Plant Ecology

Impact of Prosopis invasion on a keystone tree species in the Kalahari Desert

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Abstract:	Several Prosopis species were introduced into South Africa in the last century. Here we determine the extent to which increased mortality of Acacia erioloba E.Mey, a keystone species in the Kalahari Desert of Southern Africa, can be attributed to competition for water with Prosopis. We do this through a determination of canopy vitality, plant water stress and plant water source. We use a visual estimate to determine plant vitality. Plant water stress we determine through a combination of stable carbon isotope ratios and xylem pressure potentials. Plant water source we determine using stable hydrogen and oxygen isotope ratios. Our results show that Prosopis abundance increases in the riparian zone and that there is a good correlation between greater Prosopis abundance and Acacia erioloba mortality. We show that both species are reliant on the same water resource in the riparian zone but that Acacia erioloba is better adapted to using the deeper water away from the river. We conclude that the decline in Acacia erioloba vitality at the river is related to competition for water with Prosopis. Our study gives strong support for the eradication of Prosopis from rivers in arid parts of Southern Africa.
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	Joh Henschel, PhD EnviroMEND joh.henschel@mweb.com.na Dr Joh Henschel has decades of experience in arid land ecology (especially in the Namib Desert, Namibia), where the species under discussion are very prevalent.
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	jacobsop@grinnell.edu Prof Jacobson completed his PhD on arid rivers in Southern Africa and is still actively working in the area at times, being well-versed with the tree species that this submitted paper discusses

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Impact of *Prosopis* invasion on a keystone tree species in the Kalahari Desert

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ABSTRACT

Several *Prosopis* species were introduced into South Africa in the last century. Here we determine the extent to which increased mortality of *Acacia erioloba* E.Mey, a keystone species in the Kalahari Desert of Southern Africa, can be attributed to competition for water with *Prosopis*. We do this through a determination of canopy vitality, plant water stress and plant water source. We use a visual estimate to determine plant vitality. Plant water stress we determine through a combination of stable carbon isotope ratios and xylem pressure potentials. Plant water source we determine using stable hydrogen and oxygen isotope ratios. Our results show that *Prosopis* abundance increases in the riparian zone and that there is a good correlation between greater *Prosopis* abundance and *Acacia erioloba* mortality. We show that both species are reliant on the same water resource in the riparian zone but that *Acacia erioloba* is better adapted to using the deeper water away from the river. We conclude that the decline in *Acacia erioloba* vitality at the river is related to competition for water with *Prosopis*. Our study gives strong support for the eradication of *Prosopis* from rivers in arid parts of Southern Africa.

KEY WORDS

Kalahari Desert, water access, alien invasive, keystone species, *Acacia erioloba*, *Prosopis*

INTRODUCTION

Primarily introduced to provide shade or fodder in treeless, arid environments (Zimmerman 1991), several species of *Prosopis* (mesquite) have naturalized in desert regions throughout the world (Burkhart 1976; Nilsen et al. 1991). In its native range *Prosopis* has become extremely invasive and is now the dominant woody species on millions of hectares of semi-arid grassland (Brown and Archer 1989, van Auken 2000). However, it is the effects of the various *Prosopis* species on natural vegetation in Australia, the Indian subcontinent and 25 African countries (Mwangi and Swallow 2005) that has led the IUCN to rank the genus among the world's worst invasive species (Mwangi and Swallow 2005; Bromilow 2010). Around the turn of the 19th Century, four *Prosopis* species from central America were introduced to Namibia and the north-western parts of South Africa (Harding 1987). Since then two species, *Prosopis glandulosa* var *torreyana* (Benson) Johnson and *Prosopis velutina* Wooten have densely and rapidly invaded riparian corridors and areas with shallow groundwater (Poynton 1990; Zachariades et al. 2011; Wise et al. 2012). These species have also hybridised and may form impenetrable thickets, making invaded farmland unproductive for crop production and livestock farming. *Prosopis* is now spread over more than 1.45 million hectares in the Northern Cape Province of South Africa alone (Wise et al. 2012).

Acacia erioloba E.Mey. is one of the most important woody species of the desert regions of southern Africa (Coates Palgrave and Coates Palgrave 2002). Considered to be a keystone species in the Kalahari *A. erioloba* provides shade, shelter, nesting sites and lookout posts for birds and other animals (Milton and Dean 1995). There are, however, growing concerns that there is an increase in mature *A. erioloba* mortality in the south western Kalahari. The proposed reasons for these concerns include an increase in fire frequency (Seymour 2008), increasing groundwater abstraction (Powell, 2005) and competition for resources from alien invasives such as *Prosopis* (Robertson and Woodborne 2002; Zachariades et al. 2011).

In arid savannas such as the southern Kalahari, where mean annual precipitation is around 280 mm, rainfall is a strong constraint on the determinants of woody cover (Sankaran et al. 2005, 2008). As an adaptation to survival in low rainfall environments, both *Prosopis* and *A. erioloba* have deep root systems with records of *Prosopis juliflora* at 53 m (Canadell et al. 1996) and *A. erioloba* at 60 m (Jennings 1974). These deep root systems allow these species to exploit deep aquifers in the sands on which they grow. Recent stable isotope research has shown that *A.erioloba* may source groundwater as deep as 70 metres below the surface (Obakeng 2007). The argument that *Prosopis* invasion is responsible for *A.erioloba* mortality is based on the premise that both species are accessing deep groundwater with *Prosopis* driving the water table down faster than *A. erioloba* may follow (Robertson and Woodborne 2002; Zachariades et al. 2011). Here we test this hypothesis by determining the relationship between canopy vitality, plant water stress and plant water source for *A. erioloba* growing in conjunction with and without *Prosopis.* We do this on a farm in the Northern Cape Province of South Africa that had been partially cleared of *Prosopis*.

METHODS

Site description

The study was conducted on the farm Gannavlakte (26 57.578 S- 21 50.234 E) in the southern Kalahari, along the middle reaches of the ephemeral Kuruman River. While the river may flow in its middle and lower reaches after unusually high rainfall (Meyer et al. 1985), the average groundwater depth is 56 metres (Dept. of Water Affairs borehole records). The climate of the area is characterised by cold, dry winters and hot, wet summers with average minimum and maximum temperatures of 13.2ºC and 31.3ºC respectively and an average annual rainfall of 280 millimetres (van Rooyen et al. 2001). The area is largely covered with aeolian sand underlain by superficial silcretes and calcretes of the Cenozoic Kalahari Group (Mucina and Rutherford 2006). The riverbed typically consists of finer silt soils than those of the surrounding area, as water carries organic material, minerals and other alluvial components into the lower lying riverbeds (van der Walt and le Riche 1999).

The landscape is shaped by parallel dunes about 3 to 8 metres high, which are vegetated by *Stipagrostis amabilis* (Schweick.) De Winter, *Acacia heamatoxylon* Willd. and *Acacia mellifera* (Vahl) Benth (Mucina and Rutherford, 2006). The interdune plains are dominated by *Rhigozum trichotomum* Burch. The river fringes are lined with riverine woodland, consisting primarily of *Acacia erioloba* and other species such as *Acacia haematoxylon*, *Acacia mellifera*, *Boscia albitrunca* Burch., *Ziziphus mucronata* Willd., *Rhigozum trichotomum* and *Prosopis* (van Rooyen et al. 2001).

Woody plant density

Prosopis was cleared in the Kuruman River, along half of the farm, by the national alien invasive plant clearing programme ‘Working for Water’ (van Wilgen et al. 1998), while the other half remained un-cleared. Before we established our plots we determined the density of all the trees in the cleared and un-cleared (invaded) areas. For this, six transects were established, three in cleared and three in un-cleared areas. Each transect was 5 metres wide and 300 metres long, moving diagonally away from the river. Along each transect all mature trees were identified and counted.

Subsequent to the survey, four 20 m by 100 m plots were laid out, of which one was located along the river and one 300 m away from the river in a upland invaded area. This setup was repeated in a cleared area. The plots in the invaded area were densely overgrown with *Prosopis* while there were no mature *Prosopis* in the cleared plots. In each plot we randomly selected six mature *A.erioloba* and six *Prosopis*.

Percentage canopy dieback

In April 2007 two observers scored canopy dieback as a percentage of dead woody material relative to the total canopy area on the study trees in each plot. Scores were made in 10% increments, with 0% dieback a full healthy canopy and 100% dieback equating to a dead tree. The score average between the two observers was recorded as the percentage canopy dieback for each tree.

Water source

Sampling and measurements were carried out three times a year over two years, in the dry season (June 2004 and July 2005), the early wet season (November 2004 and 2005) and the late wet season (April 2004 and March 2005).

We use the stable isotopes of hydrogen and oxygen in water extracted from woody tissue to show the water source for both *Prosopis* as well as *A. erioloba* (Busch et al. 1992; February et al. 2007a,b). The method is based on the assumption that water extracted from non-suberized wood will have the same isotope ratio as the source water of the tree (White et al. 1985). We collected twig samples (c. 0.5 cm x 6 cm) from six randomly selected individual trees of each species in each plot. These twig samples of non-suberized wood were collected into borosilicate tubes (Kimax–Kimble, Vineland, USA) which were subsequently inserted onto a cryogenic vacuum extraction line to extract the xylem water for isotope analysis. At the same time as the twig samples were collected, we also collected groundwater samples from three different boreholes close to the study site. Rain water was collected during every rainfall event and decanted into a sealed bottle after each event. During one wet season (April 2004) the soil was sufficiently wet to auger 50 cm deep soil samples. To minimise evaporation this soil was put into a polythene bag, inserted into a second bag, each of which was securely and individually sealed with adhesive tape.

All water samples were analysed for ^{2}H/H ratios using a variation of the zinc closed tube reduction method of Coleman et al. (1982), while ^{18}O/^{16}O ratios were obtained using the CO_2 equilibrium method of Socki et al. (1992). Isotopic ratios of both ^{2}H/H and ^{18}O/^{16}O were then determined using a Thermo Delta Plus XP Mass Spectrometer (Hamburg, Germany) at the University of Cape Town.

Plant moisture stress

Leaf stable carbon isotope ratios

Leaf carbon isotope ratios are correlated with leaf gas exchange. Carbon assimilation is determined by stomatal aperture which in turn is determined by available water. As plants become more water stressed, the stomatal aperture closes which results in less discrimination against the heavy ^{13}C isotope, resulting in less negative δ^{13}C values (Ehleringer 1993). Using stable carbon isotope ratios we establish the amount of water stress that both *Prosopis* and *A. erioloba* are under. In April 2007 a total of twenty fully expanded, mature leaves were collected for stable carbon isotope analysis from each of our six trees in each plot. Prior to mass spectrometry using a Thermo Delta Plus XP Mass Spectrometer (Hamburg, Germany) the leaves were oven dried at 70˚C for 24 hours and ground to a fine powder using a Retsch MM200 ball mill (Retsch, Haan, Germany).

Xylem Pressure Potentials

Xylem pressure potentials are a determination of the tension that the water column of the plant is under. The less water available to the plant the greater the tension on the water column (Scholander et al. 1965; Miller et al. 1984). We use predawn Xylem Pressure Potentials on our study trees to determine plant moisture stress. We do this three times a year over two years, in the dry season (June 2004 and July 2005), the early wet season (November 2004 and 2005) and the late wet season (April 2004 and March 2005), using a Scholander type pressure chamber (PMS Instrument Company, Corvallis, Oregon, USA).

Data analyses

All statistical analyses for δ^{18}O, δ^{2}H, δ^{13}C isotopes and canopy dieback were conducted using Statistica 8.0. We used Student T-tests and one-way ANOVA's with Tukey post hoc tests to detect any significant differences ($p < 0.05$). A non-parametric Kruskall-Wallis test was used when assumptions of normality and heterogeneity of variance were not met. Repeated-measures ANOVA were used for predawn XPP in SPSS version 15.0, as described in ACITS (1997). Time was used as the within-subjects factor and tree groups as the between-subject factors. The multivariate hypothesis testing approach (Wilks' Lambda test) was used throughout.

RESULTS

Woody plant density

Our results for the belt transect show that *A. mellifera* and *Ziziphus mucronata* are absent from areas with high *Prosopis* density. In both the cleared and invaded transects *A. erioloba* density was highest immediately adjacent to the river with another increase in density approximately 300 metres from the river. *Prosopis* density was highest adjacent to the river, decreasing rapidly with increasing distance from the river. In the riparian zone there is a 50% increase in the number of *A.erioloba* trees where Prosopis had been cleared (Fig.1).

Percentage canopy dieback

There was a significant difference in the amount of dead material on *A. erioloba* between the different treatments. In the invaded river plot there was 50% more dieback than in the cleared river plot. As the number of *Prosopis* trees decline with distance from the river the amount of dead material on *A. erioloba* trees also declines ($F_{3,20} = 5.3$, $p = 0.008$) (Fig.2).

Water source

There is a linear relationship between $\delta^{18}O$ and $\delta^{2}H$ for fresh water samples described by the global meteoric water line (GMWL) with the equation $\delta^{2}H = 8\delta^{18}O + 10$ (GMWL) (Craig 1961). Evaporatively enriched water (shallow soil water) plots below the meteoric water line with a slope that is less than 8 and an intercept less than 10. We constructed a local meteoric water line (LMWL) from our rainfall data ($\delta^{2}H = 6.1 * \delta^{18}O + 2.6$ ‰). (Fig. 3). Values for groundwater isotope ratios are consistent over time and across the three sampling boreholes. The three soil core values (0.5 metre depth) show isotopic enrichment, relative to rainfall isotope ratios. These values plot below the LMWL (Fig. 3).

All isotope ratios for xylem water in the cleared river plot are located below the LMWL and intermediate between rainfall and groundwater (Fig. 3a). At the end of the wet season *A. erioloba* xylem water isotope ratios differ significantly from groundwater (Kruskall-Wallis nonparametric $\delta^{18}O$; $p < 0.001$). There are no significant differences between *A. erioloba* xylem water and ground water at the upland plot (Fig 3b).

Both *Prosopis* and *A. erioloba* xylem water isotope ratios in the invaded river plot (Fig. 3c) differ significantly from groundwater in the wet season (Kruskall-Wallis nonparametric $\delta^{18}O$; $p \leq 0.02$), but are not significantly different in the dry season.

In the invaded upland plot *A. erioloba* and *Prosopis* isotope ratios are similar to groundwater values (Fig. 3d). At the end of the wet season, however, values for *Prosopis* xylem water in this plot are significantly different from groundwater values (Kruskall-Wallis nonparametric $\delta^{18}O$; $p \leq 0.012$), but not significantly different from rain.

Plant moisture stress

Leaf stable carbon isotope ratios

There were significant differences in $\delta^{13}C$ values between plots ($p < 0.001$). *Prosopis* $\delta^{13}C$ values are significantly more enriched than values for *A. erioloba* (Fig. 4). The results for *A. erioloba* show significant differences in $\delta^{13}C$ values between cleared (-26.25‰) and invaded (-24.99‰) river plots ($p = 0.03$). There are no significant differences between cleared and invaded upland plots for *A. erioloba*. There are also no significant differences in $\delta^{13}C$ values for *Prosopis* invaded river and upland plots.

Xylem pressure potentials

Predawn XPP's for all upland plots are stable across seasons, relative to the river plots (Fig. 5). There are, however, significant differences between the invaded river plot and both the upland and cleared river plots for both *Prosopis* and *A. erioloba* (Tukey post hoc; $p < 0.001$).

DISCUSSION

Our belt transect results show that *Prosopis* density is highest in the riparian zone declining with distance from the river. The average groundwater depth in the river channel is 56 m, which is within the recorded range for *Prosopis* rooting (Canadell et al. 1996). While deep rooting may allow *Prosopis* access to deep water, *Prosopis* also has an extensive lateral root development which allows the genus to take advantage of sparse precipitation by growing outward and upward with roots extending to 5 cm of the soil surface (Gile et al. 1997). Combined with its extensive rooting system, the xylem anatomy of *Prosopis* is able to withstand a wide range in xylem pressure potentials which allow the species to grow in environments where the water table may fluctuate over more than 4 m in a year (Stromberg 1992, Pockman and Sperry 2000). This ability to utilise water at all depths in the soil combined with an ability to adapt to all soil conditions makes *Prosopis* one of the most prolific invasives in low rainfall environments (Gile et al. 1997).

Our belt transect results also show that the two native species *Ziziphus mucronata* and *Acacia mellifera* are only evident in those transects where *Prosopis* had been cleared. We speculate that the absence of these two species is because *Prosopis* is able to out-compete them for resources. Our stable water isotope results show that in the riparian zone both *A. erioloba* and *Prosopis* are using the same water source as both species use evaporatively enriched water during the wet season and deeper ground water during the dry season when shallow water is depleted. This competition for water is evident in our leaf $\delta^{13}C$ results which show less discrimination of the heavy ^{13}C isotope for *A. erioloba* in plots cleared of *Prosopis,* indicating more water available to the plant. Xylem pressure potentials, an indicator of plant moisture stress, show that both *Prosopis* and *A. erioloba* on the invaded riparian plot are more water stressed than on both the cleared river plot and the upland plot.

There is a significant increase in dead material on *A. erioloba* in the invaded river plot relative to the cleared river plot. We speculate that because *A. erioloba* is more water stressed in the invaded river plot this increase in dead material is related to plant moisture stress. Our belt transect data show that *Prosopis* abundance decreases significantly with distance from the river. In this upland area, where distance to the water table is greater, *Prosopis* is not able to establish as easily as in the riparian zone. With no significant differences in the amount of dead material and $\delta^{13}C$ values of *A. erioloba,* our results show that this species is better adapted than *Prosopis* to accessing resources in the upland plots.. It is only with an increase in competition for water with *Prosopis* (as in the riparian plots) that there is also a significant increase in the amount of dead material on *A. erioloba*.

We believe that our results do show that there is competition for water between *Prosopis* and *A. erioloba* at our study site. This competition for water results in *Prosopis* outcompeting *A. erioloba* for water in the riparian zone resulting in severe canopy die back and even death of *A. erioloba.* Because of its economic potential, there is reluctance among authorities to introduce biological control agents to mitigate the spread of *Prosopis* in South Africa (Zachariades et al. 2011). Such reluctance can only be overcome by studies such as ours that show the negative effects of *Prosopis* not only on available water but also on species diversity and ecosystem functioning through the decline in viability of a keystone species. Our study gives strong support for programs not only to remove *Prosopis* from rivers in the arid parts of South Africa but also for the release of well researched biological control agents (Zachariades et al. 2011).

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Figure Captions

(Figures created in MS Office)

Fig. 1 Results of the belt transect showing the decline in *Prosopis* density with distance from the river and the increase in both *Ziziphus mucronata* and *Acacia mellifera* in the cleared area. Values are for the total number of trees for three transects in and invaded and three transects in a cleared area

Fig. 2 Mean and standard error for percentage canopy dieback showing the difference between upland and riparian *A. erioloba* trees where the amount of dead material increased in those trees in the invaded riparian plot but there were no significant differences between invaded upland and cleared upland plots

Fig. 3 Mean $\delta^{18}O$ and $\delta^{2}H$ values (± 1 SE) for xylem water of *A. erioloba* for the dry season (□), start of the wet season (■) and end of the wet season (■) for (a) cleared river, (b) cleared upland, (c) invaded river and (d) invaded upland. Also shown are values for xylem water of *Prosopis* for the dry season (○), start of the wet season (●) and end of the wet season (●). These values are plotted relative to the local meteoric water line (—) as well as average soil (×), rain (▲) and groundwater (▲)

Fig. 4 Mean and standard error for leaf $\delta^{13}C$ values for *A. erioloba* and *Prosopis* showing differences between upland and riparian trees

Fig. 5 Mean and standard error (n=6) predawn XPP’s (MPa) for **(a)** cleared river (□) and upland (■) *A. erioloba*, **(b)** invaded river (□) *A. erioloba* and invaded upland (■) *A. erioloba* and **(c)** invaded river (○) *Prosopis* sp. and invaded upland (●) *Prosopis* sp

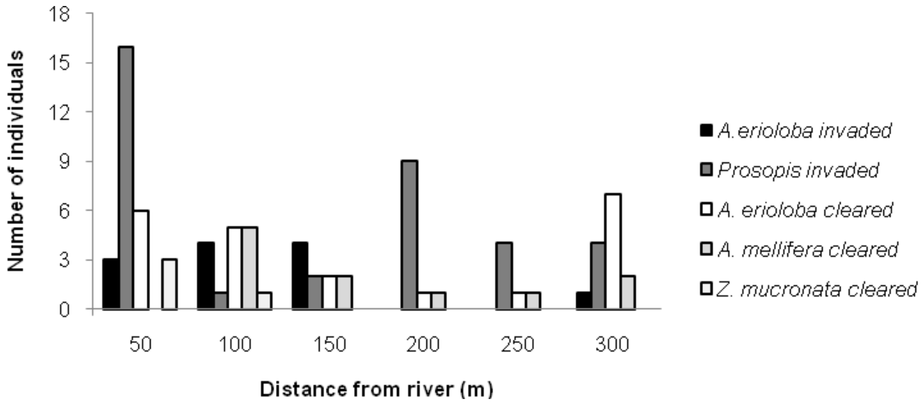

18
15
12
9
6
3
0
Number of individuals
50
100
150
200
250
300
Distance from river (m)
A.erioloba invaded
Prosopis invaded
A. erioloba cleared
A. mellifera cleared
Z. mucronata cleared

Fig. 1

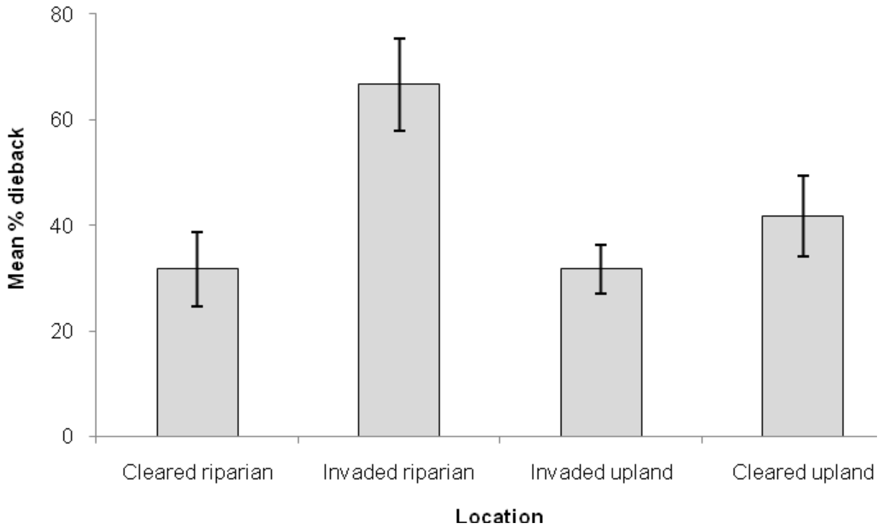
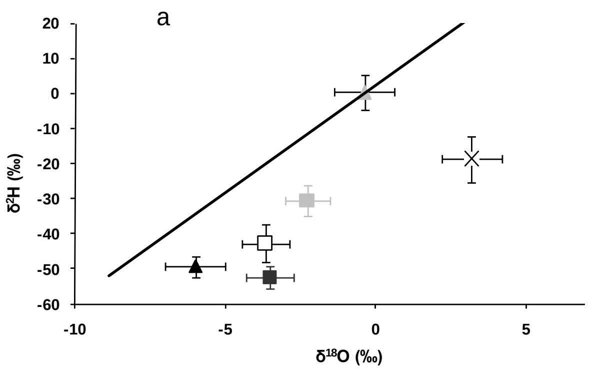
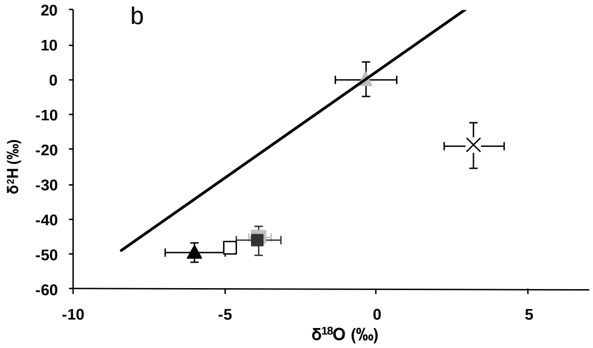
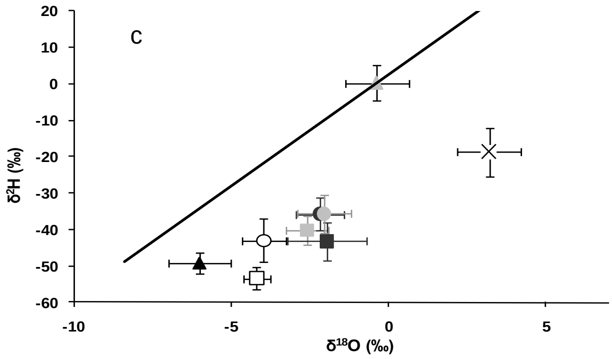

80
60
40
20
0
Mean % dieback
Cleared riparian
Invaded riparian
Invaded upland
Cleared upland
Location

Fig. 2


a
$\delta^{2}H$ (‰)
20 10 0 -10 -20 -30 -40 -50 -60
-10 -5 0 5
$\delta^{18}O$ (‰)


b
$\delta^{2}H$ (‰)
20 10 0 -10 -20 -30 -40 -50 -60
-10 -5 0 5
$\delta^{18}O$ (‰)


c
$\delta^{2}H$ (‰)
20 10 0 -10 -20 -30 -40 -50 -60
-10 -5 0 5
$\delta^{18}O$ (‰)

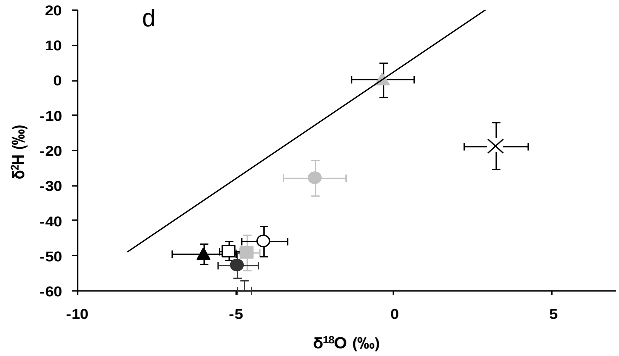

d
20
10
0
-10
-20
-30
-40
-50
-60
δ²H (‰)
-10
-5
0
5
δ¹⁸O (‰)

Fig. 3

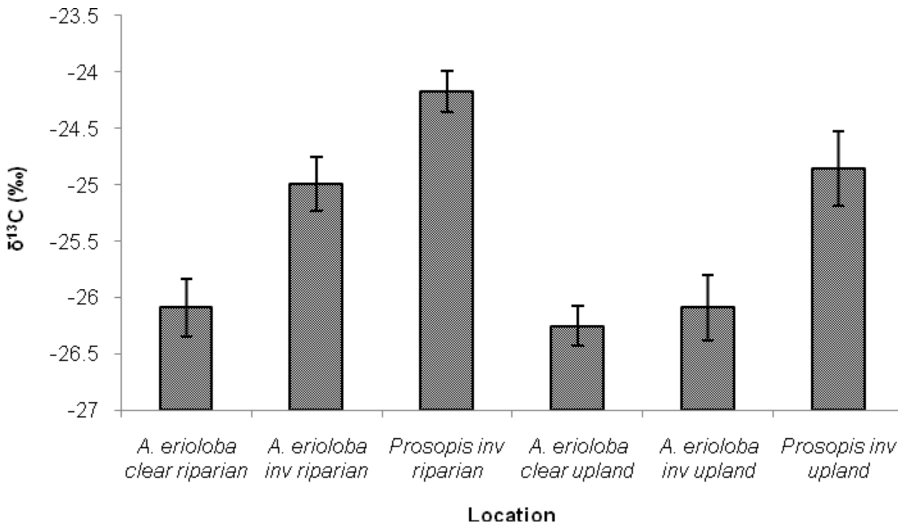

-23.5
-24
-24.5
-25
-25.5
-26
-26.5
-27
δ¹³C (‰)
A. erioloba clear riparian
A. erioloba inv riparian
Prosopis inv riparian
A. erioloba clear upland
A. erioloba inv upland
Prosopis inv upland
Location

Fig. 4

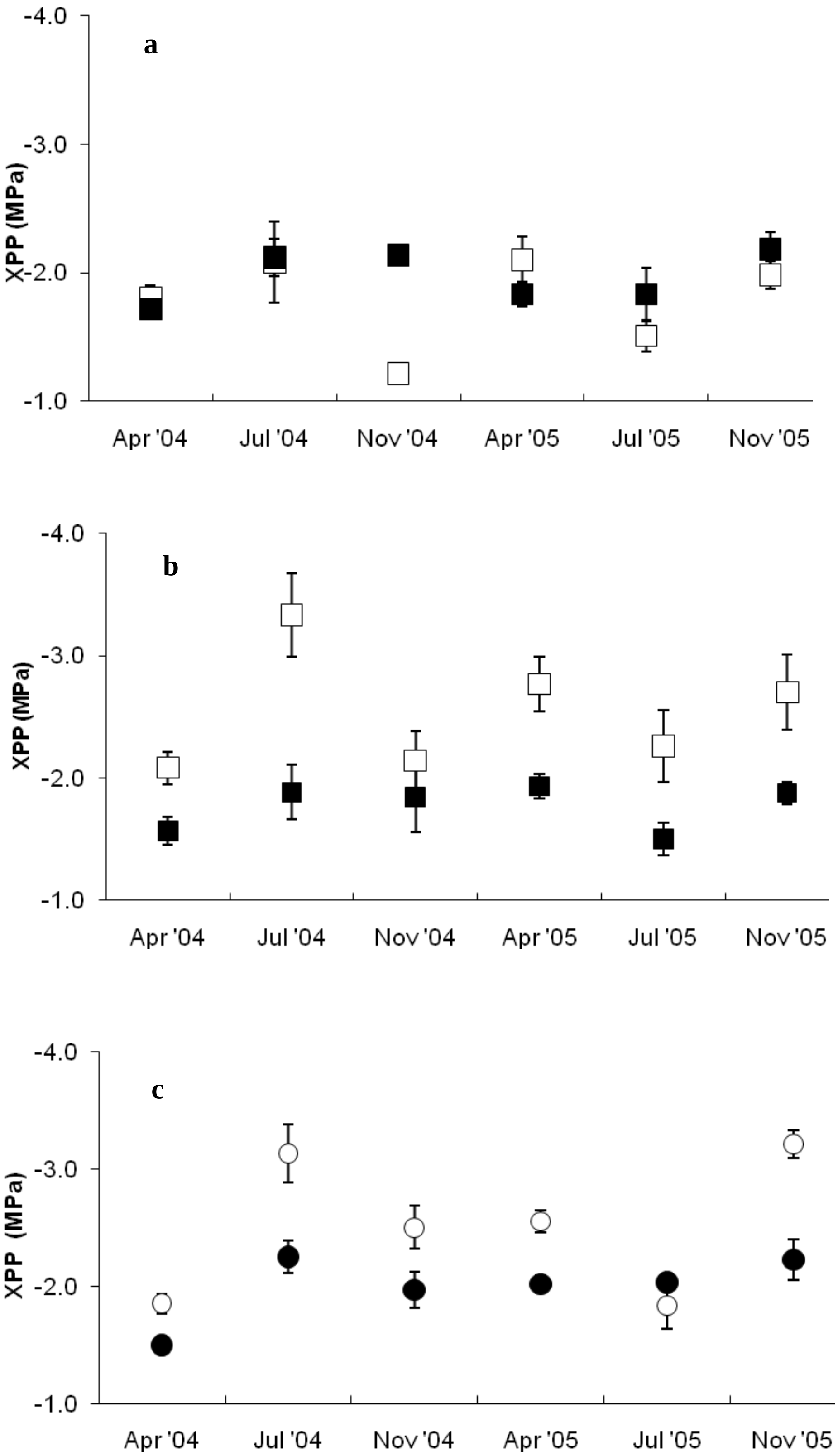


Fig. 5