

Comparing ecophysiological traits and evapotranspiration of an invasive exotic, *Pinus halepensis* in native woodland overlying a karst aquifer

Brooke A. Swaffer^{1,2*} and Kate L. Holland³

¹ South Australia Water Corporation, GPO Box 1751, Adelaide, South Australia, 5000, Australia

² Flinders University, GPO Box 2100, Adelaide, SA, 5000, Australia

³ CSIRO Land and Water, PMB 2, Glen Osmond, South Australia, 5064, Australia

ABSTRACT

Invasion by exotic plant species into water-limited environments has the potential to change the ecosystem water balance and may further exacerbate water scarcity issues. Here, we compared ecophysiological traits related to tree water use (sap flux, sapwood density, leaf and soil water potentials) and actual evapotranspiration (ET_a) of the invasive *Pinus halepensis* to native tree and shrub species. We hypothesized that the invasive pine species would possess traits that are consistent with the potential to use more water than native species, which would be supported by higher ET_a in areas invaded by pine. We found higher rates of sap flux for the invasive *P. halepensis* (5.5 cm h^{-1}) per unit sapwood area compared with the native species ($<3.5 \text{ cm h}^{-1}$). In addition, *P. halepensis* sapwood was significantly less dense than the sapwood of the native species, suggesting higher sapwood conductivity facilitated the faster sap flux. Comparison of remotely sensed ET_a before and after *P. halepensis* removal within a *Eucalyptus camaldulensis* stand demonstrated a reduction in ET_a by an average of $50 (\pm 11 \text{ SE}) \text{ mm year}^{-1}$ in the 2 years after removal, relative to the ET_a from an undisturbed, intact *E. camaldulensis* stand. This study suggests that active management of this invasive species should reduce overall ET_a losses and thereby exert a positive influence on the availability of soil moisture for groundwater recharge. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS exotic species; groundwater; transpiration; evapotranspiration; sapwood density; water balance

Received 21 January 2013; Revised 3 April 2014; Accepted 20 April 2014

INTRODUCTION

Exotic plant invasions have the potential to adversely affect natural systems (Wilcox, 2002), driving the need to understand the impact of their presence. This is particularly critical in water-limited environments, where invasive plants may exacerbate water scarcity by increasing stand density, transpiration, canopy interception or altering soil moisture flux (Sala *et al.*, 1996; Nagler *et al.*, 2008; Cavaleri and Sack, 2010; Doody and Benyon, 2011; Doody *et al.*, 2011; Rascher *et al.*, 2011). Variability between plant species' water use capacity has been recognized (Calder and Dye, 2001; Asbjornsen *et al.*, 2007; Owens and Moore, 2007) with ecosystems dominated by invasive tree species capable of consuming a greater volume of water per unit area compared with systems dominated by native species (Cavaleri and Sack, 2010). This has been attributed to differences in invasive plant density, total leaf area and relative sapwood area (Sala *et al.*, 1996) and suggests that plant invasions can substantially impact the local water balance.

Recognizing this, resource managers have sought to remove invasive species as a means of returning water to a system (Wilcox, 2002; Shafroth *et al.*, 2005). The concept of enhancing water availability through invasive species' control is not new (introduced in the USA in the 1930s) (Chew, 2009) and has recently been quantified under Australian conditions (Doody and Benyon, 2011). Several attempts to increase water availability through vegetation control have been carried out in the USA, with most of the research effort focussed on *Tamarix* spp. (Sala *et al.*, 1996; Owens and Moore, 2007; Nagler *et al.*, 2008; Hultine *et al.*, 2010; Moore and Owens, 2012). Generally, these suggest that widespread *Tamarix* spp. control appears capable of delivering only modest water savings (Glenn and Nagler, 2005; Doody *et al.*, 2011; Moore *et al.*, 2012). Nagler *et al.* (2008) calculated approximately $0.2 \text{ ML year}^{-1} \text{ ha}^{-1}$ of additional water after *Tamarix* spp. control (assuming the *Tamarix* spp. monoculture was replaced by a mixture of native species), which was in the order of 0.2% of mean annual river flow.

However, Doody and Benyon (2011) examined potential water savings from *Salix* spp. control in Australian riparian zones and propose an average saving of $5.5 \text{ ML year}^{-1} \text{ ha}^{-1}$ of crown projected area could be made, provided that

*Correspondence to: Brooke A. Swaffer, South Australia Water Corporation, GPO Box 1751, Adelaide, South Australia 5000, Australia.
E-mail: brooke.swaffer@sawater.com.au

individuals situated in-stream were controlled, rather than trees on the stream bank. Similar to the findings of Nagler *et al.* (2008), they conclude that control of stream bank willows would be unlikely to result in net water savings, as the native species would replace willows to re-attain maximum canopy coverage. This finding suggests that considering niche occupancy can be a critical factor when assessing the potential for successful water salvage.

In addition to niche occupancy, ecophysiological characteristics related to hydraulic conductivity could also explain variability in water use patterns between invasive and native species, assuming water is not a limiting factor. Physiological variation in xylem characteristics (density of vessel elements and tracheids) may influence the volume of water capable of being processed by a species, as hydraulic conductance of a plant is strongly correlated to maximum transpiration (Bucci *et al.*, 2004; Eamus *et al.*, 2006; O'Grady *et al.*, 2008). Therefore, the density of sapwood can serve as to compare the potential effect of invasive species to their native counterparts.

Due to the multitude of ecosystem impacts attributed to invasive species, literature will often focus on biological, ecological or environmental changes rather than the hydrological influences of invasive plants. This is somewhat surprising considering global freshwater shortages (Vorosmarty *et al.*, 2000), especially in Australia, with its dry climate and recent severe drought. So far, examining the influence of invasive plants has been restricted largely to riparian zones (Doody and Benyon, 2011), with systems characterized by fresh groundwater resources receiving little attention, despite their importance in many areas across Australia. One notable exception was the use of karstic groundwater resources by plantation *Pinus radiata* (Benyon *et al.*, 2006), where up to 72% of transpiration requirements were met by groundwater, with negligible recharge to the karstic aquifer once the tree canopy had closed.

Karst is a geological formation where recharge and discharge processes are particularly variable across a small spatial scale (Schwinning, 2008). Highly soluble rock is eroded to form a complex pathway of dissolution features, caves and sinkholes, causing preferential water movement and resulting in diverse recharge pathways to the water table (Herczeg *et al.*, 1997; White, 2002). Concern regarding the potential detrimental influence of the invasive *Pinus halepensis* on recharge processes of a karstic aquifer was the driver for this work. *P. halepensis* has naturalized across many regions of southern Australia (Virtue and Melland, 2003) and commonly invades the dry, rocky limestone soils often associated with karstic systems. The species has the ability to form dense monocultures and out-compete the native woodland areas (Virtue and Melland, 2003; Quarmby, 2004). An understanding of the comparative water use characteristics of the invasive and native species in

this geological setting is required to inform resource management of *P. halepensis*.

We hypothesized that the invasive *P. halepensis* would possess traits that would facilitate higher rates of water use per unit sapwood area compared with the native tree and shrub species. Furthermore, we suggested that this increased water use would correspond to higher actual evapotranspiration (ET_a) in areas that have been invaded by *P. halepensis* in comparison with areas occupied only by native species. We tested these hypotheses in two ways: (1) we compared ecophysiological traits related to tree water use (sap flux, sapwood density, leaf and soil water potentials) of the invasive and native species at the plot scale and (2) used satellite-derived estimates of ET_a to estimate net recharge under different vegetation types, including areas of *P. halepensis* invasion and removal. Satellite-derived ET_a estimates are becoming increasingly popular because of the need to understand water flux patterns across a broader spatial and temporal span than are usually available with more traditional ET_a methods (Glenn *et al.*, 2011). Here, it has enabled a water balance to be estimated at the basin scale and for different vegetation types, from 2001 to 2010.

METHODS

Study site and plant species

The study was located in Uley Wanilla water reserve, southern Australia (34.62 S, 135.63 E). Groundwater from the reserve has been an important historical drinking water source for the region (Department for Water, 2012a), supplying ~50% of the reticulated groundwater supply (circa 1970s) (Department for Water, 2012b). Since 1985, groundwater levels have declined, on average 4 m (± 1 m standard deviation), despite reduced extractions beginning in the early 1990s. Postulated causes include reduced rainfall, historical groundwater extraction, interception of rainfall and direct use of groundwater by vegetation, including the invasive *P. halepensis* (Department for Water, 2012a) (Figure 1).

Average potential evapotranspiration (FAO56) was 1081 mm year⁻¹ and average annual rainfall was 564 mm year⁻¹ (station # 18017) (1900–2010) (Bureau of Meteorology, 2010). Soils in the area were generally very shallow and typically comprise of skeletal calcareous or shallow sandy and clayey loams (Harrington *et al.*, 2006). A sheet limestone sub-stratum was often present, visible on local topographic rises, with soil pockets occupying local depressions.

Open woodlands and shrublands consisting of trees such as *Eucalyptus diversifolia* subsp. *diversifolia* Bonpl. (coastal white mallee), *Allocasuarina verticillata* (Lam.) L.A.S. Johnson (drooping she-oak), *Melaleuca lanceolata* Otto (dryland tea tree) and shrubs comprising of *Acacia longifolia* var. *sophorae* Labill. Court (coastal wattle), *Pittosporum angustifolium* Lodd., G. Lodd. & W. Lodd. (native apricot) and *Leucopogon*

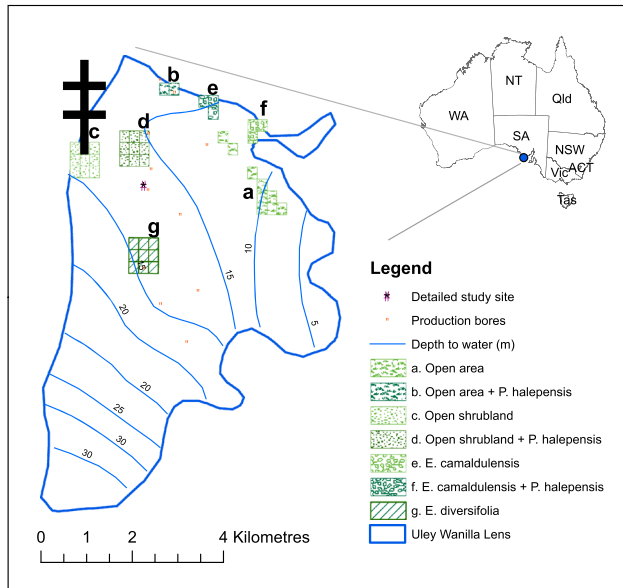


Figure 1. Location of Uley Wanilla groundwater lens showing production bores used for public drinking water supply, location of detailed study site and 250 m grid locations for reference vegetation classes used for ET_a comparisons. Depth to water contours modified from Harrington *et al.* (2006).

parviflorus (Andrews) Lindl. (coastal beard heath) dominate the landscape across the Uley Wanilla groundwater lens. Isolated stands of *Eucalyptus camaldulensis* Denh. (river red gum) were present across the northern section of the reserve, where the water table was relatively shallow. *P. halepensis* Mill. (Aleppo pine), introduced in the early 1800s (Way, 2006), has invaded across the region, with density estimates ranging from isolated plants to canopy coverage of 70–100% (Quarmby, 2004).

A 900 m² plot was used for detailed sampling of a mixed stand containing each of the species described above with the exception of *E. camaldulensis*. Species basal area within the plot was calculated by summing tree and shrub diameter at breast height measurements. Leaf Area Index (LAI) was calculated from digital photographs using Matlab R2011b and the Image Processing Toolbox (The Mathworks Inc., MA, USA). Five digital photos were taken at 2-m intervals along seven transects at 10-m intervals, generating 35 images to calculate plot LAI, following Macfarlane *et al.* (2007) and Fuentes *et al.* (2008). The gap criterion was set to 0.75 and an extinction coefficient of 0.5 was used (appropriate for eucalypt woodlands), following Macfarlane *et al.* (2007).

Tree water use

Tree transpiration (T) was estimated from heat pulse measurements of sap flow velocity on 17 stems every 30 min for 50 days between 28 April and 17 June 2010 (Table I). The technique was based on the compensation method originally proposed by Huber and Schmidt (1937)

Table I. Plot and sap flow tree site details, including wood and water fractions (%) and number of sap flow probes installed in each species, used to calculate median sap flow velocity (cm h^{-1}) and species water use (mm day^{-1}).

	Form T = tree S = shrub	Stem <i>n</i>	Basal area $\text{m}^2 \text{ha}^{-1}$	Basal area %	Sapwood density g cm^{-3}	Probes <i>n</i>	Transpiration parameters			
							Wood fraction %	Water fraction %	cm h^{-1}	mm day^{-1}
<i>Pinus halepensis</i>	T	22	1.98	15	0.513 ^a	8	22	36	5.5 ^a	0.20
<i>Eucalyptus diversifolia</i>	T	70	3.12	23	0.606 ^b	6	26	25	3.5 ^b	0.15
<i>Allocasuarina verticillata</i>	T	3	2.25	17	0.709 ^b	4	40	36	3.4 ^b	0.04
<i>Melaleuca lanceolata</i>	T	72	4.85	36	0.618 ^b	8	30	34	3.2 ^c	0.24
<i>Acacia longifolia</i>	S	5	0.05	<1	0.600 ^b	1	23	31	1.2 ^d	<0.01
<i>Pittosporum angustifolium</i>	S	13	0.23	2	0.681 ^b	3	34	28	1.0 ^d	<0.01
<i>Leucopogon parviflorus</i>	S	102	0.88	7	0.719 ^b	30				
TOTAL		287	13.37	100					0.63	100

Significant pairwise comparisons ($p < 0.05$) are differentiated by ^{a, b, c, d}.

and later refined (Marshall, 1958; Swanson and Whitfield, 1981). Sap flow velocity was measured using thermistor probes attached to a logger (SF 300 probes, Greenspan Technology, Warwick, Queensland), which can be used to accurately estimate sap flow provided appropriate calibration procedures (sapwood wood and water fractions, probe separation distance and species-specific wound widths) are followed (Thorburn *et al.*, 1993b; Vertessy *et al.*, 1997; Cramer *et al.*, 1999; Bleby *et al.*, 2004).

Sapwood wood and water fractions were determined using 5-mm diameter cores, collected at the commencement of sap flow measurements (Benyon, 1999). Probe separation values were checked by inserting blank probes at equivalent depth to the sensor and measuring variation from 10 mm above and 5 mm below the heater probe. Drillholes were rejected where variance was greater than 1 mm and the holes redrilled. Species-specific wound widths of 0.34 mm for *E. diversifolia*, 0.31 mm for *A. verticillata*, 0.34 mm for *M. lanceolata*, 0.31 mm for *P. angustifolium*, 0.37 mm for *P. halepensis* and 0.34 mm for *A. longifolia* were determined following Swanson and Whitfield (1981).

Depth of conducting wood for the instrumented trees was determined by incrementally adjusting probe depth on a sunny day until the measured heat pulse velocity was lower than the minimum reading taken between midnight and 5 AM the previous night (Benyon, 1999) and accounting for bark thickness. A linear regression between tree basal area (using diameter at breast height) and conducting wood area allowed species-specific mean sap flow velocity to be scaled to daily transpiration at the stand level following Hatton *et al.* (1990).

Sapwood density

The density of sapwood as an indicator of potential conductance was determined following O'Grady *et al.* (2009) using cuttings from 66 stems from the seven study species located within the plot. First, sapwood cross-sectional area was measured using manual calipers, and then bark and phloem layers were removed with a sharp knife. Samples were placed in distilled water for 24 h to fully saturate. Using the Archimedes principle, an object immersed in fluid has a volume equal to the weight of the fluid displaced by the object. Therefore, density was calculated by dividing the dry weight of the object (g) by the weight of the displaced water volume (equivalent to cm³). The dry weight of the sapwood was determined by oven-drying at 105 °C for 24 h.

Tree water sources

Analyses of the stable isotopes of water ($\delta^{18}\text{O}$ and $\delta^2\text{H}$) have become standard tools for tracing plant water sources (Ehleringer and Dawson, 1992; Dawson *et al.*, 2002). Matching twig isotopic signatures to their potential sources found throughout the environment is possible as plants do not alter the isotopic composition of water during uptake by roots (Thorburn *et al.*, 1993a, 1993b; Cramer *et al.*, 1999). However,

the method relies on each water source having a distinctive isotopic signature. Twig cuttings were collected from trees instrumented with sap flow loggers, ensuring twigs were selected where heartwood was yet to develop. Approximately 200 mm of twig sample was collected, immediately cut into pieces and immersed in airtight 150-ml glass jars filled with kerosene to minimize isotopic fractionation. Surface soil samples were taken within 2 m of the base of four sample trees by hand. The shallow nature of the soil and the hardness of sheet limestone prevented the use of an auger to obtain deeper samples. Soil samples were placed into 500-ml glass jars and sealed for later analysis of both isotopic composition and matric potential. Groundwater samples were obtained by first purging three well volumes, to ensure the sample was representative of the aquifer (Barber and Davis, 1987). Five rainfall samples collected approximately 15 km away were also used in this isotopic comparison (Swaffer *et al.*, 2014). All water samples were analysed by the CSIRO Isotope Analysis Service, Adelaide. All isotopic concentrations are reported in standard delta notation in units per mil (‰) relative to the Vienna-Standard Mean Oceanic Water.

A mixing line was used to estimate the proportion of twig water being used from each of the potential tree water sources, by placement of the twig isotope data along the distance of the source water mixing line, compared with the length of the line (Thorburn *et al.*, 1993b).

Leaf and soil water potentials

Leaf water potential (Ψ) (MPa) (a measure of the suction gradient and an indicator of plant water stress) was measured on three replicate twigs for each tree instrumented with sap flow loggers using a PMS 1000 pressure chamber (PMS Instrument Company, Albany, Oregon) (Scholander *et al.*, 1965). Twig samples were collected, bagged and placed into a humidified chamber to minimize water loss (Turner, 1988). Time between sample collection and measurement was <1 min. Measurements commenced before dawn (Ψ_p) (0400–0600 h), when the plant was assumed to be in equilibrium with the water potential of its water source. Fresh twig samples from the same trees were collected and measured every 2 h (approximately) therein until dusk (1730–1830 h). Midday leaf water potentials (Ψ_m) (1130–1330 h) were used to measure plant water status when evaporative demands on the vegetation would be expected to be strongest.

Soil water potentials (Ψ) (MPa) represent the sum of matric (dryness) and osmotic (saltiness) potential, where a water potential of 0 MPa is equivalent to free water. Osmotic potential was assumed to exert minimal influence because of the fresh nature of the karst system (salinity 480–620 mg l⁻¹, DEWNR, 2012). Soil matric potentials were determined using the filter paper technique (Greacen *et al.*, 1989), where three replicate filter papers were equilibrated in contact with

the soil for 7 days in a temperature controlled environment. The papers were removed, weighed immediately after the surplus soil was removed, oven-dried at 105 °C for 24 h and reweighed. Using known calibrations, the matric potential was estimated from the water content of the filter papers. Reported values were the average of the three replicates.

Water balance using satellite-derived estimates of evapotranspiration

A water balance (Q_{wt}) (mm) was calculated using the difference between rainfall (P) (mm) and actual evapotranspiration (ET_a), (mm) assuming negligible runoff and changes in soil moisture content (Equation (1)).

$$Q_{wt} = P - ET_a \quad (1)$$

Groundwater discharge was assumed where Q_{wt} was negative; conversely, water available for deep drainage and groundwater recharge was represented by positive Q_{wt} . Where Q_{wt} results are in dimensionless units, the result has been normalized by rainfall received for the corresponding period (Q_{wt} [mm]/ P [mm]). Where Q_{wt} is presented in millimetres per year, error margins are provided based on the standard error of the data. Estimates of ET_a were derived using CSIRO's MODIS Reflectance-based Scaling EvapoTranspiration (CMRSET) algorithm (developed by Guerschman *et al.*, 2009 and assessed against a range of ET -estimate algorithms by Glenn *et al.*, 2011; King *et al.*,

2011). Briefly, the method uses 8-day aggregated Enhanced Vegetation Index and Global Vegetation Moisture Index data to scale ET_a estimates from potential evapotranspiration (ET_o) on a 250-m resolution grid. Data were available from 2001 to 2010. The rainfall and ET_o data used in this assessment was measured by the aforementioned weather station. Reference vegetation classes were assigned to specific cells to examine the differences in ET_a attributable to vegetation types that were selected based on the location of uniform, continuous stands of each vegetation association. Each reference association was initially identified using aerial photography and ground-truthed in February 2014 (Figure 2). During ground-truthing, the extent of the continuous vegetation stand was mapped and the corresponding CMRSET cell reference assigned using the coordinates of the mapped vegetation coverage. Only CMRSET cells that were completely within the mapped vegetation stand were assigned a reference vegetation class.

Reference vegetation classes included the following:

- an open area covered by bare soil, exposed calcrete and annual grasses;
- an open area containing 10% coverage of a dense stand of *P. halepensis*;
- open shrubland dominated by *L. parviflorus* and *M. lanceolata*;
- open shrubland dominated by *L. parviflorus*, *M. lanceolata* and *P. halepensis*;

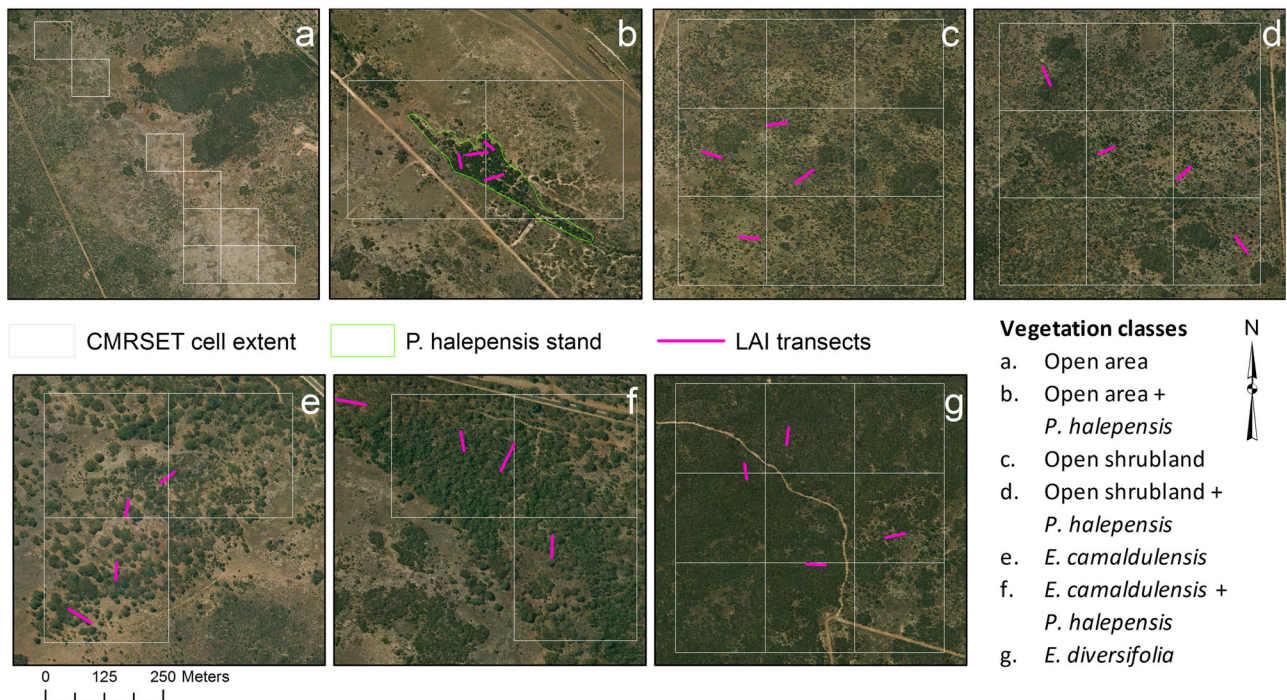


Figure 2. Aerial imagery of the grids for each reference vegetation class used to compare ET_a and Q_{wt} from 2001–2010. Site codes are as follows: (a) open area; (b) open area + *Pinus halepensis*; (c) open shrubland; (d) open shrubland + *P. halepensis*; (e) *Eucalyptus camaldulensis*; (f) *E. camaldulensis* + *P. halepensis*; (g) *Eucalyptus diversifolia*. Photo: 2008.

- *E. camaldulensis* woodland;
- *E. camaldulensis* woodland, which underwent a *P. halepensis* removal program at the end of 2008;
- *E. diversifolia* woodland (Table II).

Leaf Area Index transects were randomly located within the reference vegetation classes; digital images were taken every 2 m along a 50-m transect ($n = 104$ per reference class) and LAI was estimated following Macfarlane *et al.* (2007) and Fuentes *et al.* (2008). Actual ET estimates for the open area+10% *P. halepensis* reference class were scaled (using proportion coverage of 10%) to estimate *P. halepensis* ET_a of a CMRSET cell comprised entirely of *P. halepensis*.

Statistical analyses

Comparisons of sap flow velocity were made using one-way analysis of variance (ANOVA) on ranks, followed by Dunn's method for pairwise comparisons. Sapwood density comparisons were made using a one-way ANOVA, followed by Tukey Tests for pairwise comparisons. Comparisons of reference vegetation ET_a estimates derived from satellite imagery were performed using a repeated measures ANOVA. Differences in ET_a before and after *P. halepensis* removal were assessed using t -tests. All statistical analyses were conducted using SigmaPlot version 11.0 (Systat Software Inc., USA). All spatial analyses were performed using ArcGIS version 10.0 (ESRI Inc., USA).

RESULTS

Plot characteristics

Seven tree and shrub species were recorded within the plot; composition, basal area and location were measured on 28 April 2010. *L. parviflorus* was the most commonly recorded species but contributed only 7% of the total plot basal area. The stems were too narrow for the installation of sap flow probes; therefore, T was not measured for this species. *M. lanceolata* and *E. diversifolia* were the major contributors to plot biomass, recording 36% and 23% of the plot basal area, respectively. Twenty-two individual *P. halepensis* stems were present, comprising 15% of the plot basal area. Three large *A. verticillata* were present (17% plot basal area). *A. longifolia* (<1%) and *P. angustifolium* (2%) were minor contributors to plot basal area. Overall, the plot contained 287 plant stems, and $13.37 \text{ m}^2 \text{ ha}^{-1}$ of basal area (Table I). LAI was $1.0 (\pm 0.20 \text{ SE})$, which is consistent with that of an open woodland (Eamus *et al.*, 2006).

Tree water use

Sap flow was measured over 50 consecutive days during mid-autumn and early winter. Over this time, 72 mm of

precipitation fell across the site, the majority in the latter half of the measurement period. The increased moisture corresponded to a 45% increase in sap flow velocity for *P. halepensis* and 35% increase for *E. diversifolia*. In contrast, the remaining tree and shrub species did not respond (Figure 3).

Median sap flow velocity of *P. halepensis* ($5.5 \pm 2.4 \text{ cm h}^{-1}$) was significantly greater ($p < 0.05$) than the median velocity for *E. diversifolia* ($3.5 \pm 3.6 \text{ cm h}^{-1}$), *A. verticillata* ($3.4 \pm 0.9 \text{ cm h}^{-1}$), *M. lanceolata* ($3.2 \pm 1.7 \text{ cm h}^{-1}$), *P. angustifolium* ($1.2 \pm 0.3 \text{ cm h}^{-1}$) and *A. longifolia* ($1.0 \pm 0.3 \text{ cm h}^{-1}$), indicating greater transport of water per unit area compared with the native species (Table I) (Figure 4). The volume of water transpired by the vegetation in the plot was 32 mm over the 50-day study period, which corresponds to an average of 0.63 mm day^{-1} . Approximately, 32% of daily transpired water was attributed to *P. halepensis* (0.20 mm day^{-1}), comprising only 15% of plot basal area. However, the majority (38%) of transpired water originated from *M. lanceolata* (0.24 mm day^{-1}), attributed to its greater proportion of basal area (36%) within the plot (Table I) (Figure 4).

Sapwood density, used here as a proxy for hydraulic conductivity, was lowest in *P. halepensis*, averaging $0.513 \pm 0.035 \text{ g cm}^{-3}$ ($n = 13$); moderate in *A. longifolia* ($0.600 \pm 0.013 \text{ g cm}^{-3}$, $n = 7$), *E. diversifolia* ($0.606 \pm 0.024 \text{ g cm}^{-3}$, $n = 6$), *M. lanceolata* (0.618 ± 0.031 , $n = 12$) and *P. angustifolium* ($0.681 \pm 0.032 \text{ g cm}^{-3}$, $n = 10$); and highest in *A. verticillata* ($0.709 \pm 0.008 \text{ g cm}^{-3}$, $n = 6$) and *L. parviflorus* ($0.719 \pm 0.030 \text{ g cm}^{-3}$, $n = 12$) (Figure 5). *P. halepensis* sapwood density was significantly less than the native species' sapwood density (F -value = 61.964, $p < 0.001$) (Table I).

Tree water sources

The isotopic composition of rainfall was variable and ranged between -1.81‰ to -6.26‰ $\delta^{18}\text{O}$ and 0.7‰ to -36.5‰ $\delta^2\text{H}$. Groundwater samples from two bores ($\sim 500 \text{ m}$ apart) within 350 m of the study site averaged -4.55‰ $\delta^{18}\text{O}$ and -26.0‰ $\delta^2\text{H}$. Surface soil water samples were enriched relative to rainfall, consistent with evaporative demands and likely represent the end-member for isotopic enrichment at the time of sampling. Twig water samples were variable, but differences between the native and non-native species were not marked (Figure 6). Native species twig isotope ratios ranged between -2.90‰ to -0.01‰ for $\delta^{18}\text{O}$ and -20.2‰ to -7.2‰ for $\delta^2\text{H}$. *P. halepensis* twig isotope ratios varied between -3.47‰ to -0.64‰ for $\delta^{18}\text{O}$ and -23.4‰ to -12.8‰ for $\delta^2\text{H}$.

Twig water samples fell along a mixing line between surface soil and ground water end members (Figure 6). The third source of water, subsurface soil water, was not sampled because of the hardness of the karst material. There was no obvious match between the twig isotope ratios and two of its

Table II. Net recharge (Q_{wr}) across the Uley Wanilla basin and the seven reference vegetation classes, shown for each year as a proportion of received rainfall, and also as cumulative net recharge spanning 2001 to 2010, estimated using the CSIRO's MODIS Reflectance-based Scaling EvapoTranspiration water balance approach.

	Invaded	Cells <i>n</i>	LAI ^a		Annual net recharge as a proportion of rainfall			Cumulative net recharge (2001–2010)		
			Mean	SE	Median	Min	Max	SE	mm	% rainfall ^b
a Open area		9			0.16	–0.18	0.35	0.013	826	15
b Open area + <i>Pinus halepensis</i> ^c	x	2	2.24	0.13	–0.03	–0.40	0.24	0.043	–151	–3
c Open shrubland		9	0.44	0.09	0.09	–0.21	0.28	0.013	458	8
d Open shrubland + <i>Pinus halepensis</i>	x	9	1.09	0.14	0.02	–0.32	0.20	0.014	135	2
e <i>Eucalyptus camaldulensis</i> 2001–2008		3	1.20	0.07	–0.16	–0.46	0.16	0.032	–566	–13
2009–2010		3			0.02	–0.07	0.12	0.027	–8	–0.2%
f <i>Eucalyptus camaldulensis</i> + <i>Pinus halepensis</i> 2001–2008	x	3	0.83	0.05	–0.27	–0.52	0.01	0.030	–1067	–25%
2009–2010		3			–0.01	–0.12	0.07	0.032	–34	–1%
g <i>Eucalyptus diversifolia</i> Uley Wanilla basin	x	9	1.15	0.07	–0.18	–0.66	0.03	0.020	–1213	–22%
		703			–0.08	–1.04	0.35	0.003	–482	–9%

LAI, Leaf Area Index.

^a LAI measured 19 February 2014.^b Total rainfall (2001–2010) = 5532 mm.^c Estimates have been scaled on the basis of the ratio of *Pinus halepensis* stand area (12 283 m²) and CSIRO's MODIS Reflectance-based Scaling EvapoTranspiration cell areas (125 000 m²).

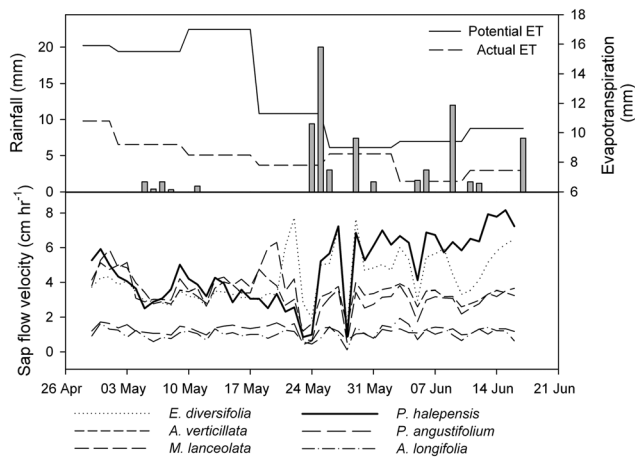


Figure 3. Project timeline showing daily rainfall (mm) and average sap flow velocity (cm h^{-1}) for the six species instrumented with sap flow loggers. Potential evapotranspiration (FAO56) and actual evapotranspiration (ET_a , mm) are presented as 8-day composites.

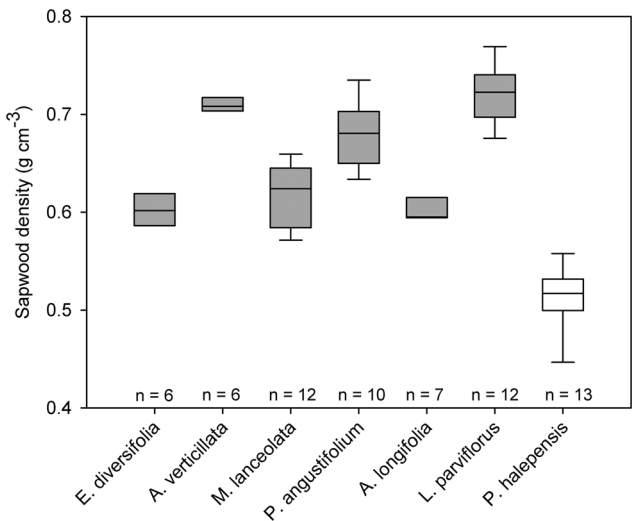


Figure 5. Sapwood density of replicate twigs (g cm^{-3}) from multiple individuals of each of the species within the plot. Box plots extend from the 25th to 75th percentile, median values within. Whiskers show 10th and 90th percentile.

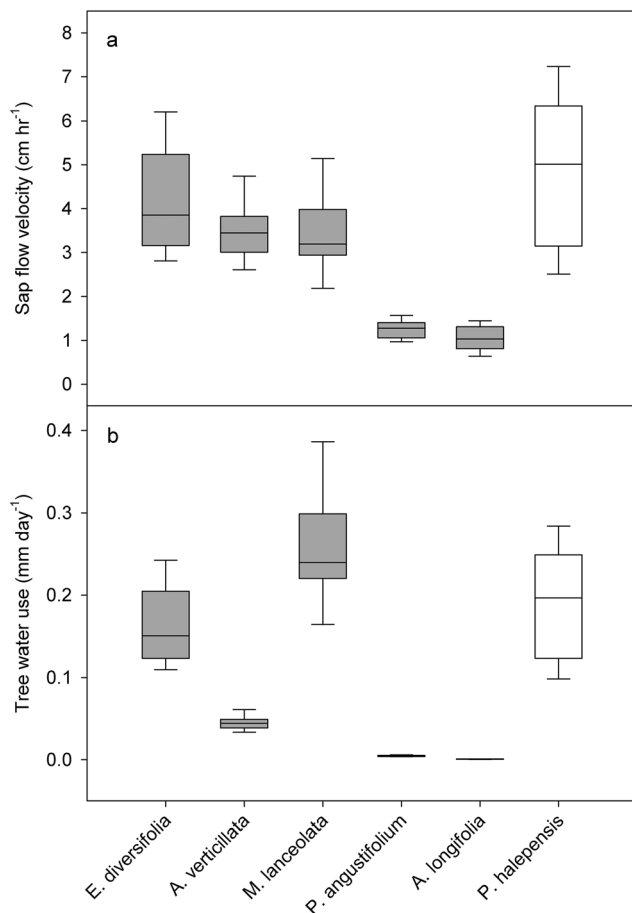


Figure 4. (a) Sap flow velocity (cm h^{-1}) averaged over replicate probes within each species. (b) Tree water use (mm day^{-1}) averaged across each instrumented species. Box plots extend from the 25th to 75th percentile, median values within. Whiskers show 10th and 90th percentile. All data $n=49$.

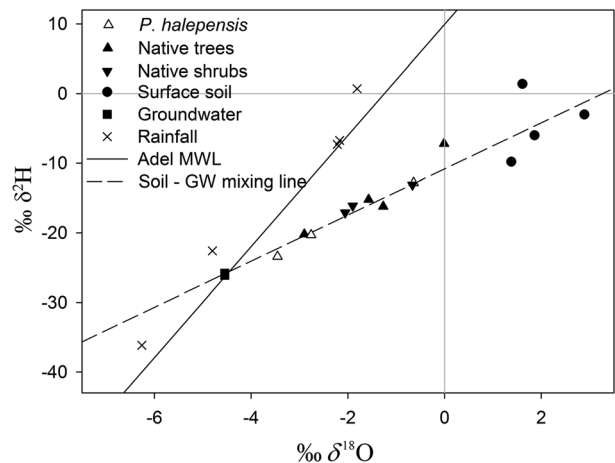


Figure 6. Plots of $\delta^{18}\text{O}$ (‰) versus $\delta^2\text{H}$ (‰) for groundwater (■), surface soils (●), *Pinus halepensis* (Δ), native tree (▲) and native shrubs (▼) collected 28 April 2010. Rainfall samples are cumulative monthly samples collected from March to July 2010. The solid line is the Adelaide Meteoric Water Line, and the dashed line represents an evaporative series inferred from the position of the groundwater and surface soil water samples on the plot.

potential sources (surface soil water or groundwater). This ambiguity may be the result of simultaneous uptake from surface soil and groundwater or that subsurface soil water may represent a mixture of evaporatively enriched surface soil water and depleted rainfall (similar to the groundwater signature).

Leaf and soil water potentials

Native species predawn water potentials were variable (-2.1 to -0.9 MPa), suggesting that species-specific or location-specific variability was present within the site. The

relatively low predawn Ψ values suggest that these individuals had limited access to water reserves at the time of sampling. The native species predawn Ψ were not significantly different to *P. halepensis* predawn Ψ values (-1.5 to -1.3 MPa) ($p > 0.05$). Midday leaf water potentials also lacked statistical differences between native species (-3.3 to -1.9 MPa) and *P. halepensis* (-2.6 to -2.3 MPa). Surface soil matric potentials ranged between -5 and -1 MPa ($n = 4$) (Figure 7).

Water balance using satellite-derived estimates of evapotranspiration

Evapotranspiration from the Uley Wanilla groundwater basin exceeded the volume of rainfall received from 2001 to 2010, indicating a total net discharge of 9% of the rainfall received (5532 mm). A discharging basin is consistent with the region experiencing what is commonly referred to as the 'Millennium Drought' (2001 and 2009) (Van Dijk *et al.*, 2013), amplified by the extremely low rainfall years of 2002, 2006 and 2008. Q_{wt} was spatially variable across the basin for all water balance years (2001–2010) (Figure 8). There were detectable ET_a differences between the reference vegetation classes relative to the volume of rainfall received. Median Q_{wt} was positive (recharging) for open areas (0.16) largely devoid of vegetation. Median Q_{wt} was also positive in shrublands, regardless of the presence (0.02) or absence (0.09) of *P. halepensis*. However, median Q_{wt} was negative (discharging) for regions covered by *P. halepensis* (-0.03), *E. camaldulensis* with (-0.21) and without (-0.11) *P. halepensis*, and *E. diversifolia* woodland (-0.18) (Figure 9) (Table II).

The hydrological effect of *P. halepensis* infestation was particularly evident upon closer examination of the two *E. camaldulensis* stands. *Pinus halepensis* removal took place in 2008; prior to this, median net recharge relative to rainfall

for the stand was -0.27 . In the 2 years after clearance, median net recharge increased to -0.01 (gain of 0.26 relative to rainfall). A comparison stand of *E. camaldulensis* without *P. halepensis* invasion demonstrates a similar trend; during 2001 to 2008, net recharge for the intact site was -0.16 , which increased to 0.02 during 2009 and 2010 (gain of 0.18 relative to rainfall). After accounting for the corresponding increase in ET_a in the intact site in 2009 and 2010 (0.26–0.18), the pine removal equated to a reduction in ET_a of $50 (\pm 11 \text{ SE}) \text{ mm year}^{-1}$ over the 2 years of measurement in the invaded site.

Net recharge was significantly lower in the invaded *E. camaldulensis* stand during 2001–2008, compared with the intact *E. camaldulensis* site ($F\text{-value} = 37.249$, $p < 0.001$). However, importantly, there was no significant difference in net recharge between the intact and invaded sites post-clearance (2009 and 2010) ($F\text{-value} = 1.589$, $p = 0.263$). Within each site but comparing across the two periods (pre-clearance and post-clearance), net recharge was significantly lower in 2001–2008, in comparison with 2009–2010 for both vegetation types (*E. camaldulensis* with *P. halepensis*, $p < 0.001$; *E. camaldulensis* without *P. halepensis* $p < 0.05$), consistent with the timing of the end of the drought (Figure 10).

On the basis of the median net recharge estimates in Table II and adopting the average rainfall of 564 mm year^{-1} , we can postulate the changes to annual ET_a with future removal of *P. halepensis*. For example, removing *P. halepensis* in the open shrubland site may result in a reduction of ET_a by $39 (\pm 1 \text{ SE}) \text{ mm year}^{-1}$. Removing a dense, closed canopy *P. halepensis* stand and replacing it with open grassland may reduce ET_a losses by $109 (\pm 17 \text{ SE}) \text{ mm year}^{-1}$. Allowing encroachment of open shrubland by dense *E. diversifolia* woodland would increase ET_a by $50 (\pm 19 \text{ SE}) \text{ mm year}^{-1}$. Caution is recommended when considering these figures, as other location-specific variables may influence ET_a besides

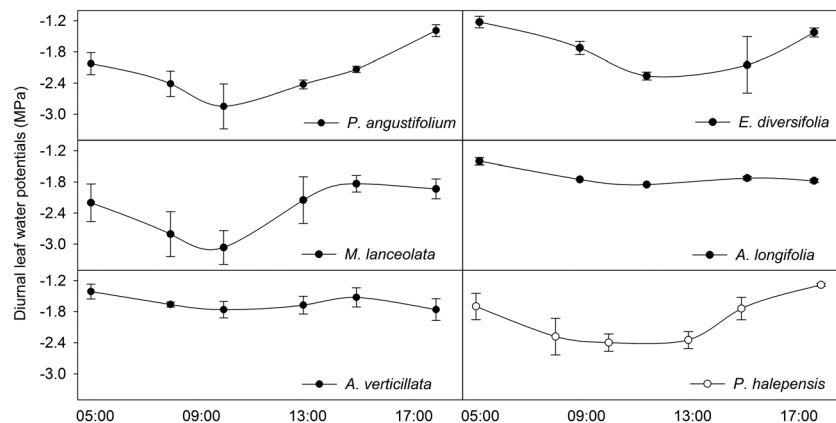


Figure 7. Diurnal pattern of leaf water potential (Ψ , MPa, mean \pm standard deviation) for native species (solid circles) and *Pinus halepensis* (open circles) measured on 28 April between 5 AM and 5 PM. Multiple trees per species were sampled, except *Pittosporum angustifolium* and *Acacia longifolia*, where only one individual was sampled. Three twig samples were measured per tree per time and averaged.

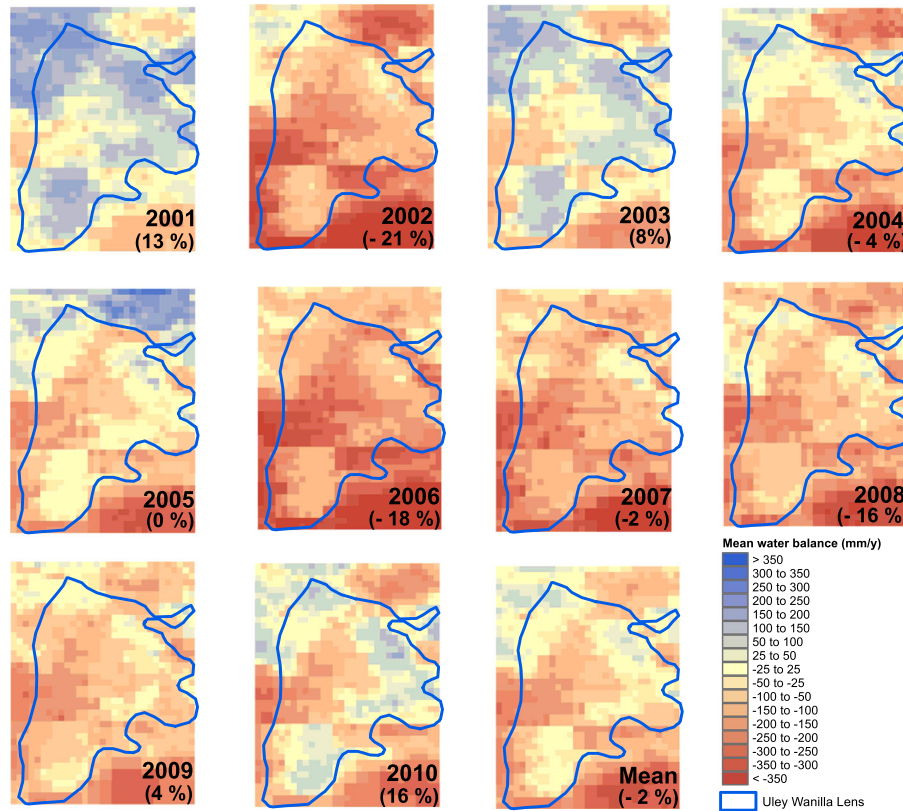


Figure 8. Annual net recharge (mm year^{-1}) for each year from 2001 to 2010. Received rainfall relative to the long term average of 564 mm year^{-1} is shown in brackets.

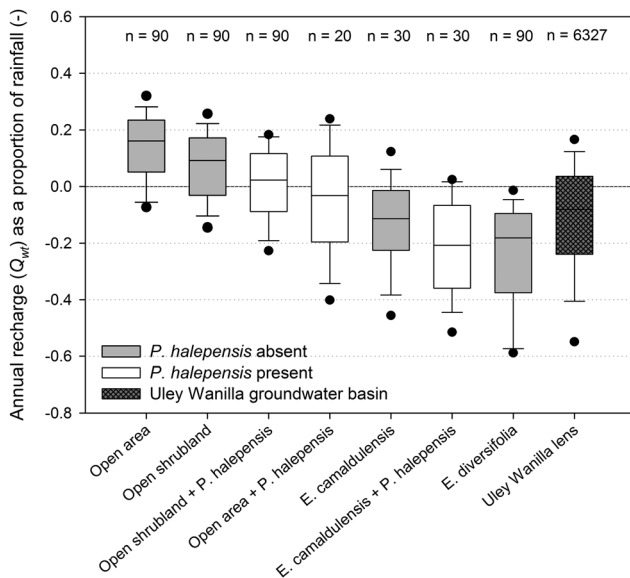


Figure 9. Annual net recharge over the period of 2001 to 2010, normalized by rainfall for each vegetation class and the extent of the Uley Wanilla groundwater basin. *Pinus halepensis* vegetation estimate has been calculated (scaled using stand extent and CSIRO's MODIS Reflectance-based Scaling EvapoTranspiration cell coverage). Box plots extend from the 25th to 75th percentile, median values within. Whiskers show 10th and 90th percentile.

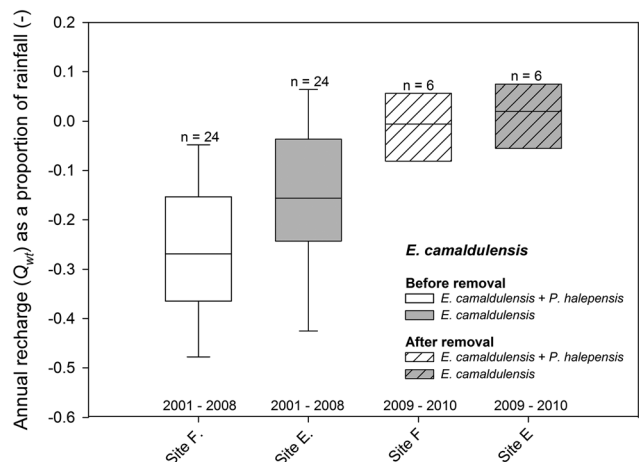


Figure 10. Annual net recharge (Q_w) as a proportion of rainfall received before (2001–2008) and after (2009–2010) *Pinus halepensis* removal within an *Eucalyptus camaldulensis* stand (Site F). A comparative *E. camaldulensis* stand with no history of *P. halepensis* infestation (Site E) is shown for comparative purposes for both periods (filled boxes).

vegetation cover (depth to groundwater, soil depth, etc), which were not considered in this work. Perhaps the most reliable water saving estimate was evident for the *E.*

camaldulensis stand, before and after removal within a single site, where measured ET_a was reduced by $50(\pm 11 \text{ SE}) \text{ mm year}^{-1}$ once *P. halepensis* was removed.

DISCUSSION

Ecophysiological traits

The declining status of a freshwater aquifer prompted this investigation into tree water use and ET_a losses associated with the invasive pine species. Differences between the ecophysiological traits and ET_a of *P. halepensis* and the native tree and shrub species were detected. *P. halepensis* had the highest median sap flux rate, and its transpiration rate (0.20 mm day^{-1}) was comparable with previously reported values ($0.15\text{--}2.1 \text{ mm day}^{-1}$; Schiller and Cohen, 1998; Yaseef *et al.*, 2010). The higher sap flow velocity was consistent with the lower sapwood density of *P. halepensis*. Wood density can be used as a predictor of a range of parameters that relate to plant water use (O'Grady *et al.*, 2009; McCulloh *et al.*, 2011), with sapwood density negatively correlated with sapwood conductivity (Stratton *et al.*, 2000; Bucci *et al.*, 2004) and positively correlated to specific leaf area (O'Grady *et al.*, 2009). This indicates that removal of *P. halepensis* and replacement by native species (with higher sapwood density and lower transpiration rates) may reduce the volume of water lost as transpiration. We note that, however, species-specific transpiration differences may be compensated by variable soil evaporation or canopy interception rates for different trees and result in similar net ET_a values (Swaffer *et al.*, 2014).

Water balance using remotely sensed ET_a

We examined the water balance of the aquifer system and above ground vegetation using 10 years of ET_a data derived using the CMRSET algorithm. When all years were combined, the data suggested net discharge was occurring for the Uley Wanilla groundwater basin, which is consistent with the observed water level trends. It is important to note that the region was in severe drought during most of the 10 years of available ET_a data, which was likely to have increased the amount of discharge relative to historical levels. Regardless, higher ET_a , which can be attributed to the presence of *P. halepensis*, was detected by comparisons between the open shrubland and *E. camaldulensis* vegetation associations with and without *P. halepensis*.

We compared ET_a from two *E. camaldulensis* sites: one where *P. halepensis* was removed at the end of 2008 and another where there was no history of *P. halepensis* invasion. We showed that removal of *P. halepensis* reduced ET_a by $50(\pm 11) \text{ mm year}^{-1}$. Considering the reported annual recharge rate for the Uley Wanilla groundwater reserve has ranged between 11 and 16 mm year^{-1} (2001/02 to 2011/12) (Government Gazette, 2012), this additional water has the

potential to increase groundwater recharge. Invasive species have been reported to negatively impact system hydrology elsewhere (Elkington, 2009; Rascher *et al.*, 2011; Boyce *et al.*, 2012). Our results suggest that there is a linkage between water use by the invasive pine and a reduction in recharge to this karst aquifer. However, we consider that more than 2 years of post-clearance ET_a data are required to confidently assess the value of these water savings.

Groundwater use by vegetation

It is difficult to separate the decline in water levels from reduced recharge or increased discharge (groundwater access) by *P. halepensis*. Not all negative Q_{wr} values indicate groundwater use, as excess soil moisture can be present in the subsurface profile from the previous year's rainfall. However, five consecutive years (2004–2008) were at or below the long term average of 564 mm year^{-1} . It seems reasonable then, in the absence of surface water expressions, that discharging sites during 2008 contain vegetation that was using groundwater to maintain transpiration.

Groundwater use, however, was not clearly demonstrated by the tree water source data (isotopes and leaf and soil water potentials) collected in 2010. The observed response of *P. halepensis* transpiration to rainfall on 24 May 2010 suggested that the trees were previously water limited. The isotope signatures do, however, suggest that different species access different water sources within the karst profile, as has been reported in similar environments (Schwinning, 2008). The *P. halepensis* isotope values were more depleted, most likely indicating deeper, water stores in the profile or groundwater compared with most of the native tree and shrub twig water signatures.

Benyon *et al.* (2006) observed groundwater uptake by plantation pines in a karst environment in areas where the water table was $< 8 \text{ m}$ below the soil surface. Groundwater depth at our detailed study site was $\sim 15 \text{ m}$, which exceeds Benyon's *et al.* (2006) threshold in a similar geological setting. A review of groundwater discharge studies in Australia and global reviews of plant rooting distributions concluded that the maximum depth of groundwater discharge was $5\text{--}10 \text{ m}$ (O'Grady *et al.*, 2010).

Groundwater use, of all the vegetation classes examined here, appears most likely for the *E. diversifolia* woodland. Here, the CMRSET data suggested that many of these areas had negative Q_{wr} ; therefore, additional water was being lost than can be met by rainfall. Following this, it appears that groundwater recharge will be adversely affected not only by the presence of *P. halepensis* but also by encroachment of some native vegetation associations. Annual ET_a was less than rainfall in open and shrubland regions, suggesting that this additional water would facilitate deep drainage and groundwater recharge.

The Q_{wr} rates in this study, normalized for rainfall received, are comparable with the 2 years of detailed plot

scale measurements in Swaffer *et al.* (2014) and provide confidence in the CMRSET application to this location. In a similar karstic setting, open area Q_{wt} was 0.28 and 0.11, similar to the 0.16 reported here, and the *E. diversifolia* Q_{wt} was -0.21 and -0.19 , which is comparable with -0.18 calculated in this study for this vegetation type.

Our results indicate that the presence of *P. halepensis* infestations and expansion of *E. diversifolia* would reduce recharge rates. In addition, it is important to recognize that much of the ET_a data used in this analysis were obtained during one of the most severe droughts to have affected south-eastern Australia; therefore, it is unsurprising to have recorded few positive (draining) Q_{wt} areas. It would be beneficial to expand the CMRSET ET_a analysis to more recent years (2011–2013), with higher rainfall totals; however, the data were unavailable at the time of this analysis.

CONCLUSION

This study demonstrated that *P. halepensis* was capable of transpiring a greater volume of water per unit of conducting wood area compared with the native tree and shrub species. We also showed that actual evapotranspiration was higher from sites where *P. halepensis* had invaded *E. camaldulensis* woodland systems and that removal of the trees can reduce ET_a by 50 mm year^{-1} . However, our analysis also showed that encroachment by other native vegetation associations (*E. diversifolia*) would reduce groundwater recharge. Groundwater discharge was consistently observed in some areas, which was most likely due to groundwater use by vegetation during the below average rainfall conditions. Our findings link the eco physiology of *P. halepensis* and the hydrology of the system to provide data to support the active management of the invasive pine and increase the volume of water available for groundwater recharge.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the advice and support from South Australia Water Corporation, the South Australian Department for Environment, Water and Natural Resources and the Eyre Peninsula Natural Resources Management Board. We thank Megan LeFournour, Michelle Caputo, Tanya Doody, Damian Stam, Glyn Ashman, Rob Hughes and Peter Samuel for their support and technical assistance. We are particularly grateful to Russell Crosbie and Phil Davies for the advice and access to the CMRSET ET_a data. Thanks also to Jodie Pritchard, Jacqueline Frizenschaf, Glyn Ashman, Caecilia Ewenz, John Hutson and each of the anonymous reviewers for review of the manuscript. The authors declare no conflict of interest regarding this research article.

Research was funded by the South Australia Water Corporation, with in-kind support provided by CSIRO Land and Water.

REFERENCES

- Asbjornsen H, Tomer MD, Gomez-Cardenas M, Brudvig LA, Greenan CM, Schilling K. 2007. Tree and stand transpiration in a Midwestern bur oak savanna after elm encroachment and restoration thinning. *Forest Ecology and Management* **247**: 209–219.
- Barber C, Davis GB. 1987 Representative sampling of ground water from short screened boreholes. *Ground Water* **25**: 581–587.
- Benyon RG. 1999. Nighttime water use in an irrigated *Eucalyptus grandis* plantation. *Tree Physiology* **19**: 853–859.
- Benyon RG, Theiveyanathan S, Doody T. 2006. Impacts of tree plantations on groundwater in south-eastern Australia. *Australian Journal of Botany* **54**: 181–192.
- Bleby TM, Burgess SSO, Adams MA. 2004. A validation, comparison and error analysis of two heat-pulse methods for measuring sap flow in *Eucalyptus marginata* saplings. *Functional Plant Biology* **31**: 645–658.
- Boyce RL, Durtsche RD, Fugal SL. 2012. Impact of the invasive shrub *Lonicera maackii* on stand transpiration and ecosystem hydrology in a wetland forest. *Biological Invasions* **14**: 671–680.
- Bucci SJ, Goldstein G, Meizner FC, Scholz FG, Franco AC, Bustamante M. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology* **24**: 891–899.
- Bureau of Meteorology. 2010. Daily rainfall data for Port Lincoln (Big Swamp) (018017). <http://www.bom.gov.au/climate/data/>. Accessed 12 June 2012.
- Calder I, Dye P. 2001. Hydrological impacts of invasive alien plants. *Land Use and Water Resources Research* **1**: 1–12.
- Cavaleri MA, Sack L. 2010. Comparative water use of native and invasive plants at multiple scales: a global meta-analysis. *Ecology* **91**: 2705–2715.
- Chew M. 2009. The monstering of Tamarisk: how scientists made a plant into a problem. *Journal of the History of Biology* **42**: 231–266.
- Cramer VA, Thorburn PJ, Fraser GW. 1999. Transpiration and groundwater uptake from farm forest plots of *Casuarina glauca* and *Eucalyptus camaldulensis* in saline areas of southeast Queensland, Australia. *Agricultural Water Management* **39**: 187–204.
- Dawson TE, Mambelli S, Planboeck AH, Templer PH, Tu KP. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology, Evolution, and Systematics* **33**: 507–559.
- Department for Water. 2012a. Southern basins PWA: groundwater level and salinity status report. Available at: <http://www.waterconnect.sa.gov.au>. Accessed 11 July 2012.
- Department for Water. 2012b. Waterconnect. Available at: <http://www.waterconnect.sa.gov.au>. Accessed 11 July 2012.
- DEWNR. 2012. Southern basins PWA: Uley Wanilla Lens groundwater level and salinity status report. Accessed online at <https://www.waterconnect.sa.gov.au/> on 17 March 2014.
- Doody TM, Benyon RG. 2011. Quantifying water savings from willow removal in Australian streams. *Journal of Environmental Management* **92**: 926–935.
- Doody TM, Nagler PL, Glenn EP, Moore GW, Morino K, Hultine KR, Benyon RG. 2011. Potential for water salvage by removal of non-native woody vegetation from dryland river systems. *Hydrological Processes* **25**: 4117–4131.
- Eamus D, Hutton T, Cook P, Colvin C. 2006. *Ecohydrology: Vegetation Function, Water and Resource Management*. CSIRO Publishing: Melbourne.
- Ehleringer JR, Dawson TE. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell and Environment* **15**: 1073–1082.
- Elkington RJ. 2009. Species-specific differences in spring plant water use of invasive brush on the Edwards Plateau, Texas. Msc Thesis. Available form: http://igitur-archive.library.uu.nl/student-theses/2009-1203-200139/Bec_Final_Thesis.pdf. Accessed 19 July 2012.
- Fuentes S, Palmer AR, Taylor D, Zeppel M, Whitely R, Eamus D. 2008. An automated procedure for estimating leaf area index (LAI) of

- woodland ecosystems using digital imagery, MATLAB programming and its application to an examination of the relationship between remotely sensed and field measurements of LAI. *Functional Plant Biology* **35**: 1070–1079.
- Glenn EP, Nagler PL. 2005. Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U. S. riparian zones. *Journal of Arid Environments* **61**: 419–446.
- Glenn EP, Doody TM, Guerschman JP, Huete AR, King EA, McVicar TR, Van Dijk AIJM, Van Niel TG, Yebra M, Zhang Y. 2011. Actual evapotranspiration estimation by ground and remote sensing methods: the Australian experience. *Hydrological Processes* **25**: 4103–4116.
- Government Gazette. 2012. South Australian Government Gazette. Available from: <http://www.governmentgazette.sa.gov.au/>. Accessed 18th October 2012.
- Greacen EL, Walker GR, Cook PG. 1989. Evaluation of the filter paper method for measuring soil water suction. In 'International meeting at University of Utah on measurement of soil and plant water status'. p 137–145.
- Guerschman JP, Van Dijk AIJM, Mattersdorf G, Beringer J, Hutley LB, Leuning R, Pipunic RC, Sherman BS. 2009. Scaling of potential evapotranspiration with MODIS data reproduces flux observations and catchment water balance observations across Australia. *Journal of Hydrology* **369**: 107–119.
- Harrington N, Evans S, Zulfic D. 2006. Uley basin groundwater modelling Project. Volume 1: Project overview and conceptual model development. Report DWLBC 2006/01. Department of Water, Land, Biodiversity and Conservation, Adelaide. <http://www.waterconnect.sa.gov.au/TechnicalPublications/Pages/Default.aspx>. [Accessed 11 July 2012].
- Hatton TJ, Catchpole EA, Vertessy RA. 1990. Integration of sapflow velocity to estimate plant water use. *Tree Physiology* **6**: 201–209.
- Herczeg AL, Leaney FWJ, Stadler MF, Allan GL, Fifield LK. 1997. Chemical and isotopic indicators of point-source recharge to a karst aquifer, South Australia. *Journal of Hydrology* **192**: 271–299.
- Huber B, Schmidt E. 1937. Eine kompensationsmethode zu thermoelektrischen messung langsamer saftströme. *Bericht der Deutschen botanischen Gesellschaft* **55**: 514–529.
- Hultine KR, Nagler PL, Morino K, Bush SE, Burch KG, Dennison PE, Glenn EP, Ehleringer JR. 2010. Sap flux-scaled transpiration by tamarisk (*Tamarix* spp.) before, during and after episodic defoliation by the saltcedar leaf beetle (*Diorhabda carinulata*). *Agricultural and Forest Meteorology* **150**: 1467–1475.
- King E, Van Neil T, Van Dijk A, Paget M, Wang Z, Raupach T, Haverd V, Raupach M, Zhang Y, Guerschman JP, McVicar T, Miltenburg I, Renzullo L. 2011. Actual evapotranspiration estimates for Australia. Inter-comparison and Evaluation. Water Information Research and Development Alliance Science Symposium, Melbourne, Australia, 1–5 August.
- Macfarlane C, Hoffman M, Eamus D, Kerp N, Higginson S, McMurtrie R, Adams M. 2007. Estimation of leaf area index in eucalypt forest using digital photography. *Agricultural and Forest Meteorology* **143**: 176–188.
- Marshall DC. 1958. Measurement of sap flow in conifers by heat transport. *Plant Physiology* **6**: 385–396.
- McCulloh KA, Johnson DM, Meinzer FC, Voelker SL, Lachenbruch B, Domec J-C. 2011. Hydraulic architecture of two species differing in wood density: opposing strategies in co-occurring tropical pioneer trees. *Plant, Cell and Environment* **35**: 116–125.
- Moore GW, Owens MK. 2012. Transpirational water loss in invaded and restored semiarid riparian forests. *Restoration Ecology* **20**: 346–351.
- Moore GW, Barre DA, Owens MK. 2012. Does shrub removal increase groundwater recharge in southwestern Texas semiarid rangelands? *Rangeland Ecology and Management* **65**: 1–10.
- Nagler PL, Glenn EP, Didan K, Osterberg J, Jordan F, Cunningham J. 2008. Wide-area estimates of stand structure and water use of *Tamarix* spp. on the lower Colorado River: implications for restoration and water management projects. *Restoration Ecology* **16**: 136–145.
- O'Grady AP, Worledge D, Battaglia M. 2008. Constraints on transpiration of *Eucalyptus globulus* in southern Tasmania, Australia. *Agricultural and Forest Meteorology* **148**: 453–465.
- O'Grady AP, Cook PG, Eamus D, Duguid A, Wischusen JDH, Fass T, Worledge D. 2009. Convergence of tree water use within an arid-zone woodland. *Oecologia* **160**: 643–655.
- O'Grady AP, Carter JL, Holland KL. 2010. *Review of Australian Groundwater Discharge Studies of Terrestrial Systems*. CSIRO: Water for a Healthy Country National Research Flagship; 60.
- Owens MK, Moore GW. 2007. Saltcedar water use: realistic and unrealistic expectations. *Rangeland Ecology and Management* **60**: 553–557.
- Quarmby JP. 2004. Aleppo Pine survey of Uley Wanilla, Uley South and Lincoln Basins. Report on the distribution and abundance of Aleppo Pine and recommendations for control. South Australian Water Corporation, Adelaide.
- Rascher KG, Große-Stoltenberg A, Máguas C, Werner C. 2011. Understorey invasion by *Acacia longifolia* alters water balance and carbon gain of a Mediterranean pine forest. *Ecosystems* **14**: 904–919.
- Sala A, Smith SD, Devitt DE. 1996. Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave desert floodplain. *Ecological Applications* **6**: 888–898.
- Schiller G, Cohen Y. 1998. Water balance of *Pinus halepensis* Mill. Afforestation in an arid region. *Forest Ecology and Management* **105**: 121–128.
- Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA. 1965. Sap pressure in vascular plants. *Science* **148**: 339–346.
- Schwinning S. 2008. The water relations of two evergreen tree species in a karst savanna. *Oecologia* **158**: 373–383.
- Shafroth PB, Cleverly JR, Dudley TL, Taylor JP, Van Riper III C, Weeks EP, Stuart JN. 2005. Control of *Tamarix* in the Western United States: implications for water salvage, wildlife use, and riparian restoration. *Environmental Management* **35**: 231–246.
- Stratton L, Goldstein G, Meinzer FC. 2000. Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. *Plant, Cell and Environment* **23**: 99–106.
- Swaffer BA, Holland KL, Doody TM, Li C, Hutson J. 2014. Water use strategies of two co-occurring tree species in a semi-arid karst environment. *Hydrological Processes* **28**: 2003–2017.
- Swanson RH, Whitfield DWA. 1981. A numerical analysis of heat pulse velocity theory and practice. *Journal of Experimental Biology* **32**: 221–239.
- Thorburn PJ, Walker GR, Brunel JP. 1993a. Extraction of water from Eucalyptus trees for analysis of deuterium and oxygen-18: laboratory and field techniques. *Plant, Cell and Environment* **16**: 269–277.
- Thorburn PJ, Hatton TJ, Walker GR. 1993b. Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forests. *Journal of Hydrology* **150**: 563–587.
- Turner NC. 1988. Measurement of plant water status by pressure chamber technique. *Irrigation Science* **9**: 289–308.
- Van Dijk AIJM, Beck HE, Crosbie RS, de Jeu RAM, Liu YY, Podger GM, Timbal B, Viney NR. 2013. The Millennium Drought in southeast Australia (2001–2009): Natural and human causes and implications for water resources, ecosystems, economy and society. *Water Resources Research* **49**: 1040–1057.
- Vertessy RA, Hatton TJ, Reece P, O'Sullivan SK, Benyon RG. 1997. Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiology* **17**: 747–756.
- Virtue JG, Melland RL. 2003. The environmental weed risk of revegetation and forestry plants. DWLBC 2003/02. Available from: http://live.greeningaustralia.org.au/nativevegetation/pages/pdf/Authors%20V1_Virtue_Melland.pdf. Accessed 19 July 2012.
- Vorosmarty CJ, Green P, Salisbury J, Lammers RB. 2000. Global water resources: vulnerability from climate change and population growth. *Science* **289**: 284–288.
- Way S. 2006. Strategic management of Aleppo Pines on Lower Eyre Peninsula to maximise biodiversity outcomes. Department of Environment and Heritage. Available from: <http://www.epnrm.sa.gov.au/Portals/4/Aboriginal/pa-gen-aleppopines.pdf>. Accessed 11 July 2012.
- White WB. 2002. Karst hydrology: recent developments and open questions. *Engineering Geology* **65**: 85–105.
- Wilcox BP. 2002. Shrub control and streamflow on rangelands: a process based viewpoint. *Journal of Rangeland Management* **55**: 318–326.
- Yaseef NR, Yakir D, Rotenberg E, Schiller G, Cohen S. 2010. Ecohydrology of a semi-arid forest: partitioning among water balance components and its implications for predicted precipitation changes. *Ecohydrology* **3**: 143–154.