Water relations and the effects of clearing invasive *Prosopis* trees on groundwater in an arid environment in the Northern Cape, South Africa

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Abstract

Several *Prosopis* species have been introduced into South Africa in the last century and many of them have become invasive. This study investigates the water relations, effects of tree clearing, and the seasonal dynamics of groundwater use by an invasive *Prosopis* stand. The trees were growing on deep sandy soils in the floodplain of an episodic river in the arid Northern Cape Province of South Africa. Data was collected on tree water uptake, evapotranspiration and water table depth over different seasons. Effects of tree clearing on groundwater were quantified by comparing data from a *Prosopis invaded* and an adjacent cleared area. Transpiration rates were less than 1.0 mm/d throughout the year and the trees showed structural and physiological adaptations to the combined low rainfall and low water holding capacity of the soils by developing very narrow sapwood areas and by closing their stomata. The trees abstracted groundwater as evidenced by the decline in borehole water levels in the *Prosopis* stand when the trees were transpiring. Groundwater savings of up to 70 m^3/ month could be achieved for each hectare of *Prosopis* cleared. The study suggests that clearing of invasive *Prosopis* would conserve groundwater in the arid parts of South Africa.

Key words: *Hydraulic redistribution, Grassland, Groundwater level, Prosopis clearing, Sap flow, Water use model.*

Highlights

- *Prosopis* showed physiological and structural adaptations to severe water deficit;
- Hydraulic redistribution was the dominant mode of groundwater uptake
- Total transpiration in the *Prosopis* stand was 57 mm annually, and
- *Prosopis* clearing would prevent the loss of 345 m^3/ha of groundwater annually

1.0 Introduction

In South Africa, as elsewhere in the world, it is widely acknowledged that the encroachment of alien invasive plants, especially trees, has deleterious effects on water resources (Doody et al., 2011; Görgens and van Wilgen., 2004; Le Maitre et al., 2002; Naumburg et al., 2005). These alien trees pose problems particularly in water scarce areas because of their ability to alter the local hydrology, compete with and displace indigenous vegetation, and reduce human access to water. Problems with alien invasive plants are likely to be exacerbated by climate change which is expected to accelerate the rate of spread of some species (Hellmann et al., 2008; Richardson and van Wilgen, 2004). This could lead to increased pressure on ecosystems, loss of biodiversity and the disruption of ecosystem goods and services.

Therefore there is a need for enhanced environmental monitoring to better understand the mechanisms and extent to which alien invasive plants use resources such as water. Such information is crucial for the development of evidence – based policies for managing alien invasive plants, and for effectively responding to challenges such as climate change. The International Union for the Conservation of Nature (IUCN) has declared the desert adapted *Prosopis* to be one of the world's worst invasive species (Mwangi and Swallow, 2005; Bromilow, 2010). Near the turn of the 19th century, six *Prosopis* species from Central America were introduced to Namibia and the arid parts of South Africa for fodder, fuel and shade (Harding, 1987; Wise et al., 2012). Here they have hybridised and spread rapidly. The estimated extent of invasion in the Northern Cape province in South Africa grew by 363% between 1990 and 2007, from about 77,000 ha in 1990, to 147 000 ha in 2002, 203 000 ha in 2003 and 360 000 ha in 2007 (van den Berg, 2010). In the Northern Cape alone invasions have increased from 127 821 ha in 1974 to 1 473 953 ha in 2007, roughly doubling between 2004 and 2007 (Van Den Berg 2010; Wise et al. 2012). The largest density of *Prosopis* invasions occur in alluvial flood plains in the Northern Cape Province with some species occurring in upland areas. *Prosopis*, which is a deep – rooted desert phreatophyte, competes for resources with the native grassy and dwarf shrublands which are the dominant vegetation types in South Africa’s most arid Province – the Northern Cape (Mucina and Rutherford 2006).

The need for fresh water for human consumption, agriculture and other uses in the Northern Cape Province has resulted in increasing use of groundwater and has led to serious competition between humans, animals and *Prosopis* (Fourie et al., 2002). An understanding of the relationship between water use by *Prosopis* and groundwater is crucial for managing and maintaining healthy ecosystems while providing water for human needs. Currently there is a paucity of accurate quantitative information on how *Prosopis* trees interact with ground and soil water in different ecosystems in Southern Africa (Fourie et al., 2002; Versfeld et al., 1998). Accurate and direct measurements of water use by *Prosopis* using eco – physiological and micrometeorological instrumentation are mainly reported for areas in the USA, where *Prosopis* is a native species (Hultine et al., 2006; Scott et al., 2000, 2004, 2008).

The clearing of alien invasive plants such as *Prosopis* in order to salvage the water they use is a common management practice employed in countries like Australia, China, South Africa and the USA, among others (Doody et al., 2011; Richardson and van Wilgen, 2004). The overriding objective of the clearing programmes is to reduce excess water-use by the invasive species (Dye et al., 1996) so that the water demands of people and the environment can be met through increased stream flows and groundwater yields. While some studies in humid environments have reported increased stream flows and groundwater levels following the removal of invading vegetation (Prinsloo and Scott, 1999), there are studies in more arid regions where decreases in evapotranspiration due to alien vegetation clearing did not translate to increased stream flow (Hart et al., 2005; McDonald, 2010) or increased groundwater levels (Hays, 2003). Hultine et al (2006) showed that the hydraulic properties of *Prosopis* vary significantly with soil texture. But little information exists on how this translates to stand level water use and the response of different ecosystems to clearing programmes.

This study examines the effects on groundwater of clearing *Prosopis* in an arid riparian ecosystem characterized by deep sandy soils in South Africa. We investigated the water relations of invasive *Prosopis* trees, quantified the seasonal magnitudes and variability of water use, and evaluated the effects of clearing *Prosopis* trees on groundwater by comparing the responses of a *Prosopis* invaded and a cleared area where native vegetation has re – established itself.

2.0 Materials and methods

2.1 Study sites

The study was conducted within the riparian zone of the Rugseer river (29.360°; 21.186° E and 802 m.a.s.l.), approximately three kilometres southeast of the town of Kenhardt in South Africa's Northern Cape Province. The river is highly episodic only flowing for brief periods during irregular flood events. The climate is arid with the mean annual rainfall ranging from 150 to 250 mm most of which falls from late November to March usually as heavy downpours of short duration. Maximum day time air temperatures in excess of 40 °C are common in the spring and summer seasons with the annual reference evapotranspiration approaching 2 000 mm. The study area is underlain by quarternary alluvium and calcrete with superficial deposits of the Kalahari group (Mucina and Rutherford, 2006). The soils are red–yellow in colour and apedal with a coarse sandy texture and a low water–holding capacity. Soils in the riparian zone are partially interlaced with pockets of silt derived from irregular flood events. Electrical resistivity work by Noner (1979, in Fourie et al., 2002) showed that the depth of the sandy soil profile was up to 10 m in most places. Average groundwater depth ranged from seven to twelve metres (Fourie et al., 2002).

The study area falls within the Bushmanland Arid Grassland (Mucina and Rutherford, 2006). The area is dominated by *Stipagrostis* grasses, but the riparian zone is also vegetated by shrubs including *Salsola* species, *Lycium cinereum* and *Galenia africana* and trees such as

Tamarix usneoides, *Acacia karroo*, *Acacia erioloba* and *Ziziphus mucronata.* Areas densely invaded by *Prosopis* consist of stands of mixed age groups with no other understory species presumably because of allelopathic effects and competition (Schachtschneider, 2010). The number of small trees (< 1.5 m height) far exceeded the number of large trees (> 3.0 m) and Fourie et al (2002) reported that large trees were only 12% of the stand population. Mean *Prosopis* tree density was approximately 700 plants per ha and a thicket occupying approximately 5.0 ha was chosen as the 'invaded' study site.

The second study site (29.361° S; 21.189° E and 805 m.a.s.l.), approximately 3.0 ha was cleared of *Prosopis* in 2002 and is currently covered by grasses and a few indigenous shrubs and trees. It is located approximately 250 meters away from the invaded site. Both sites were situated on gently sloping terrain (< 5° slope).

2.2 Sap flow and micrometeorological measurements

Water use by individual *Prosopis* trees was measured using the heat-pulse-velocity (HPV) sap flow technique (Burgess et al., 2001). This technique was used because of its suitability for quantifying low sap velocities and its ability to detect reverse sap flows (negative flows). Five trees of different sizes were instrumented in November 2010 (late spring) with four HPV probes per tree placed equidistant around the trunk at less than 15 cm above – ground. Data were collected at hourly intervals until December 2011 (early summer). Instrumented trees were selected to be representative of the range of stem sizes in the stand based on a survey of the stem diameters of 30 randomly selected trees. The stem diameter and canopy base area of instrumented trees ranged from 6.3 to 18.9 cm, and from 0.7 to 10 m^2, respectively.

We felled trees of different sizes to study in detail the distribution of the water transport pathways across the stem cross section and the sapwood/heartwood boundaries were visually distinguishable from the wood colour. The sapwood depth was very shallow, ranging from 0.7 to 1.3 cm in thickness for all tree size categories. Thus, the thermocouple probes of the HPV system were inserted at the same depth of 0.9 cm from the outside bark to ensure that they measured the temperature of the active sapwood. Since all the HPV sap flow sensors were inserted at the same depth into the sapwood of the instrumented trees, the sap flow volume per tree was calculated by multiplying the average sap velocity of the four HPV probes with the total sapwood area of the respective trees. The sap velocity data was derived from the heat pulse velocity according to the approach by Burgess et al (2001) and corrected for wounding according to the procedure by Swanson and Whitefield (1981). Stand level transpiration (in mm/h) was estimated as the weighted sum of water use by trees in each size category per hectare of the invaded site, assuming negligible tree capacitance.

Three days before the removal of the HPV equipment in December 2011, HPV sensors from one small tree were relocated to measure the sap velocity of the tap root and two lateral roots of one of the larger instrumented trees. This was done to further investigate the water uptake dynamics of the trees. Thick roots were exposed by carefully excavating the soil around the base of the stem. Two sensors were installed in the tap root (~ 2.1 cm diameter), and one sensor in the lateral root running northwards of the main stem (~ 1.85 cm diameter) and another sensor in the southwards lateral root (~ 1.46 cm diameter). The leaf area index of the trees was measured during the spring, summer and winter seasons, respectively using a leaf area meter (Model LAI 2000, LI – COR, Inc., Lincoln NE, USA).

Stand-level evapotranspiration at both the invaded and cleared sites was measured using the open path eddy covariance system during three field measurement campaigns representing three different seasons namely spring, summer and winter. Continuous measurement of stand evapotranspiration was not possible because of equipment limitations. Concurrent measurements at the two sites were also not possible for the same reason. The evapotranspiration was measured for approximately three days per site in the middle of both the invaded and cleared sites (Table 1). The eddy covariance system comprised a three-dimensional sonic anemometer (Model CSAT3, Campbell Scientific, Inc., Logan UT, USA) and an open path infrared gas analyzer (Model LI – 7500A, LI – COR, Inc., Lincoln NE, USA) mounted 1.5 m above the mean canopy height using an eight meter lattice tower at the invaded site and at two meters height above the cleared site. Two net radiometers (Model 240 – 110 NR – Lite, Kipp & Zonnen, Delft, The Netherlands) were mounted at eight meters above the ground, one above the tree and the other above a patch of bare ground at the invaded site to obtain the net radiation which was representative of the stand. The net radiometers at the cleared site were mounted at three meters height. All the sensors were mounted at least 100 cm away from the tower to minimize the influence of the tower on the sensor readings. Air temperature and relative humidity were measured at mean canopy height (~ 3.0 m) on the invaded site and at standard two meters height at the cleared site using the HMP45C probe (Vaisala, Helsinki, Finland). The soil heat flux was measured at various positions within the sites using four clusters of soil heat flux plates (Models Hukseflux, Delft, The Netherlands and REBS, Inc., Seattle, WA, USA) installed at an average depth of six centimetres below the ground. Measurements of the rate of change of soil temperature above the soil heat flux plates at two and five centimetres depths were taken with the soil averaging thermocouples (Campbell Scientific, Inc., Logan UT, USA). The sensors were sampled at 10 Hz frequency by a CR5000 data logger while additional sensors were connected to a CR23X data logger (Campbell Scientific, Inc., Logan UT, USA) and all the loggers were programmed to process the signals at 30 minute intervals. An automatic weather station, mounted at an open area less than one kilometre from the sites, measured the solar irradiance, air temperature, relative humidity, wind speed and direction, and rainfall. All the sensors were programmed to give hourly outputs of the weather variables.

2.3 Plant water status

Soil water content was monitored continuously close to the surface (0 – 20 cm) at the invaded site, using three CS616 soil moisture probes (Campbell Scientific, Inc., Logan UT, USA) to quantify the effects of rainfall on plant available water in the shallow soil layers. Plant water status was quantified by measuring the predawn leaf water potential between 0300 and 0500 (Local time = GMT + 2 h) and the water potential of the stem's xylem (stem water potential) at midday between 1200 to 1400 local time using a Scholander – type pressure chamber (PMS Instruments, Corvallis, OR, USA). The predawn leaf water potential is often used as a surrogate for the average water status of the plant's root zone (Dzikiti et al., 2010; Jones 2004) since the plant's hydraulic system will be in equilibrium at pre-dawn.

The midday stem (xylem) water potential was determined by enclosing the plant shoots in zip–lock bags which were wrapped with aluminium foil to prevent overheating. Equilibration periods of up to three hours were allowed before measurements were taken. The plant water status measurements were taken in December 2011 at the time root sap flow was measured.

2.4 Sources of transpired water

Groundwater levels were monitored at hourly intervals in one borehole in the invaded site and another borehole on the cleared site using piezometers (Diver: Eijkelkamp/van Essen, Netherlands). Rain and groundwater samples were collected for oxygen and hydrogen isotope analysis during each field trip (Table 1). Rainfall was collected in a 25 L bucket that contained a layer of silicone oil to prevent evaporation, and groundwater samples were extracted from the boreholes. Soil samples were collected for isotopic analysis at 50 cm intervals up to two metres depth on two occasions (November 2010 and December 2011). To minimise evaporation the soil samples were stored into two individually secured air tight polythene bags per sample. Twig samples (c. 0.5 cm x 6 cm) from all sap flow instrumented trees were collected for measurements of the plants' xylem water isotopic signature. The twig samples were placed into borosilicate tubes, which were directly inserted onto a cryogenic vacuum extraction line to separate the water for isotope analysis. All extracted tree xylem, soil, rain and groundwater samples were analysed at the Council for Scientific and Industrial Research's isotope laboratory in Pretoria.

The samples were analysed with the traditional isotope ratio mass spectrometry (IRMS). The IRMS analysis procedure had all water samples disassociated into H_2 and CO with a Thermal Conversion Elemental Analyzer (TC/EA) operating at 1350 °C (Thermo Finnigan 2001). These sample gasses were then interfaced with a ConFloIV to a Delta V Plus mass spectrometer (Bremen, Germany) to determine isotopic ratios of both $^{2}H/H$ and $^{18}O/^{16}O$. Eight triplicates of each sample were run to exclude memory effect. A full set of six standards was run after every 20 samples and the running standard was run after every 10 samples to account for reference gas drift and to calibrate the results relative to Standard Mean Ocean Water (VSMOW). The analytical uncertainty was approximately 0.2‰ for $\delta^{18}O$ and 1‰ for $\delta^{2}H$.

2.5 Prosopis water use model

Lastly, we developed a simple tree-scale model for predicting the water use by the *Prosopis* invasions. The model is based on the version of the Penman–Monteith approach applied to *Prosopis* trees by Scott et al., (2004) and on grasses by Wever et al., (2002) but with some modifications. In this approach the transpiration rate (E, kg s^{-1}) is given by:

$$E=\frac{sR_nL+0.93\rho c_p g_b(e_s(T_a)-e_a)L}{\lambda\left[s+0.93\gamma(1+\frac{g_b}{g_c}\right])} \qquad (1)$$

where λ is the latent heat of vaporization of water (J kg^{-1}), "s" is the slope of the saturation vapour pressure against temperature curve (Pa $°C^{-1}$), R_n is the net radiation absorbed by the canopy (W m^{-2}), L is the mean leaf area index of the trees (-), ρ is the density of air (kg m^{-3}),

c_p is the specific heat of air at constant pressure (J kg^{-1} °C^{-1}), $e_s(T_a) - e_a$ is the vapour pressure deficit (VPD) of the air (Pa), γ is the psychrometric constant (Pa °C^{-1}), g_b and g_c are the aerodynamic and canopy conductance (m s^{-1}), respectively. The aerodynamic conductance (g_b=1/r_b) was calculated from the equation for the leaf boundary layer resistance (r_b, s m^{-1}) derived for *Prosopis* by Changgui and Sosebe (1990) as:

$$\mathrm{r_b} = \frac{1}{29.4\left(\frac{u}{d}\right)^{0.5}} \tag{2}$$

where *d* is the characteristic dimension of the *Prosopis* leaf taken to be approximately 0.0045 m and *u* is the mean wind speed (m s^{-1}) across the leaf surface.

A non – linear model of the form developed by Jarvis (1976) and modified by Wever et al. (2002) was used to derive the canopy conductance (g_c, in m s^{-1}) in which:

$$g_c = g_{\max} f(T) f(S) \tag{3}$$

where g_{max} is the maximum value of the surface conductance of the *Prosopis* while f(T) and f(S) are stress functions that vary between 0 and 1. According to Wever et al. (2002) the maximum canopy conductance was given by:

$$g_{\max} = \frac{1}{k_D (VPD)^{0.5}} \tag{4}$$

where k_D is a parameter obtained by model optimization. Because the photosynthetic photon flux density was not measured in this study, we could not use the radiation stress function applied by Wever et al. (2002) or Scott et al. (2004). Rather we used the alternative expression based on the global solar irradiance (S) stress function f(S) presented by Loustau et al. (1997) as:

$$f(S) = \frac{S}{S + k_r} \tag{5}$$

where k_r is a parameter obtained by model optimization. The temperature stress function f(T) was derived using the equation by Zhang et al. (1997) in which:

$$f(T) = \frac{(T_h - T_a)(T_a - T_L)^a}{(T_h - kT)(kT - T_L)^a} \quad \text{and} \tag{6}$$

$$a = \frac{T_h - kT}{kT - T_L} \tag{7}$$

where T_h and T_L are the upper and lower temperature thresholds at which the stomata of *Prosopis* close and these were set at 40 and 0 °C, respectively. T_a is the measured mean air temperature and *kT* is another parameter obtained by model optimization. Given the arid conditions and evidence from multiple excavations (up to 2 metres depth) which showed an extremely dry soil profile, it is reasonable to assume that the soil evaporation component was negligible compared with transpiration. Thus, tree transpiration contributed the bulk of the stand evapotranspiration flux.

3.0 Results

3.1 Prosopis and grassland site energy balance

In spring (November 2010), the mean leaf area index (LAI) of the *Prosopis* trees was approximately 1.2 and this reached a peak of around 1.5 in summer (February 2011). The LAI dropped to less than 0.2 in winter as most trees shed their leaves. Most of the available surface energy was dissipated as sensible heat in spring (Fig 1a) and a very small fraction was used for evapotranspiration (latent heat flux). This translated to low stand evapotranspiration rates which were less than 0.4 mm/d (Table 1). The low evapotranspiration rates were likely a result of the structural and physiological adaptation of the trees to the severely limited plant available water and Fig 2 illustrates how the size of the conducting sapwood area changed with stem size. Bigger trees had disproportionately large heartwood areas which occupied up to 76% of the total stem surface area while the conducting sapwood area was as small as 13% of the total area. To quantify the physiological responses of the trees we estimated the mean canopy conductance by inverting the Penman–Monteith equation according to the approach by Scott et al (2004). The canopy conductance had a very low peak value of only 0.3 mm s^{-1} on cloudless days.

The diurnal trend in the energy balance components of the grassland site in spring (16 to 18 November 2010) were similar to those of the *Prosopis* site with most of the available energy dissipated as sensible heat (Fig 1b). This culminated in correspondingly low evapotranspiration values shown in Table 1, which were generally less than 0.30 mm/d. The high evapotranspiration at the grassland site on 16 November (~ 0.48 mm/d) was a result of high soil evaporation due to light drizzle which was received the previous night. Trends in the surface energy balance components for the invaded (Fig 1c) and cleared sites (Fig 1d) differed between summer and spring. In summer significant proportions of the available energy were used for evapotranspiration at both sites resulting in water use rates that were four to seven times higher than in spring (Table 1). Between 14 November 2010 and 14 February 2011 approximately 92 mm of rainfall was received. This resulted in the re-growth of significant grass cover at the cleared site, with the LAI subsequently rising to approximately 0.8. This increased the peak grassland water use values to more than 3.0 mm/d compared with just over 2.0 mm/d at the *Prosopis* invaded site. The rates of water use by both stands during winter were much lower than the spring or summer values as expected (Table 1).

3.2 Tree water relations

There was no direct correlation between the key driving climatic variables for water use (Fig 3a) and the stem sap flow for the *Prosopis* trees (continuous line with closed circles in Fig 3b). However, the stand evapotranspiration (dotted line with open circles in Fig 3b) followed a clear diurnal trend which was consistent with the driving climatic variables. In addition, the magnitude of the evapotranspiration flux was similar to that of the stem sap flow but only during the day time. The stem sap flow data showed that substantial water uptake by the trees occurred during the night (Fig 3a). But this water was not used for transpiration since the night – time eddy covariance evapotranspiration remained equal to zero (Fig 3b). The night – time stem sap flow can be attributed to the hydraulic redistribution phenomenon and clear evidence of this was provided by the root sap flow and soil water content data. Water taken up by the tap root, which had access to the groundwater, was used partly to replenish the internal water deficit in the trees as shown by the increase in night – time stem sap flows in Figs 3b and 4a, respectively. But some of the water was redistributed to the shallow soil layers via the lateral roots as shown by the negative sap flow (away from the stem) in the lateral roots in Fig 4(b). There was a fairly strong inverse correlation between the night time tap root and lateral root sap flows as shown on the insert in Fig 4(b). Up to 56% of the changes in the lateral root sap flow during the night could be attributed to the changes in tap root sap flow. The hydraulically redistributed water led to increases in the soil water content in the shallow soil horizons during the night (data not shown).

The direction of the lateral root sap flow changed from negative to positive (flow towards the stem) during the day and even exceeded the tap root sap flow (Fig 4b). This suggested that the trees relied, to a large extent, on the water stored in the shallow soil horizons to meet their immediate transpiration demands leading to soil water depletion (data not shown). However, the fact that the tap root sap flow remained greater than zero (Fig 4b) suggests that the tap root also remained an important source of transpired water during the day time, directly contributing to the transpiration. However, if the groundwater extracted by the tap root was the only source of water used by the trees, then we would expect the total volume of water taken up by the tap root (sum of the previous night plus day time uptake) to nearly equal the total day time stem sap flow. In this study however, the daily total tap root sap flow was approximately 1.56 L/day while the whole tree transpiration, estimated from the time integral of the stem sap flow only considering the day time period was approximately 5.54 L/day suggesting that the trees were also using other sources of water, possibly hydraulically lifted water by neighbouring plants.

The predawn leaf water potential measured in December 2011 ranged from - 3.0 to - 3.8 MPa, indicating severe water stress in the root zone of the trees. The midday xylem water potential on the other hand was even more negative with values ranging from – 4.0 to less than – 4.5 MPa.

3.3 Tree water sources

Both rainwater and groundwater stable isotope values fall along the Global Meteoric Water Line (Craig, 1961). In this study soil water showed evaporative enrichment, typical for arid areas (Gat, 1996; Schachtschneider and February, 2010). The stable isotope values for *Prosopis* were separated according to season, namely the dry period corresponding to late spring (November – December), wet summer (February – March) and dry winter (June – July). In late spring when water stress was at its highest, *Prosopis* isotope values fell between the soil and groundwater isotope values (Fig 5) suggesting a mixed uptake of water from both sources. The *Prosopis* isotope values for the other two seasons suggest that the trees primarily took up evaporated and enriched rainwater.

3.4 Seasonal water use and groundwater dynamics

Monthly total water use by *Prosopis*, determined from the up–scaled sap flow measurements were very low ranging from close to 0 mm in winter to almost 8.0 mm in summer (Table 2). Although the summer evapotranspiration rates were high, actual tree transpiration rates remained relatively low because of the structural adaptation of the trees to water limitations via the reduced sapwood and transpiring surface areas. Instead, soil evaporation and the evaporation of the intercepted water, rather than transpiration contributed the bulk of the observed evapotranspiration flux in the *Prosopis* stand in summer (Table 1). The annual total transpiration by the trees was 57.0 mm compared with 211 mm of rainfall and 1439 mm reference evapotranspiration and Fig 6(a) shows the impact of the rainfall on the water content in the shallow soil layers. Total transpiration during the summer months from the beginning of the rainy season in late December to end of April was approximately 22.5 mm.

Based on the groundwater level results (Fig 6b), it is apparent that the water table was consistently lower in the *Prosopis* invaded area than at the grassland site. The grassland borehole groundwater level showed insignificant changes during the dry period and Fourie et al (2002) noted that there were some differences in the hydrogeology of the two boreholes which could partly explain the differences in water level. But there is clear evidence of groundwater abstraction at the *Prosopis* borehole from mid November to late December when the first rains fell. The water level differences between the boreholes ranged from about 20 cm in early spring to approximately 80 cm in the summer. Assuming that all the transpiration in summer was derived from rainfall, then at least 34.5 mm of the transpired water was derived from the groundwater annually.

The groundwater level showed a diurnal trend comprising periods of rapid decline during the day time and partial stabilisation during the night (Fig 7). The day time decline in groundwater level can be attributed to the active water uptake by the trees to meet their transpirational demand. An inverse relationship is also evident between the night – time tree water uptake (due to hydraulic lift) and the changes in the groundwater level (Fig 7 grey shaded areas). Cumulative daily tree water uptake and the cumulative daily decline in the groundwater level of the *Prosopis* borehole from the time of equipment installation in mid November 2010 until the first rains in late December 2011 were highly correlated (Fig 8) with an $R^2 = 0.99$ suggesting that the trees played a role in the long–term decline of the level of the water table.

3.4. Prosopis water use model

The water use model was calibrated using the transpiration data derived from sap flow collected from 13 to 17 November 2010 and the inputs to the model were the global solar irradiance, air temperature, relative humidity, wind speed and the leaf area index. The Maquardt iterative method, implemented within the ModelMaker software package (Cherwell Scientific, Ltd, UK), was used to derive values of the model parameters, kr, k_D, kT (in equations 2 to 6) that minimized the weighted sum of the squared differences between the measured and the predicted transpiration values (Table 3).

Model validation was done by simulating the hourly transpiration rates by the *Prosopis* trees over 30 days from 1 to 30 April 2011. Considerable scatter was found in the simulated sap flow, presumably because of the strong stomatal control of transpiration driven by endogeneous signalling mechanisms which require a different modelling approach (Fig 9). But, overall, the model predicted the transpiration reasonably well ($r^2 = 0.65$). In the calibration and validation data however, the non–zero night time sap flows due to the hydraulic redistribution were set to zero as this water was not lost from the plants as transpiration.

4.0 Discussion

The observed low evapotranspiration rate in the *Prosopis* stand was likely a result of a number of factors. These include the structural and physiological adaptation of the trees to limited water availability at the study site due to the combination of severe aridity, deep sandy soils which had a low water holding capacity and a relatively deep water table. Observed structural adaptations include the distinctly narrow sapwood areas which limited the volumes of water transported up the transpiration stream at any given time and reduced transpiring surface areas. Stomatal closure is a common physiological response by *Prosopis* to water deficit (Ansley et al., 1993; Changgui and Sosebe, 1990). The peak canopy conductance determined in this study was approximately 0.3 mm s^{-1} which was more than ten times lower than the maximum value of 5.0 mm s^{-1} obtained by Scott et al (2004) using the same approach on *Prosopis* growing in a riparian zone but with different soil and climatic conditions in the USA. Drought induced embolisms as a result of air pockets forming in the plant's xylem vessels are known to significantly reduce transpiration rates (Dzikiti et al., 2007; Sperry et al., 1998). These were identified by Hultine et al (2006) as key constraints to leaf water supply in *Prosopis* growing in sandy soils and we are uncertain how this affected the observed dynamics of plant water use since we did not quantify the severity of cavitation in this study.

Lack of surface energy balance closure in which some of the available energy is not fully accounted for is yet another possible source of low values of water use obtained with the eddy covariance systems (Wever et al., 2002; Scott et al., 2004). There was on average a 70% closure in the daily energy balance, consistent with the observations by Scott et al. 2004 (75% closure) who used the same technique on *Prosopis*. The missing energy could have been used for evapotranspiration, or dissipated as sensible heat, among other processes. But it was unlikely to have significantly increased the observed evapotranspiration rates since firstly, a relatively small proportion of the energy was missing and secondly, water use values obtained independently using sap flow sensors were of a similar order of magnitude to the observed eddy covariance evapotranspiration (Fig 3b) in spring providing alternative evidence of the limited impact of the lack of energy balance closure. The impact of the structural changes of the *Prosopis*' hydraulic system was evident in the rainfall season in which the isotopes data showed that most of the transpiration was derived from rainwater. However, despite the relatively abundant water in summer compared to the other seasons, maximum daily transpiration of the *Prosopis* stand was three to four times lower than the stand evapotranspiration (Table 1). This suggested that the bulk of the evapotranspiration flux emanated from soil evaporation rather than tree transpiration. As a consequence the *Prosopis* stand evapotranspiration appeared marginally lower than that of the cleared site (Table 1) where the uniform and dense grass cover was transpiring possibly at rates higher than the *Prosopis* trees.

Hydraulic redistribution was the dominant mode of groundwater uptake and this phenomenon has previously been observed on *Prosopis* and other deep rooted species (Hultine et al., 2004; Smith et al., 1999). Typically hydraulic redistribution occurs at night when transpiration is low and the water potential of the roots' xylem rises to values intermediate between the root – occupied moist and dry soil layers (Hultine et al., 2004). The water taken up by the tap root, which had access to the groundwater, was used partly to replenish the internal water deficit in the trees created by the day time transpirational losses and partly redistributed to the shallow soil layers by the lateral roots. The replenishment of the tree internal water storage pools during the night usually stops when the bulk tree water status equals the average water status of the entire root zone (Caldwell and Richards, 1989; Caldwell et al., 1998; Dzikiti et al., 2010) and this normally occurs around predawn. Predawn leaf water potential measurements at this site showed that the trees were under severe water stress. Vulnerability to cavitation tests for *Prosopis* conducted in another study in the Kuruman river north – east of Kenhardt observed 95% xylem cavitation at -4.6 MPa xylem water potential (Schachtschneider, 2010) suggesting that severe cavitation may have occurred on *Prosopis* at our study site where midday xylem water potentials lower than – 4.0

MPa were recorded. *Prosopis* can withstand low moisture conditions by a reduction in leaf area, an increase in the thickness of the leaf cuticle and almost complete cessation of growth (Changgui and Sosebe, 1990). Leaf drop, twig die–back and mortality of whole trees were prevalent at our study site which was further evidence of the severe water stress.

The stable isotope values of *Prosopis* showed a mixed uptake of soil and groundwater at the height of the dry period in late spring (Fig 5). This interpretation was supported by the root sap flow measurements that showed that the trees conduct hydraulic lift in order to access sufficient water to meet their short – term water needs during the day time. *Prosopis* stable isotope values throughout the other two seasons suggest primary uptake of evaporated and enriched rainwater. It needs to be noted that rainfall in 2011 was exceptionally late and some rain was recorded as late as June 2011, which may have facilitated the observed rainwater uptake. Similar preference of shallow water uptake over groundwater uptake was observed in the Kuruman river where seasonally available rainwater was the preferred source for *Prosopis* when available (Schachtschneider, 2010). A switch to groundwater only occurred once rainwater sources were exhausted.

Fourie et al. (2002), using hourly groundwater level data and the hydrogeological information of the same study area obtained monthly total evapotranspiration estimates of approximately 5.0 mm, a result which is similar to our observations. The diurnal trend in the groundwater levels clearly indicated water abstraction during the drier months in spring attributed to active water uptake by the trees (Fig 7). Scott et al (2004) observed a similar diurnal trend in the groundwater levels at a riparian *Prosopis* site in the USA although they did not have direct data on tree water uptake (sap flow). Up to 70 m^3 of groundwater could potentially be released per month for each hectare of *Prosopis* invasion cleared based on the total water use data in December 2010 for periods prior to the onset of the rains. On an annual scale at least 345 m^3 of groundwater could be salvaged for each hectare of *Prosopis* cleared and this figure excludes the rainy season transpiration values when the trees were likely to be dependent on rainwater (Schachtschneider, 2010). Model simulations of tree water use were reasonable and such a model which uses readily available climate data as inputs, can be used for estimating the water use by *Prosopis* invasions in similar ecosystems provided the leaf area index can be determined reliably. Remote sensing products such as MODIS LAI provide reasonably accurate estimates of the leaf area index and these have been applied on *Prosopis* in South Western USA (Nagler et al., 2005).

5.0 Conclusions

While some studies have reported high values of water use by *Prosopis* trees growing in riparian zones (Scott et al., 2004), it is apparent from this study that the water use by these trees is strongly dependent on the prevailing environmental conditions mainly the microclimate and the water holding capacity of the soils in the shallow horizons inhabited by a dense network of lateral roots. Hydraulic lift was the dominant process by which water was obtained from the groundwater reserves and distributed to the shallow soil layers. Much of the daytime transpiration was sustained from the hydraulically lifted water stored in the shallow soil horizons as evidenced by the trend in the day time root sap flow patterns and the mixed plant xylem water isotopic signature which had attributes of both the groundwater and the evaporated soil water during the dry season. The trees showed significant structural adaptations to the limited available water by developing a very narrow sapwood area and physiological adaptations such as closing their stomata. Despite the differences in the hydrogeology of the sites where the two boreholes were situated (Fourie et al., 2002), there was clear evidence of groundwater withdrawal on the *Prosopis* borehole as shown by the rapidly declining water level during the period of active tree transpiration in the spring and early summer seasons. Overall, the stand evapotranspiration and hence the amount of water withdrawn from the groundwater was low because of the severe aridity, low soil water holding capacity which kept the stomata closed, and the dominance of small trees which probably had relatively shallow root systems and thus a limited direct impact on the groundwater. This study provides support for clearing *Prosopis* trees as it suggests that such clearing would prevent the depletion of groundwater resources.

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Captions

Fig 1. Components of the surface energy balance of: (a) a *Prosopis* invaded and (b) a cleared grassland site in the Northern Cape in spring before the onset of the rainy season. Panes (c) and (d) show the energy balance components for the invaded and cleared sites during the rainy season in February 2011.

Fig 2. Allometric relationship between the total stem cross sectional area and the conducting sapwood area of the *Prosopis* trees below the first cluster of branches, ~ 15 cm above the ground.

Fig 3. (a) Diurnal course of the key climatic driving variables for plant water use namely, the solar radiation (closed rectangles) and the vapour pressure deficit of the air (open rectangles). (b) The corresponding diurnal course of the evapotranspiration over the *Prosopis* invaded site (dotted line) and the stem sap flow (continuous line) expressed in the same units as the evapotranspiration. The stem sap flow showed multiple peaks attributed to the hydraulic redistribution of the water by the trees.

Fig 4. Dynamics of water transport through the *Prosopis* trees with (a) showing the hourly stem sap flow and (b) the corresponding tap and lateral roots sap flow (in litres per hour) over one full day.

Fig 5. Average δ^{18}O versus δ^{2}H values from *Prosopis* dry summer (●), wet summer (●) and dry winter (○). All seasons are plotted against the GMWL (—), groundwater (×), soil (×) and rain water (ж).

Fig 6. (a) Soil water content over a period of one year at the *Prosopis* site. (b) Corresponding seasonal changes in the groundwater levels for a borehole located at the invaded site (continuous line) and the cleared site (dotted line). Vertical bar graphs depict the rain fall received at the study sites at Kenhardt.

Fig 7. The effect of water uptake by the Prosopis trees on the groundwater level at the invaded site over a three day period.

Fig 8. Cumulative tree water extraction and the corresponding changes in the groundwater levels for the borehole at the invaded site over a period of several weeks before the onset of the 2010/11 rainfall season.

Fig 9. Comparison of the measured and the predicted Prosopis water use using the Penman–Monteith model adapted for the arid study area in the Northern Cape. The graph shows the model validation with hourly sap flow data collected during the entire month of April 2011.

Tables

Table 1. Comparison of the different components of the evaporation fluxes from an invaded site and a cleared site (now covered with the native grass) during the spring, summer and winter measurement campaigns. ET is the actual stand evapotranspiration measured by the eddy covariance system and ET_0 is the reference evapotranspiration.

Date	**Water use**			**ET_o (mm/d)**	***Season***
	Prosopis		**Grassland**		
	ET (mm/d)	**Transpiration (mm/d)**	**ET (mm/d)**		
12 November 2010	0.24	-	-	-	Late spring
13 November 2010	0.26	0.24	-	7.69	
14 November 2010	0.33	0.28	-	9.04	
16 November 2010	-	0.23	0.48	9.02	
17 November 2010	-	0.29	0.20	8.06	
18 November 2010	-	0.30	0.30	10.11	
13 February 2011	2.10	0.31	-	8.48	Summer
14 February 2011	1.57	0.45	-	7.28	
15 February 2011	-	0.46	3.28	9.12	
16 February 2011	-	0.63	2.00	6.08	
22 July 2011	0.17	0.00	-	2.64	Winter
23 July 2011	0.23	0.00	-	4.19	
24 July 2011	0.14	0.00	-	2.94	
25 July 2011	-	0.00	0.20	1.35	
26 July 2011	-	0.00	0.31	2.70	
27 July 2011	-	0.00	0.31	3.47	
28 July 2011	-	0.00	0.19	1.55	

Table 2. Summary of the monthly climatic conditions and the groundwater withdrawals via transpiration by *Prosopis* over a period of one year in the Northern Cape Province. T_{max} and T_{min} are the maximum and minimum monthly air temperatures.

Month	**ET_o (mm)**	**T_{max} (°C)**	**T_{min} (°C)**	**Transpiration (mm)**	**Rainfall (mm)**
Dec 2010	194.84	43.12	9.47	7.12	7.62
Jan 2011	177.20	41.86	17.66	7.90	59.94
Feb 2011	156.07	40.05	13.34	7.97	44.40
Mar 2011	137.75	39.08	10.51	6.84	34.03
Apr 2011	101.15	36.60	-1.08	4.12	11.18
May 2011	68.89	31.20	-0.49	3.60	22.86
Jun 2011	52.94	25.82	-4.75	2.09	23.37
Jul 2011	52.25	28.13	-7.34	0.00	1.52
Aug 2011	77.99	32.90	-3.30	1.06	2.03
Sep 2011	112.67	35.70	-0.34	3.81	0.00
Oct 2011	145.63	38.78	2.01	5.95	0.00
Nov 2011	161.99	42.38	5.52	6.56	3.56
Total	**1439.37**			**57.02**	**210.51**

Table 3. Parameters of the *Prosopis* tree water use model derived during calibration of the Penman – Monteith model.

Parameter	**Value**	**Units**
k_D	12.24	kPa^{-1}
kr	270.01	$W\ m^{-2}$
kT	16.95	°C
d	0.0045	M

Figures

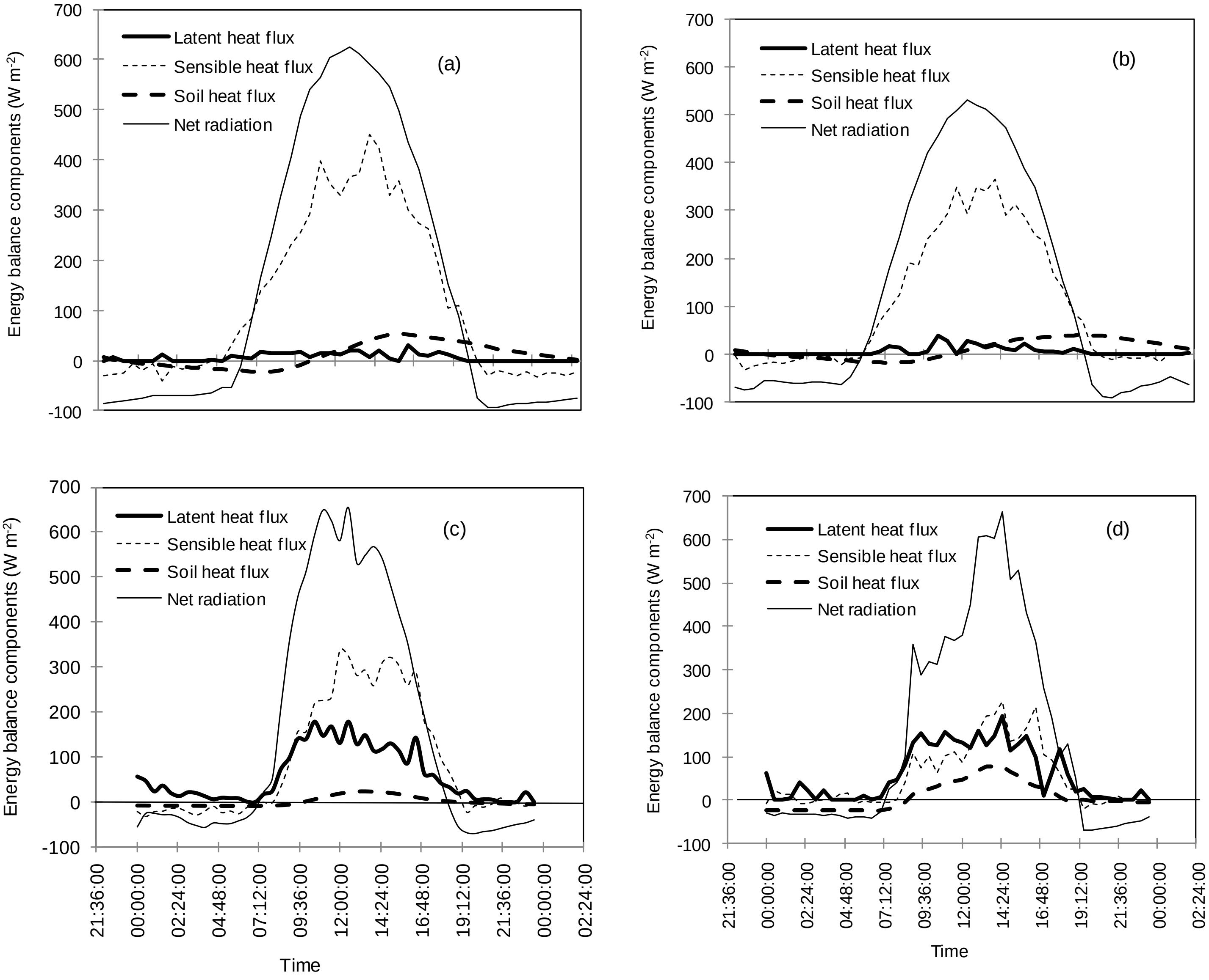
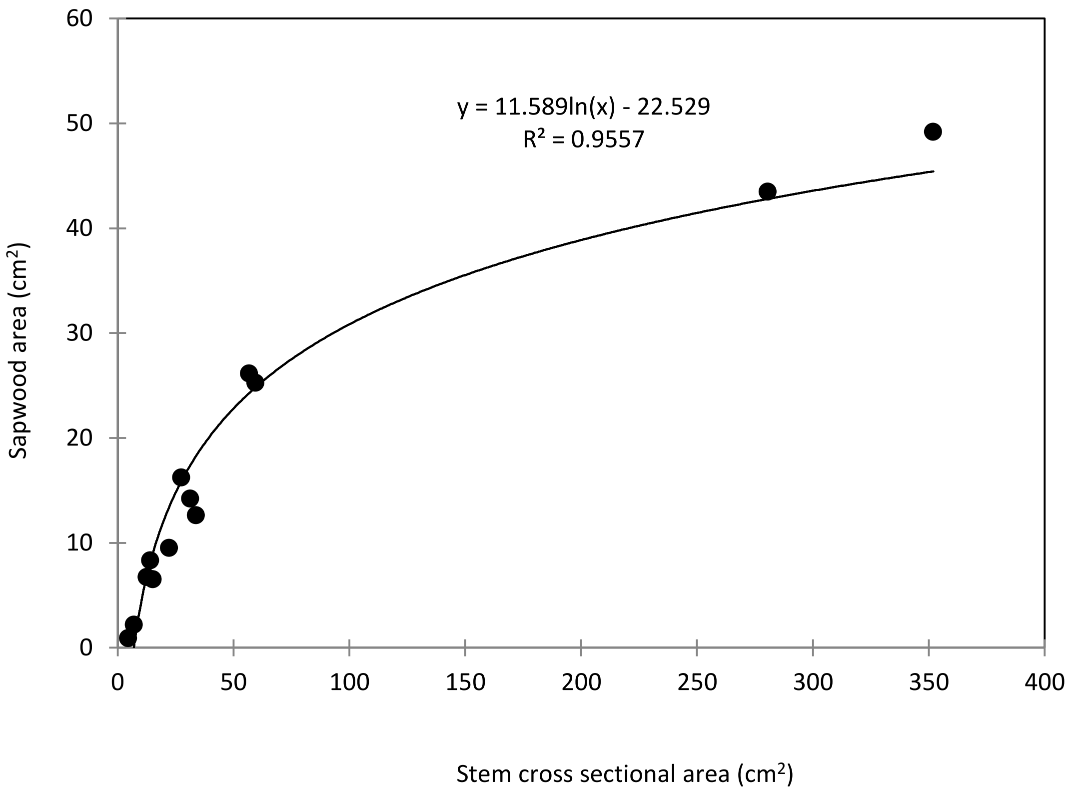


Fig 1



y = 11.589ln(x) - 22.529
R² = 0.9557
Sapwood area (cm2)
Stem cross sectional area (cm2)
0
10
20
30
40
50
60
0
50
100
150
200
250
300
350
400

Fig 2.

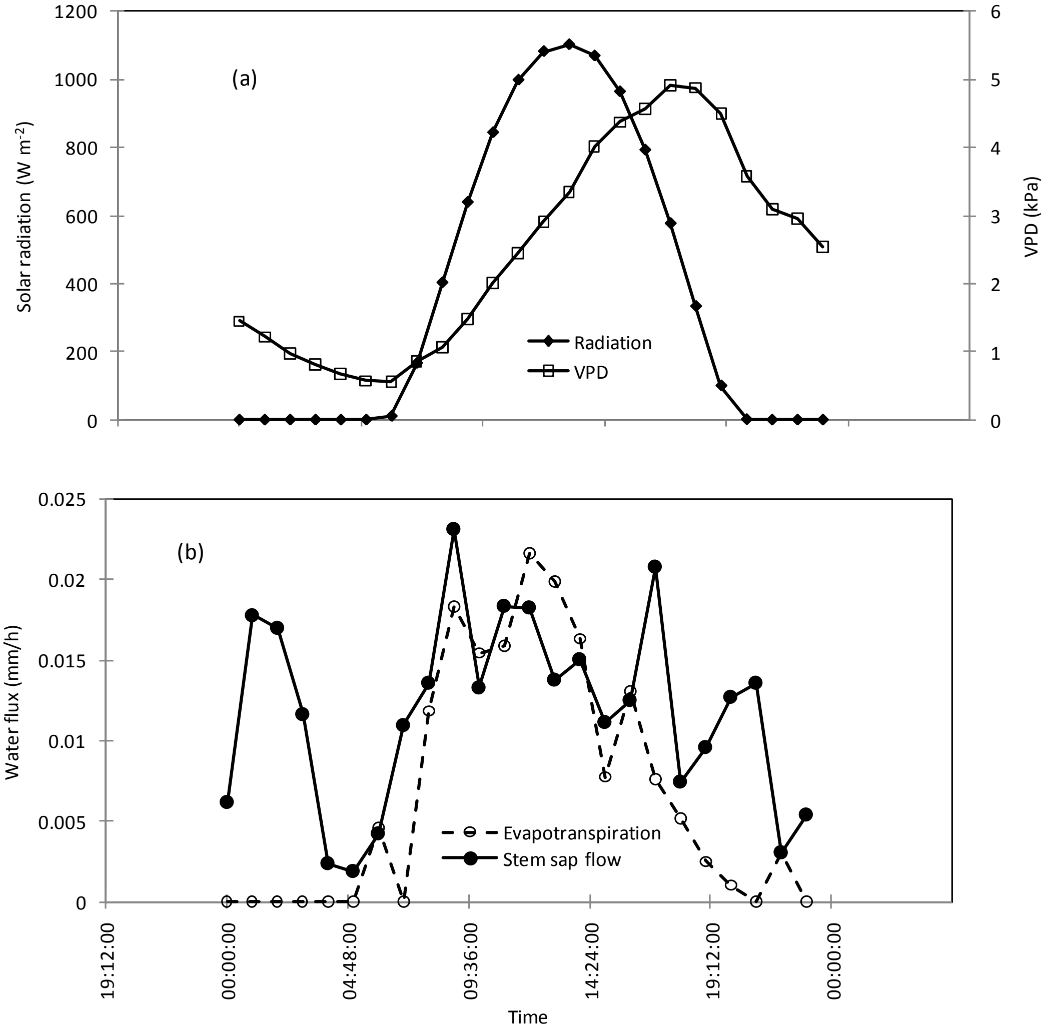

(a)
Solar radiation (W m-2)
VPD (kPa)
0
200
400
600
800
1000
1200
0
1
2
3
4
5
6
Radiation
VPD
(b)
Water flux (mm/h)
0
0.005
0.01
0.015
0.02
0.025
Evapotranspiration
Stem sap flow
19:12:00
00:00:00
04:48:00
09:36:00
14:24:00
19:12:00
00:00:00
Time

Fig 3

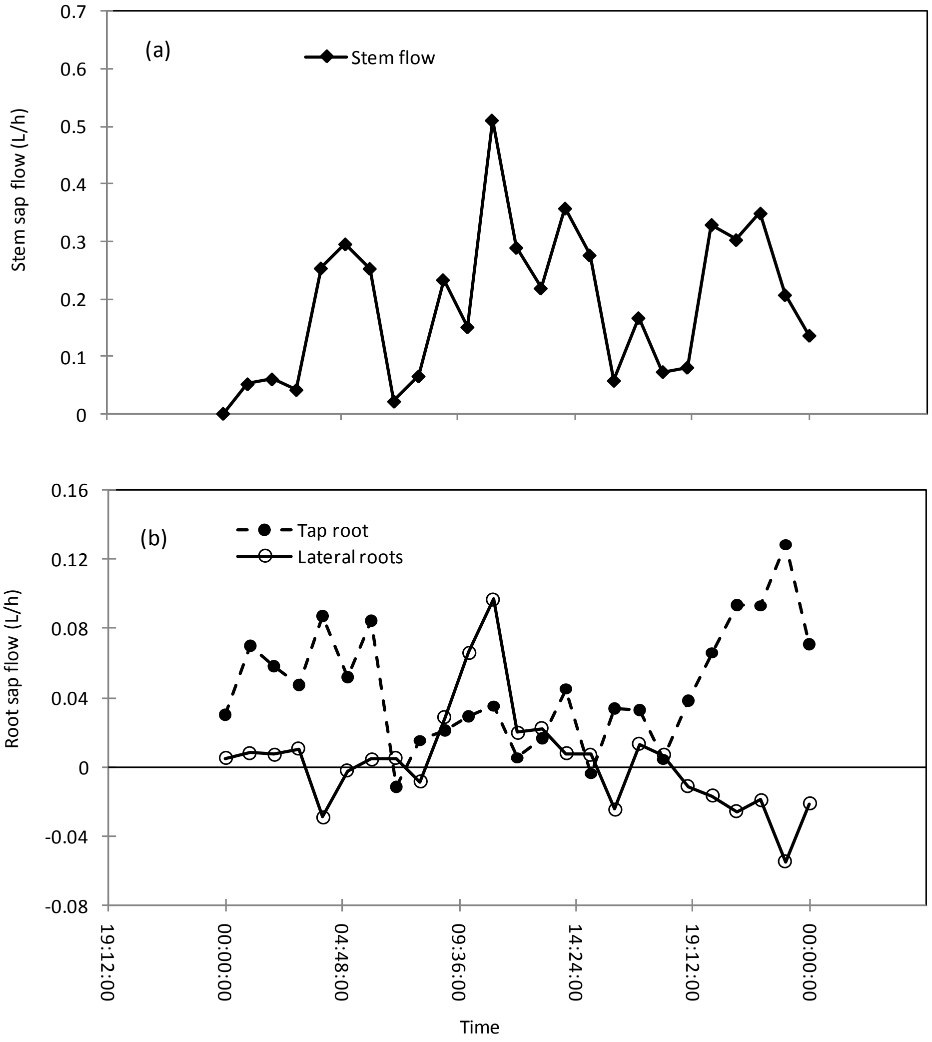

(a)
Stem flow
Stem sap flow (L/h)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
(b)
Tap root
Lateral roots
Root sap flow (L/h)
0.16
0.12
0.08
0.04
0
-0.04
-0.08
19:12:00
00:00:00
04:48:00
09:36:00
14:24:00
19:12:00
00:00:00
Time

Fig 4

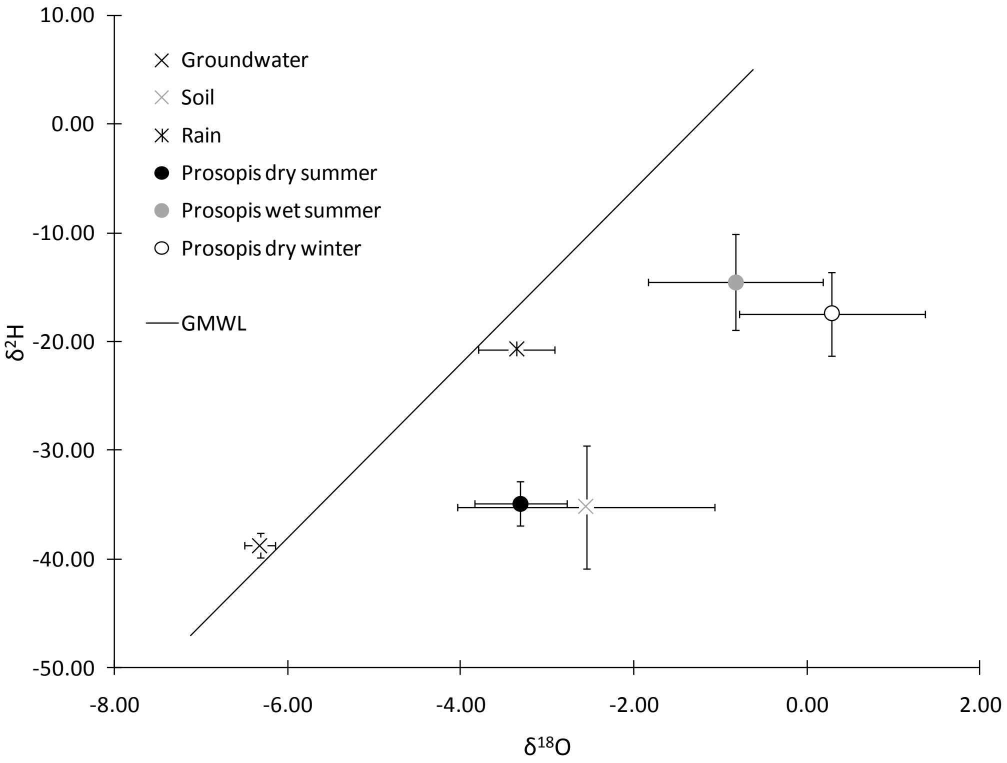

10.00
0.00
-10.00
-20.00
-30.00
-40.00
-50.00
δ^2H
-8.00
-6.00
-4.00
-2.00
0.00
2.00
$\delta^{18}O$
Groundwater
Soil
Rain
Prosopis dry summer
Prosopis wet summer
Prosopis dry winter
GMWL

Fig 5

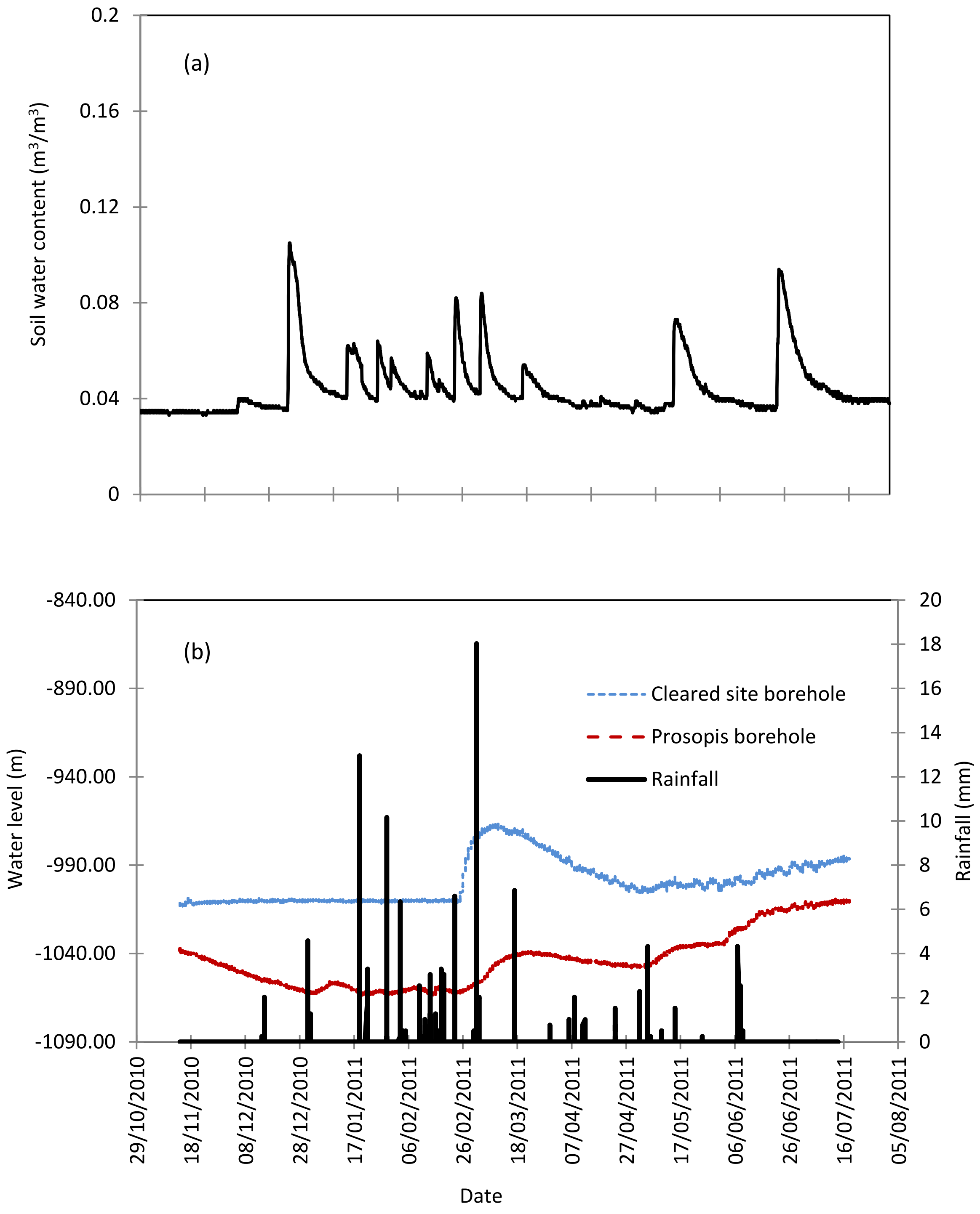

(a)
Soil water content (m³/m³)
0.2
0.16
0.12
0.08
0.04
0
(b)
Water level (m)
-840.00
-890.00
-940.00
-990.00
-1040.00
-1090.00
Rainfall (mm)
20
18
16
14
12
10
8
6
4
2
0
Cleared site borehole
Prosopis borehole
Rainfall
29/10/2010
18/11/2010
08/12/2010
28/12/2010
17/01/2011
06/02/2011
26/02/2011
18/03/2011
07/04/2011
27/04/2011
17/05/2011
06/06/2011
26/06/2011
16/07/2011
05/08/2011
Date

Fig 6

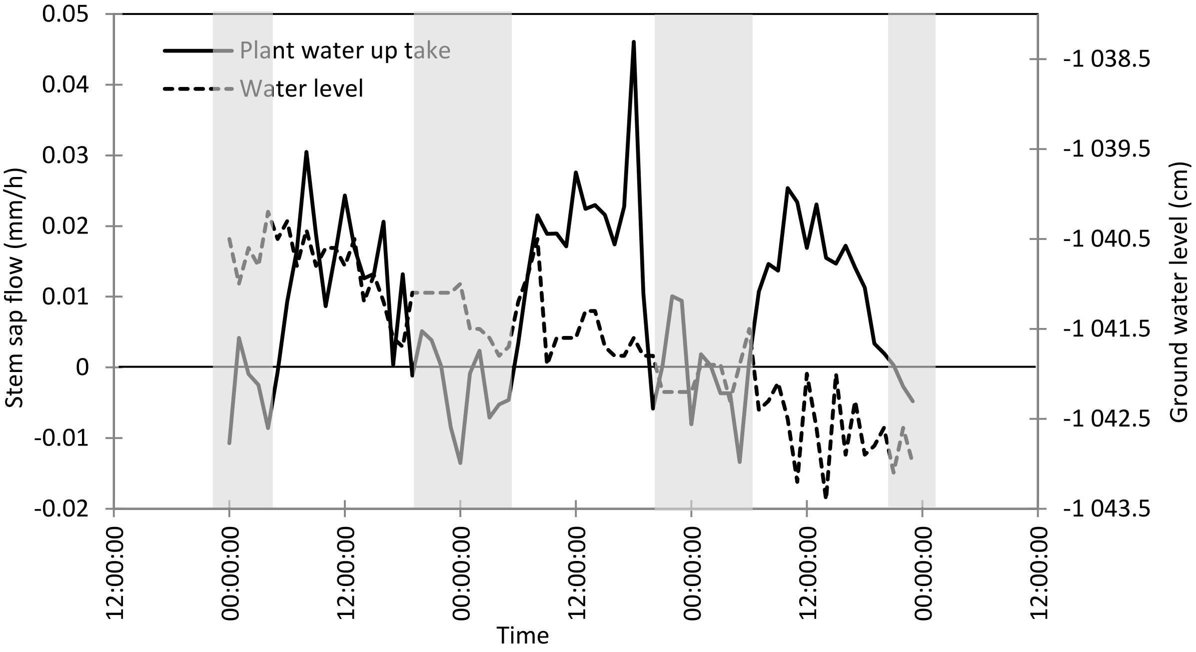

0.05
0.04
0.03
0.02
0.01
0
-0.01
-0.02
Stem sap flow (mm/h)
Plant water up take
Water level
-1 038.5
-1 039.5
-1 040.5
-1 041.5
-1 042.5
-1 043.5
Ground water level (cm)
12:00:00
00:00:00
12:00:00
00:00:00
12:00:00
00:00:00
12:00:00
00:00:00
12:00:00
Time

Fig 7

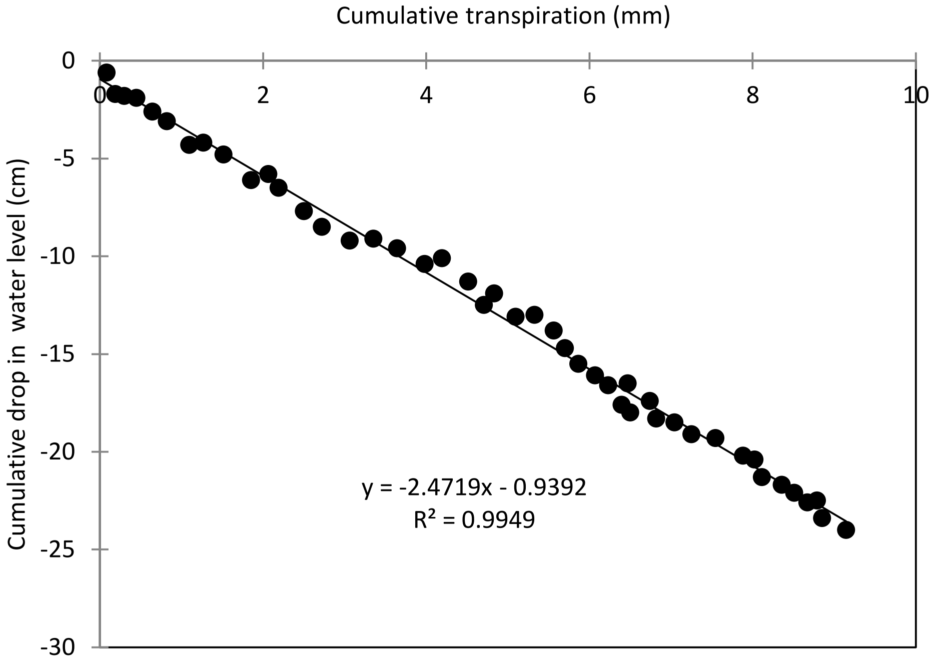

Cumulative transpiration (mm)
0
2
4
6
8
10
0
-5
-10
-15
-20
-25
-30
Cumulative drop in water level (cm)
y = -2.4719x - 0.9392
R² = 0.9949

Fig 8

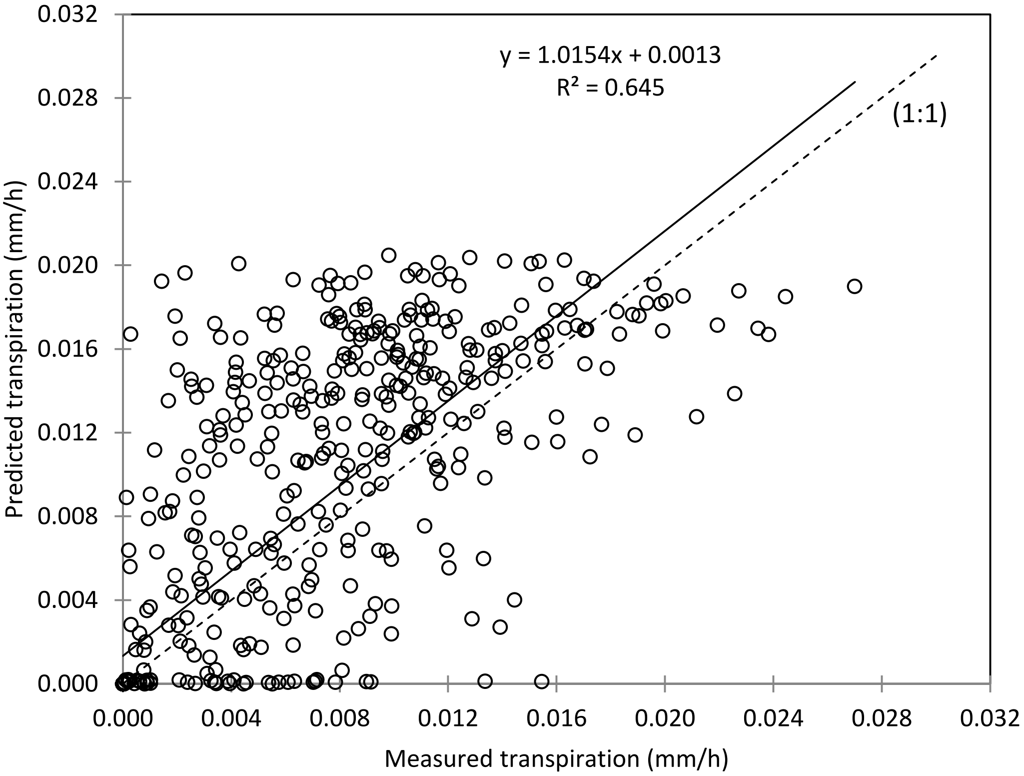

y = 1.0154x + 0.0013
R² = 0.645
(1:1)
Predicted transpiration (mm/h)
Measured transpiration (mm/h)
0.000
0.004
0.008
0.012
0.016
0.020
0.024
0.028
0.032

Fig 9