use efficiency (net photosynthetic rate per stomatal conductance), suggesting a constraint to unlimited groundwater absorption. In this young volcanic environment where rainfall is low and quite episodic, the success of this species likely stems from its anisohydric strategy even at the risk of cavitation, and it is altering the hydrological cycling of the areas where it is dominant. Copyright © 2015 John Wiley & Sons, Ltd.

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## INTRODUCTION

Non-native species invasions have been definitively linked to changes in energy, water, carbon and nutrient cycles in many ecosystems (Vitousek *et al.*, 1987; D'Antonio and Vitousek, 1992). In arid systems, phreatophytes are often among the most effective invaders because they are able to access groundwater typically unavailable to native vegetation (Smith *et al.*, 1998; Stromberg *et al.*, 2007; Milton and Dean, 2010). Access to, and use of, groundwater provides a considerable competitive advantage because it allows trees to transpire, assimilate carbon and thereby increase live biomass under limited rainfall conditions that typically occur during the dry seasons in savanna and tropical seasonal ecosystems (Hutley *et al.*, 2000; Cleverly *et al.*, 2006; O'Grady *et al.*, 2009; Pfautsch *et al.*, 2011), while photosynthesis and transpiration of non-phreatophytic native

plants are constrained by the difficulties in water uptake from relatively dry soil. As such, restrictions on water absorption from the dry soil of non-phreatophytic native plants under drought conditions help to determine the degree to which invasive phreatophytes alter local hydrological processes (Hultine and Bush, 2011), nutrient cycling (Dudley *et al.*, 2014) and ultimately plant community structure (Breshears *et al.*, 2005).

Hawai'i Island is an excellent place to examine the impacts of invasive species on ecosystem function. Communities of plants and animals in the Hawaiian Islands have been profoundly altered by introduced species brought from other regions of the world, especially since the late 18th century (Cuddihy and Stone, 1990). Today, approximately half of Hawai'i's flora is non-native (Wagner *et al.*, 1999). In addition, the chemical homogeneity of the lava that forms the basis of Hawai'i's soil substrates provides uniform settings in which to examine impacts of non-native species on processes such as nutrient availability (Vitousek *et al.*, 1987; Hughes and Denslow, 2005), carbon cycling (Sandquist and Cordell, 2007; Litton

\*Correspondence to: Yoshiyuki Miyazawa, Research Institute for East Asia Environments, Kyushu University, 744 Motoooka, Fukuoka 819-0395, Japan. E-mail: sclerophyll@gmail.com

*et al.*, 2008) and hydrological cycling (Cordell and Sandquist, 2008) in native ecosystems.

Throughout the dry coastal shrublands of leeward Hawai'i, many native plant communities have been replaced by invasive grasses and non-native N-fixing tree species, particularly *Leucaena leucocephala* and the phreatophytic tree *Prosopis pallida* (D'Antonio and Vitousek, 1992; Wagner *et al.*, 1999). *P. pallida*, known as 'kiawe' in Hawai'i and mesquite elsewhere, is native to Peru, Colombia and Ecuador and naturalized in Puerto Rico and Australia as well as Hawai'i, where it is the more common of the two *Prosopis* species introduced to the Hawaiian Islands from South America (Gallaher and Merlin, 2010). Following its introduction at the end of the 19th century, *P. pallida* has proliferated across leeward coastal areas, including much of the leeward coast of Hawai'i Island where it has altered the ecology and possibly the hydrology of these dry forest ecosystems (Gallaher and Merlin, 2010). It typically dominates dry, disturbed, low-elevation areas, often abutting leeward beaches and occupying raised limestone reefs, dry slopes and gulches, and degraded dry forests from sea level to ~600 m above sea level (Wagner *et al.*, 1999).

Because of the high permeability of the soils and underlying basalt rock, groundwater flow constitutes the primary means of land-to-sea freshwater transport on leeward coasts of Hawai'i Island. This groundwater, derived primarily from high-altitude recharge, is a critical resource to coastal human communities as well as terrestrial flora and fauna. Groundwater also transfers terrestrially derived nutrients to marine environments (Knee *et al.*, 2010), helping to sustain economically and culturally important marine ecosystems along these coasts (Duarte *et al.*, 2010). Unfettered groundwater use by *P. pallida*, a species capable of high rates of transpiration (Scott *et al.*, 2004), has the potential to reduce freshwater inputs and alter nutrient transport to near-coastal marine environments.

Dudley *et al.* (2014) documented *P. pallida*'s access to groundwater along leeward coasts and found that this access resulted in considerable increases in the size and density of *P. pallida* individuals. However, high stable carbon isotope ratio, low predawn leaf water potential and midday leaf water potential values close to the critical level for cavitation in other *Prosopis* species (Dzikiti *et al.*, 2013) suggest that groundwater uptake may be constrained to lower levels than those demanded by the transpiring foliage and that transpiration rates are likely to be different from those of trees under wet soil conditions, in both magnitude and the response to the varying environmental drivers. During drought periods, many species elsewhere exhibit ecophysiological traits that maintain transpiration rate at low levels and have specific responses to water restriction, characterized by reduced stomatal conductance under increasing atmospheric evaporative demand in order to maintain the minimum leaf water potential at a constant

level (isohydric stomatal control, Oren *et al.*, 1999). Leaves reduce stomatal conductance at low leaf water potential (Epron and Dreyer, 1993; Sala and Tenhunen, 1996) to avoid increasing transpiration, which would result in reduction in leaf water potential beyond the minimum level and avoidance of cavitation (McDowell *et al.*, 2008a), especially under high air vapour pressure deficits that occur near midday. This response to drought is also characterized by sharp increases in transpiration and stomatal conductance when leaf water potential rises following episodic rainfall events, as seen in other *Prosopis* species (Scott *et al.*, 2006; Dzikiti *et al.*, 2013).

A potential alternative response to restricted groundwater access is to maximize stomatal conductance, continue high transpiration rates and further reduce leaf water potential, a strategy that increases transpiration rates, carbon gain (Farquhar and Sharkey, 1982) and the risk of cavitation (McDowell *et al.*, 2008a; Manzoni *et al.*, 2013). If *P. pallida* exhibits this latter type of stomatal control (anisohydric stomatal control), stomatal conductance should not decline during rainless periods, nor should transpiration rates increase in response to rainfall events, allowing higher transpiration rates than the level that is expected to be achieved under isohydric stomatal control (Oren *et al.*, 1999).

In this study, we monitored the sap flux of *P. pallida* stands with ample access to shallow groundwater and compared the annual transpiration rate with annual rainfall to evaluate the influence of *P. pallida* invasion on local hydrology. We examined several hypotheses, under the basic assumption that transpiration characteristics of *P. pallida* follow those of other *Prosopis* species (isohydric stomatal control and reduced transpiration rates during rainless periods) (Scott *et al.*, 2006; Dzikiti *et al.*, 2013; but see Martínez-Vilalta *et al.*, 2014). First, we hypothesized that sap flux increases with vapour pressure deficit but that its increase is saturated at low atmospheric vapour pressure deficit on diurnal and longer timescales. Second, we hypothesized that stomatal conductance declines with increasing vapour pressure deficit and maintains a stomatal conductance–vapour pressure deficit relationship that corresponds to the theoretical relationship for optimum maintenance of leaf water potential (Oren *et al.*, 1999). Third, we hypothesized that sap flux and the stomatal conductance–vapour pressure deficit relationship would change substantially in response to rainfall events and that the leaf-level ecophysiological traits would vary in close relation to stomatal conductance (Collatz *et al.*, 1991; Katul *et al.*, 2003). In light of projected future decreases in rainfall in dry leeward areas of Hawai'i in response to global climate warming (Elison Timm *et al.*, 2015), the response of *P. pallida* stomatal control to drought and episodic rainfall

will likely be important in dictating future ecosystem-level impacts of this species.

## MATERIALS AND METHODS

### *Study site and species*

Our study site was located near Kīholo Bay, Hawai'i Island, Hawai'i (19.85466°N, 155.92416°W), on the coastal margin of a basaltic formation derived from a 3000- to 5000-year-old lava flow emanating from Hualālai Volcano (Wolfe and Morris, 1996). The substrate is poorly weathered, largely owing to low rainfall, and soil at the study site is shallow and discontinuous, with a mean depth of less than 5 cm (Dudley *et al.*, 2014). Roots extend into the ground through cracks in the rock. Kīholo Bay receives considerable shallow submarine groundwater discharge near its shoreline via freshwater flow from montane areas (Peterson *et al.*, 2009). Dominant vegetation consists of *P. pallida* stands and ephemeral herbaceous species, primarily *Sida fallax* ('Ilima) and *Waltheria indica* ('Uhaloa), which partially cover the area following heavy rain events. Although *P. pallida* trees may attain heights >20 m in areas with abundant moisture (Y. Miyazawa, personal observation), stands surveyed along the coast of Kīholo Bay were approximately 8 m in height. Our study site was established in a closed *P. pallida* stand in May 2010 at the same location as Dudley *et al.* (2014). Annual rainfall of the study site averaged 270 mm over the 30-year period ending in 2007 (Giambelluca *et al.*, 2013). Between August 2010 and August 2011, annual air temperature averaged 25 °C, and annual rainfall was 188 mm, approximately two-thirds of the long-term annual average for the area. A weather station equipped with a pyranometer (CMP3, Kipp & Zonen, Delft, the Netherlands), a photosynthetically active radiation (PAR) sensor (LI-190SB, Li-Cor, Lincoln, NE, USA), a tipping-bucket rain gauge (TE525, Texas Electronics, Dallas, TX, USA), air temperature–humidity sensors (HMP45C, Vaisala, Vantaa, Finland) and an anemometer (014a, Met One Instruments, Grants Pass, OR, USA) was established in an open area adjacent to the sap flow monitoring site. Sensors were monitored by a data logger (CR3000, Campbell Scientific, Logan, UT, USA), which sampled data at a 10-s interval and recorded mean values (sums in the case of rainfall) at a 10-min interval. Because of a power supply interruption, weather data were not collected for 24 days in January 2011. Air temperature and relative humidity data were used to calculate atmospheric vapour pressure deficit ( $D$ , kPa). Because transpiration is linked to  $D$  in daylight, mean  $D$  was calculated for both daytime (6:00–18:00 hours) and complete 24-h periods.

In order to scale up transpiration ( $E$ ,  $\text{g m}^{-2} \text{s}^{-1}$  or  $\text{mm day}^{-1}$ ) from mean stand xylem sap flux ( $J_s$ ,  $\text{g m}^{-2} \text{s}^{-1}$ ) as  $E = J_s \times \text{stand-scale sapwood area/ground area}$ , we measured *P. pallida* stem metrics in five 20-m radius plots

established within coastal *P. pallida* stands known to have access to groundwater as determined by oxygen isotope measurements (Dudley *et al.*, 2014). Within each plot, diameters of all stems present at 2.5 m above the ground were measured at that point – a height coinciding with the location at which sap flow sensors were installed in selected trees. We estimated stand-level sapwood area from a regression relationship that predicted sap wood area from stem diameter and was derived from 72 *P. pallida* stem cross sections ranging in diameter from 2.9 to 59 cm at 2.5 m above the ground (sapwood area =  $2.18 \text{ diameter}^{0.954}$ ,  $r^2 = 0.733$ ,  $p < 0.001$ , Figure S1). For details about the calculation of sapwood area, see Supporting Information 1.

Leaf area index (LAI,  $\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$ ) of the stand was periodically measured using paired LAI-2000 instruments (Li-Cor); one sensor was located in an open site, and the second at designated points within *P. pallida* stands. In each of the five plots, we measured LAI at four permanent points, facing towards, and equidistant from, the plot centre. During any given measurement, the sensor in the open area collected data at the same time and in the same direction as the within-canopy sensor. Measurements were always collected during overcast sky conditions.

### *Sap flow measurements*

The  $J_s$  ( $\text{g m}^{-2} \text{ s}^{-1}$ ) was estimated using Granier-type sap flux sensors (Granier, 1987) modified slightly with respect to the length of the probes (James *et al.*, 2002). A data logger (CR1000, Campbell Scientific) attached to a multiplexer (AM16/32, Campbell Scientific) scanned the output from the sensors at a 30-s interval, and average values were recorded at 10-min intervals. We installed sap flux sensors at a height of 2.5 m because bark and stems at lower positions were observed to be frequently damaged by feral goats. Sensors were installed on 17 selected trees in May 2010. Details about the sensors, installation and the calculation of sap flux are given in Supporting Information 2.

As  $J_s$  and  $E$  are functions of atmospheric  $D$  and leaf stomatal conductance (Jarvis and McNaughton, 1986), stomatal conductance was calculated on a unit leaf area basis ( $G_s$ ,  $\text{mol m}^{-2} \text{ leaf s}^{-1}$ ) and on a unit sapwood area basis ( $G_{s\_sap}$ ,  $\text{m s}^{-1}$ , Meinzer *et al.*, 2013) during periods for which LAI data were not available, based on  $J_s$  and  $D$  (Supporting Information 3). We determined the relationship between  $G_s$  and  $D$  by performing boundary line analysis under high solar radiation (solar radiation > 600  $\text{W m}^{-2}$ ) (Supporting Information 3). The selected  $G_s$  points were regressed against  $\ln(D)$ :

$$G_s = G_{s\text{ref}} - m \ln(D) \quad (1)$$

where  $m$  is the slope  $\partial G_s / \partial \ln D$  ( $\text{mol kPa}^{-1} \text{ m}^{-2} \text{ s}^{-1}$ ) and  $G_{s\text{ref}}$  is the intercept at  $D = 1 \text{ kPa}$  ( $\text{mol m}^{-2} \text{ s}^{-1}$ ). The ratio

of  $m$  to  $G_{sref}$  was obtained for each month for comparison with the theoretical value (0.6) for isohydric leaves with perfect stomatal control of minimum leaf water potential (Oren *et al.*, 1999). When LAI data were not available, a similar analysis was carried out using  $G_{s,sap}$  and obtained  $G_{s,sapref}$  and  $m_{sap}$ .

We employed  $G_{sref}$  and  $m$  obtained in the boundary line analysis to model  $G_s$  during midday (10:00–15:00 hours) for two cases with different assumptions on the stomatal control ( $m-G_{sref}$  relationship). In case 1, modelled  $G_s$  was calculated as  $G_s = G_{sref} - m \ln D$ . Similarly in case 2, which assumed isohydric stomatal control (i.e.  $m/G_{sref} = 0.6$ ), modelled  $G_s$  was computed as  $G_s = G_{sref} - 0.6 G_{sref} \ln D$ . If *P. pallida* does not adopt isohydric stomatal control, i.e. if it exhibits species-specific  $m/G_{sref}$  values, modelled  $G_s$  in case 1 should differ from modelled  $G_s$  in case 2; if modelled  $G_s$  in case 1 is larger than modelled  $G_s$  in case 2, increased  $G_s$  of *P. pallida* should be partly attributed to the species-specific stomatal control represented by the  $m/G_{sref}$  value. Modelled  $G_s$  values in cases 1 and 2 were compared to evaluate the extent to which *P. pallida* exhibited enhanced or reduced  $G_s$  during midday by adopting species-specific stomatal control, rather than isohydric stomatal control.

#### Measurements of leaf ecophysiological traits

During periods preceded by rainfall events (January and August 2011 and July 2012), leaf-level ecophysiological traits were measured using an LI-6400 portable photosynthesis system (Li-Cor). We obtained a relationship between net photosynthetic rate ( $A$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and intercellular  $\text{CO}_2$  concentration using intact leaves from the trees selected for sap flow measurements in order to determine the parameter described by Farquhar *et al.* (1980): the maximum rate of RuBP carboxylation at a common leaf temperature 25 °C ( $V_{\text{cmax}25}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Leaves were selected from the sun-exposed crown surface within reach (1–1.5 m height). A total of 8–12 leaves from each of the three trees were used to determine  $V_{\text{cmax}25}$  on each sample day.

In addition to  $V_{\text{cmax}25}$ , we also determined leaf-level intrinsic water use efficiency (iWUE,  $\text{mmol mol}^{-1}$ ) and the intercellular  $\text{CO}_2$  concentration relative to the air  $\text{CO}_2$  concentration ( $C_i/C_a$ ) for sunlit leaves and partially shaded leaves, respectively. Leaf-level iWUE was calculated as the ratio of  $A$  to the stomatal conductance for water vapour ( $g_{\text{sw}}$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ). We derived mean iWUE from the diurnally varying leaf gas exchange rate data collected between 10:00 and 15:00 hours when 70–80% of daily transpiration typically occurs. Details about photosynthesis measurements, samplings and the calculation of the parameters are shown in Supporting Information 4.

#### Statistical analysis

We used *t*-tests (Sokal and Rohlf, 1995) to compare  $V_{\text{cmax}25}$  and iWUE among periods that varied with regard

to the amount of preceding rainfall. Similarly, *t*-tests were used to compare between sun-exposed leaves and shaded leaves.

## RESULTS

#### Environmental variation and tree water status

Solar radiation (Figure 1a) exhibited a large annual cycle, reaching its lowest levels in winter. High rainfall events occurred in winter–spring (December 2010–May 2011), and a period of very low rainfall occurred from June to October 2011. Monthly rainfall was 81 mm in December 2010 but was less than 20 mm in other months (Figure 1a). Despite these variations in rainfall, LAI did not differ between seasons (Figure 1d).

Mean daytime and whole day  $D$  remained high throughout the study period (Figure 1b), and neither approached zero, even during predawn hours.

#### Sap flux and its response to the environment

Daily  $J_s$  of *P. pallida* stand exhibited a clear annual cycle, with high levels in summer and lower levels in winter (Figure 1c). Low  $J_s$  was observed in January–February, attaining only 60–70% of the levels exhibited in July–September. Annual stand-level  $E$  was  $350 \text{ mm year}^{-1}$  (August 2010–July 2011) and exceeded annual rainfall by  $160 \text{ mm year}^{-1}$  (84%), indicating that water sources other than rainfall supported transpiration. Importantly, we did not observe decreasing trends in  $J_s$  during long rainless periods (June–September 2011) or sudden increases after the high rainfall event in December 2010.

$J_s$  was positively correlated with varying seasonal patterns of  $D$  (Figure 2). The  $J_s$ – $D$  relationships did not differ between the rainless period from June to September 2011 and the post-rainfall period in December 2010. Patterns clearly indicated that variation in transpiration was a function of  $D$  and provide no evidence of saturation of the increase of  $J_s$  with  $D$  in response to limitation by other factors.

At a fine temporal resolution (i.e. 10 min), we observed a negative correlation ( $r^2 = 0.646$ – $0.922$ ,  $p < 0.01$ , in each month) between  $D$  and  $G_s$  when upper envelopes of the  $G_s$ – $D$  relationship were compared (Figure 3a). Although the ratio of  $m_{\text{sap}}$  to  $G_{s,sapref}$  approached 0.6 in three of the 14 months, the slope was less than 0.5 for seven months (Figure 4b).  $G_{s,sapref}$  and  $m_{\text{sap}}/G_{s,sapref}$  changed seasonally without a clear relationship with the preceding month's rainfall, suggesting that rainfall did not influence the  $G_s$ – $D$  or  $E$ – $D$  relationship of *P. pallida*.

Irrespective of rainfall during the preceding month,  $G_s$  did not exhibit a clear midday depression at high PAR levels ( $\sim 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ , Figure 4b). Reductions in  $G_s$  in the afternoons during July coincided with reductions in PAR. In February 2011 when  $m/G_{sref}$  was near 0.6,

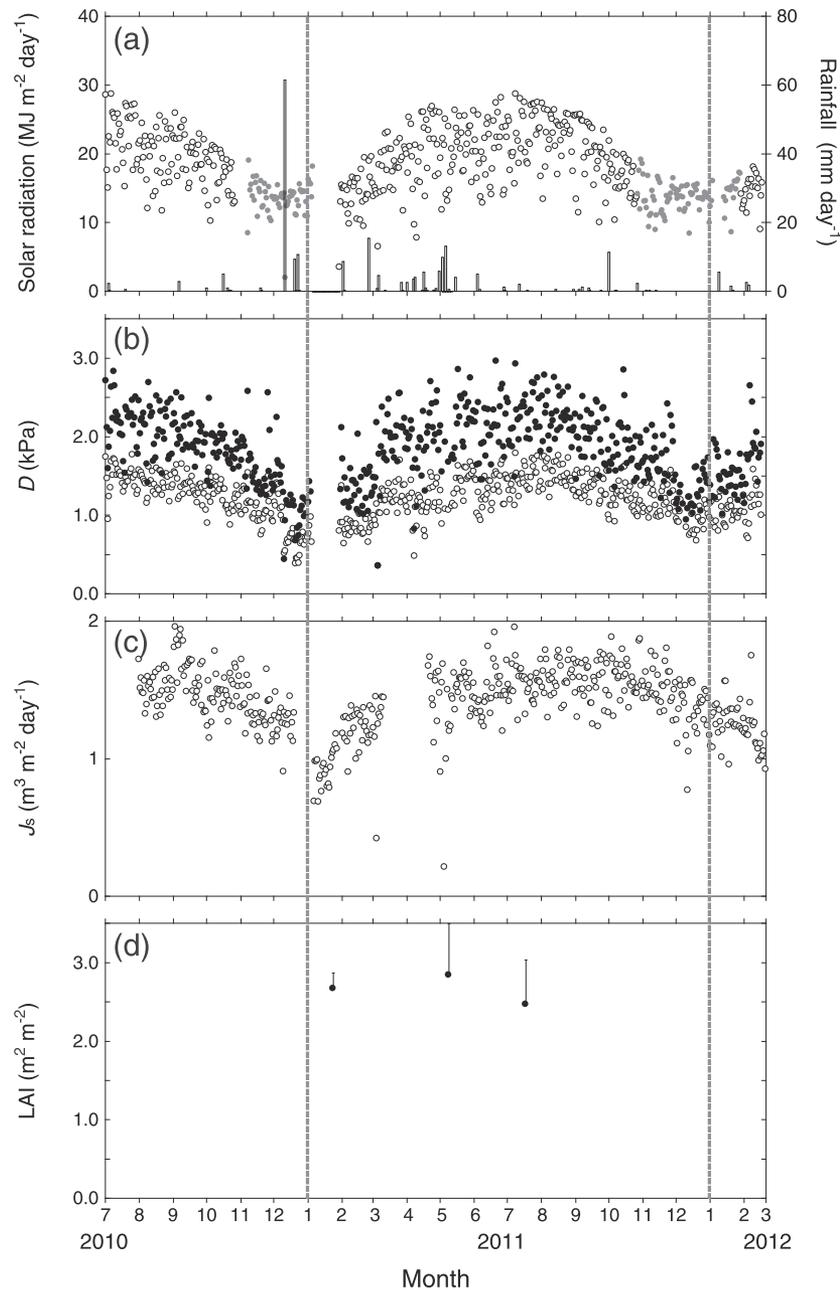


Figure 1. Seasonal trends in (a) daily solar radiation (circles) and rainfall (bars), (b) whole day (open circles) and midday (10:00–14:00 hours, closed circles) atmospheric vapour pressure deficit ( $D$ ), (c) sap flux ( $J_s$ ) and (d) leaf area index (LAI) of the study site (mean  $\pm$  standard deviation,  $n = 5$ ). For solar radiation (a), grey symbols show daily values adjusted to correct for the influence of shading by nearby trees (Section on Materials and Methods).

modelled  $G_s$  in cases 1 and 2 exhibited similar diurnal trends to the measured  $G_s$ ; that is, values were similar to means + 1 standard deviation of  $G_s$  (Figure 4c). In July, a period when  $m/G_{sref} = 0.4$ , modelled  $G_s$  in case 2 continued to decrease with increasing  $D$  between 10:00 and 12:00 hours and was consistently lower than the measured  $G_s$ . Large differences of modelled  $G_s$  values between cases 1 and 2 were due to the differing assumptions for stomatal control inherent in these two measures (i.e. anisohydric or isohydric stomatal control).

#### Photosynthesis measurements

Photosynthetic capacity, or  $V_{cmax25}$  of sun-exposed leaves, remained high and exhibited no differences between February 2011 and August 2010–2011 despite large differences in antecedent rainfall amount between these periods (Figure 5). Seasonal trends and interannual variation in  $V_{cmax25}$  were less clear. Shaded and sun-exposed leaves did differ with regard to  $V_{cmax25}$  over each measurement period ( $p < 0.05$ ) (Table I).

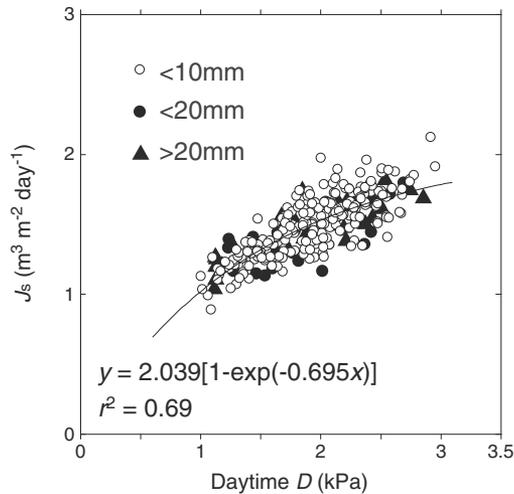


Figure 2. The relationship between sap flux density ( $J_s$ ) and daytime atmospheric vapour pressure deficit ( $D$ ) for days with rainfall amount in the precedent one month: <10 mm (open circles), <20 mm (closed circles) and >20 mm (closed triangles). The equation is for the regression line for all the pooled data.

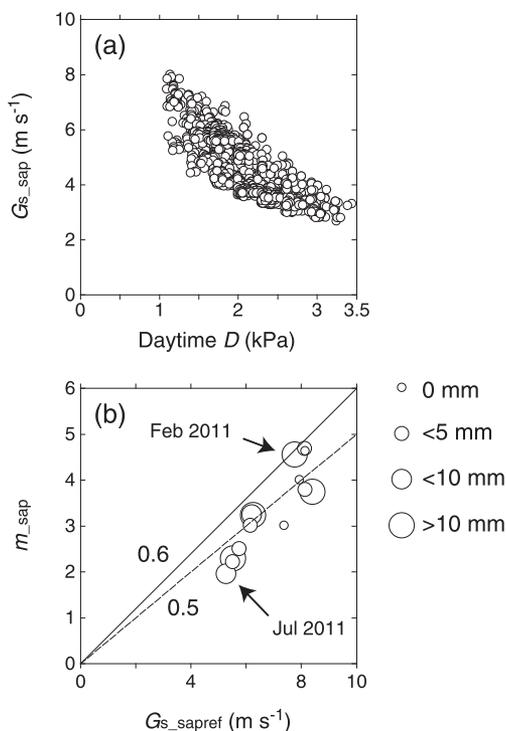


Figure 3. (a) The relationship between stomatal conductance ( $G_{s\_sap}$ ) and atmospheric vapour pressure deficit ( $D$ ) for upper boundary data under non-limiting solar radiation ( $600 \text{ W m}^{-2}$ ). (b) The relationship between the slope of Equation 1 for stomatal conductance on a unit sapwood area basis ( $G_{s\_sap}$ ),  $m_{sap}$ , and intercept,  $G_{s\_sapref}$ . Each point indicates the values for one month. The diagonal line with slope 0.6 shows the theoretical value for perfect stomatal control of minimum leaf water potential (Section on Materials and Methods).

Around midday, peak  $g_{sw}$  of sun-exposed leaves was higher in February 2011 than in August 2012 and that of partially shaded leaves and was higher than  $G_s$  by three to

four times in each period (Table II). In each period, in contrast to the diurnal trend in  $G_s$ ,  $g_{sw}$  of sun-exposed leaves showed strong midday depression to 30–50% of the peak after 9:00 hours (data not shown). Sun-exposed leaves did not exhibit differences in iWUE around midday between August and February 2011, despite the differing antecedent precipitation regimes between those periods. Leaves maintained high iWUE values characterized by low  $C_i/C_a$  (Table II). Despite differences in  $V_{cmax25}$ ,  $g_{sw}$  and PAR, sun-exposed leaves and partially shaded leaves did not differ with respect to iWUE (Table II).

## DISCUSSION

### Access to groundwater for transpiration

Despite the low rainfall of Kīholo Bay, fairly unweathered pāhoehoe basalt substrate and very patchy, shallow soils that characterize these leeward coastal environments of Hawai'i Island, our results clearly indicate that *P. pallida* stands were able to successfully access and utilize groundwater and subsequently transpire substantially (~80%) more water than was supplied via rainfall. This capacity has been documented for other phreatophyte species in other environments (Sala *et al.*, 1996; Scott *et al.*, 2006; Canham *et al.*, 2012). *Prosopis* species are known to extend their tap roots to great depths in their native habitat (*Prosopis juliflora*, Canadell *et al.*, 1996) to maintain transpiration, although soil conditions in these native conditions may differ considerably from the young basaltic substrates of Hawai'i Island.

Because other woody species in nearby areas do not exhibit the capacity to access groundwater and so typically reduce transpiration in response to dry periods (Sandquist and Cordell, 2007; Cordell and Sandquist, 2008), our results support the idea that invasion of *P. pallida* has altered the hydrological processes of this region, which is now characterized by a negative water budget through groundwater uptake and continuous transpiration.

### Transpiration characteristics of *Prosopis pallida* trees in arid Kīholo Bay

Low predawn leaf water potential is known to induce stomatal closure in many species (Pereira *et al.*, 1987; Epron and Dreyer, 1993; Sala and Tenhunen, 1996) – a mechanism to avoid hydraulic failure by restricting  $E$  (Sperry *et al.*, 2002; McDowell *et al.*, 2008a). We hypothesized that leaves of *P. pallida* with low predawn leaf water potential would restrict  $G_s$  to low levels in midday and avoid excessive increase in  $E$  under high  $D$  (Irvine *et al.*, 1998; Williams *et al.*, 1998). In contrast to our first hypothesis, transpiration by *P. pallida* was characterized by a positive  $J_s$ – $D$  relationship (Figure 2)

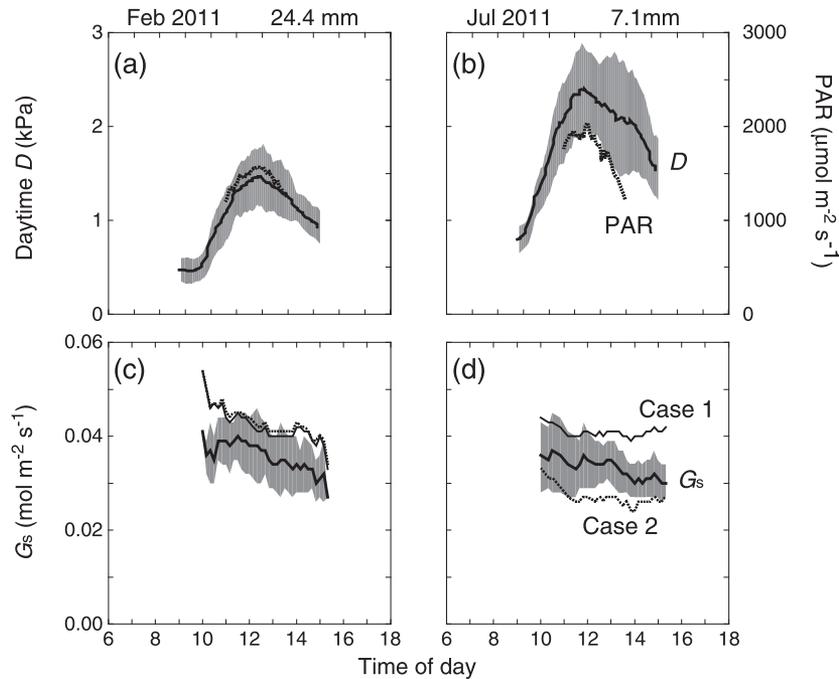


Figure 4. Monthly mean diurnal cycles in (a and b) atmospheric vapour pressure deficit ( $D$ , solid line) and photosynthetically active radiation (PAR, broken line) and (c and d) measured stomatal conductance ( $G_s$ , bold line) and modelled  $G_s$  in case 1 (thin line) and case 2 (broken line). The grey areas indicate means  $\pm$  standard deviation for  $D$  (a and b) and  $G_s$  (c and d). The plots shown are for February 2011 (a and c) and July 2011 (b and d). The numbers above the panels indicate the mean rainfall in the preceding month.

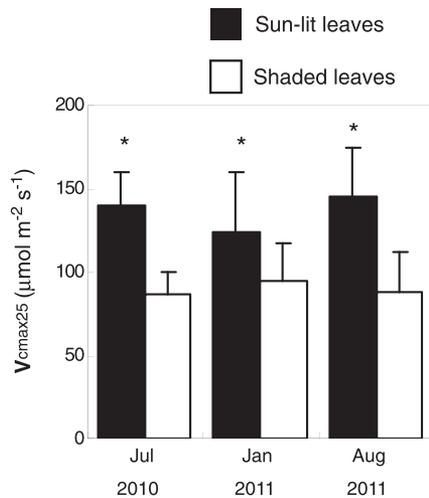


Figure 5. Photosynthetic capacity (means  $\pm$  standard deviation) of *Prosopis pallida* leaves at 25 °C ( $V_{max25}$ ) for sun-exposed leaves at the upper canopy surface (black bars) and deeply shaded leaves at the bottom of the canopy (white bars) obtained in periods with different antecedent rainfall amounts (high: January 2011, low: July 2011 and August 2012). Vertical bars indicate the standard deviation among measured leaves. Asterisks indicate significant difference at  $p=0.05$  between sun-exposed leaves and the deeply shaded leaves ( $t$ -test).

and the absence of midday depression (Figure 4), suggesting that water uptake from groundwater was sufficient to meet the seasonally and diurnally variable  $D$  (Sala *et al.*,

1996; Hutley *et al.*, 2000). Despite low predawn leaf water potential, *P. pallida* was able to take up water to meet daytime demand by creating a high gradient of water potential between groundwater and leaf (Meinzer *et al.*, 1995); resulting midday leaf water potential values ( $-3$  to  $-4$  MPa, Dudley *et al.*, 2014) were near the critical level for cavitation in other *Prosopis* species in South Africa (Dzikiti *et al.*, 2013).

*Prosopis pallida* exhibited anisohydric stomatal control, and the assumption of isohydric stomatal control ( $m=0.6G_{sref}$ ) in our second hypothesis would considerably underestimate  $G_s$  and  $E$  of *P. pallida* during most periods (Figure 4d). During most periods, the ratio of  $m$  to  $G_{sref}$  was lower than the theoretical value for perfect control of minimum leaf water potential: 0.6 (Oren *et al.*, 1999) (Figure 3). This suggests that *P. pallida* controlled stomata at the risk of reducing leaf water potential with increasing  $D$  (McDowell *et al.*, 2008a; Manzoni *et al.*, 2013). Anisohydric behaviour of *P. pallida* leaves was supported by leaf water potential values in the native region (Martínez-Vilalta *et al.*, 2014) and at the site during the period of study; midday leaf water potential was not constant but varied between approximately  $-2$  and  $-4$  MPa (Dudley *et al.*, 2014). Similarly, high risk for cavitation coincides with the observation of many dead branches and stems in this region. Even within a single individual, there are dead branches and stems. Comparison of modelled  $G_s$  values between cases 1 and 2 in this study suggested

Table I. List of abbreviations.

Abbreviations	Units	Definition
$A$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Net photosynthetic rate
$C_i/C_a$	—	$C_i$ relative to the air $\text{CO}_2$ concentration
$D$	kPa	Air vapour pressure deficit
$E$	$\text{mm day}^{-1}$	Daily canopy-scale transpiration rate estimated using sap flux sensors
$G_s$	$\text{mol m}^{-2} \text{s}^{-1}$	Stomatal conductance on a unit leaf area basis
$g_{\text{sw}}$	$\text{mol m}^{-2} \text{s}^{-1}$	Leaf-scale stomatal conductance for water vapour
$G_{\text{sref}}$	$\text{mol m}^{-2} \text{s}^{-1}$	$G_s$ at 1 kPa
iWUE	$\text{mmol mol}^{-1}$	Intrinsic water use efficiency ( $A/g_{\text{sw}}$ )
$J_s$	$\text{g m}^{-2} \text{s}^{-1}$	Stand mean xylem sap flux over the total stand sapwood area
LAI	$\text{m}^2 \text{m}^{-2}$	Leaf area index
$m$	$\text{mol kPa}^{-1} \text{m}^{-2} \text{s}^{-1}$	Slope of $G_s$ - $\ln(D)$ relationship
PAR	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Photosynthetically active radiation
sap (subscript)	—	Values calculated on a unit sapwood area basis
$V_{\text{cmax25}}$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Maximum rate of ribulose-1,5-bisphosphate carboxylation normalized at 25 °C

Table II. Leaf-level ecophysiological traits of *Prosopis pallida* around midday.

Leaf type	Season	Year	Parameters	
Sun-exposed leaf	Winter	2011	Peak $g_{\text{sw}}$	$0.152 \pm 0.059$
			$A/g_{\text{sw}}$	$119.66 \pm 55.42$
			$C_i/C_a$	$0.471 \pm 0.226$
Sun-exposed leaf	Summer	2011	Peak $g_{\text{sw}}$	$0.111 \pm 0.031$
			$A/g_{\text{sw}}$	$116.75 \pm 44.97$
			$C_i/C_a$	$0.410 \pm 0.208$
Partially shaded leaf	Summer	2012	Peak $g_{\text{sw}}$	$0.132 \pm 0.022$
			$A/g_{\text{sw}}$	$96.28 \pm 6.63$
			$C_i/C_a$	$0.564 \pm 0.028$

Peak  $g_{\text{sw}}$ , leaf-scale stomatal conductance for water vapour at the peak between 10:00 and 15:00 hours;  $A$ , net photosynthetic rate;  $C_i/C_a$ , intercellular  $\text{CO}_2$  concentration relative to the air  $\text{CO}_2$  concentration.

anisohydric stomatal control was responsible for high midday  $G_s$  and the observed positive  $J_s$ - $D$  relationship (Figure 2). Interestingly, neither  $G_{\text{sref}}$  nor  $m/G_{\text{sref}}$  showed a clear relationship with antecedent rainfall events (Figure 3b). Therefore, the processes underlying temporal variation in  $G_{\text{sref}}$  and  $m/G_{\text{sref}}$  remain unclear.

#### Transpiration characteristics under the requirement for low leaf water potential

Although midday depression of  $G_s$  was modest or absent, daily peak  $G_s$  was low (Kelliher *et al.*, 1995), indicating that *P. pallida* held  $E$  at low levels in adaptation to this environment where low leaf water potential is required for water uptake. The ecophysiological basis for low  $G_s$  is clearly shown by relatively low  $g_{\text{sw}}$ , which is a function of high iWUE (negatively correlated with  $g_{\text{sw}}$ ) and high  $V_{\text{cmax25}}$  (positively correlated with  $g_{\text{sw}}$ ) for this species (Collatz *et al.*, 1991; Katul *et al.*, 2003). Measured daily

peak  $g_{\text{sw}}$  values were lower than for other tropical species with similar or lower  $V_{\text{cmax25}}$  or  $A$  values than *P. pallida* (Liu *et al.*, 2003; Holscher *et al.*, 2006; Forrester *et al.*, 2012). High iWUE results were supported by high canopy leaf stable carbon isotope ratio throughout the stand over the period of the study (Dudley *et al.*, 2014). Trees are known to balance leaf gas exchange traits against hydraulic limitation on water transport from soil to leaves (e.g. stem conductivity and leaf water potential) (Katul *et al.*, 2003), as demonstrated by positive correlations between plant hydraulic conductance and stomatal conductance (Meinzer *et al.*, 1999) or photosynthetic rates (Brodribb and Feild, 2000). In order to achieve such balance in this study site, *P. pallida* maintained  $E$  in midday at low levels not by inducing a midday depression (Williams *et al.*, 1998) or reducing  $V_{\text{cmax25}}$ , but rather by maintaining high iWUE and relatively low LAI, which restrict transpiration during the period of highest stomatal conductance (high light intensity under low  $D$  in the morning).

From the viewpoint of carbon acquisition, we suggest that high  $V_{\text{cmax25}}$  typical in N-fixing species and the avoidance of midday depression via anisohydric stomatal control contribute to the increased net carbon gain in this environment. Avoidance of midday depression in  $G_s$ , and possibly photosynthesis, is likely to be an acclimation by *P. pallida* to increase carbon gain, instead of photosynthesizing only within a short period in the early morning each day. Similarly, *Quercus ilex*, a species that does not reduce photosynthetic capacity and  $g_{\text{sw}}$  in the dry season, is successfully established in dry Mediterranean forests (Ferrio *et al.*, 2003; Valladares and Sanchez-Gomez, 2006). As is the case for Russian olive (*Elaeagnus angustifolia*) in the south-western United States (Hultine and Bush, 2011), these leaf ecophysiological

traits of *P. pallida* would have allowed this species to avoid carbon starvation and establish as a successful invader in environments with very low and infrequent rainfall.

#### *Invasion impacts of coastal Prosopis pallida* stands

In contrast to our third hypothesis,  $J_s$  (and  $E$ ) of *P. pallida* increased with daytime  $D$  without clear responses to preceding rainfall events (Figure 2). These patterns contrast with those of tree species in nearby higher-altitude dry forests that experience greater rainfall (Sandquist and Cordell, 2007; Cordell and Sandquist, 2008) and with other *Prosopis* species (Scott *et al.*, 2004; Dzikiti *et al.*, 2013), which show transpiration and leaf gas exchange rates strongly dependent on rainfall. A potential explanation for a lack of response of  $E$  in *P. pallida* is an overwhelming contribution of groundwater uptake to the water supply of these trees.

Owing to the strong dependence on groundwater,  $E$  values of *P. pallida* showed a regular seasonal trend predicted by  $D$ , regardless of the occurrence of episodic rainfalls and their amount. The lack of episodic rainfall influence on  $E$  was in contrast to findings from other dry ecosystems (Schwarz *et al.*, 2004; McDowell *et al.*, 2008b), where changes in the frequency of light rainfall under global climatic changes (Easterling *et al.*, 2000) should have strong impacts on the  $E$ .

While annual transpiration calculated as  $E$  was ~80% higher than rainfall over the year of the study, our estimate of  $E$  may be a conservative one, with implications for impacts by this species on regional hydrological processes. Although lower  $G_s$  than  $g_{sw}$  may be partly due to the different calculation methods (Equation S3), midday  $G_s$  was about half of independently obtained  $g_{sw}$  for sun-exposed leaves and partially shaded leaves (Figure 4 and Table II). This finding can be explained by recent studies that found sap flux to be underestimated using Granier's sensors (Bush *et al.*, 2010; Sun *et al.*, 2012). Hence, our findings of a negative water budget through groundwater uptake and continuous transpiration by *P. pallida* through drought periods suggest this invasion has altered the historical hydrological cycle of this region and separates the impacts of this species from the shallow-rooted, ephemeral vegetation currently present. It is reasonable to expect that increased net carbon gain in coastal bands of *P. pallida* increases the biogeochemical and ecological impacts of this species as an invader.

## CONCLUSIONS

Access to groundwater by *P. pallida* resulted in transpiration rates that were higher than annual rainfall and that lacked clear responses to episodic rainfall

events. However, low leaf water potential, high iWUE and high canopy leaf stable carbon isotope ratio (Dudley *et al.*, 2014) suggest constraints to groundwater absorption by this species and partly explain the modest transpiration rates and stomatal conductance at their daily peaks. Nevertheless, *P. pallida* has unique ecophysiological traits that enhance both transpiration rates and photosynthesis for survival in this dry leeward coastal area on a young basaltic substrate; such traits include high photosynthetic capacity and anisohydric stomatal control capable of maintaining high midday stomatal conductance even at the risk of cavitation. Our results obtained by *in situ* measurements have helped to avoid possible erroneous predictions of variations in transpiration rates in response to changing vapour pressure deficit by *P. pallida*, responses by this species to episodic rainfall events and future climate change scenarios. The invasion of *P. pallida* into leeward coastal areas of Hawai'i has likely promoted increased groundwater uptake, altering local hydrological processes including probable reductions in submarine groundwater discharge. Additionally, our observations of vigorous photosynthesis due to high photosynthetic capacity and sustained stomatal conductance throughout daylight hours are consistent with the premise that groundwater access by *P. pallida* increases alterations to carbon and nutrient cycling in invaded areas (Dudley *et al.*, 2014).

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