

Intraspecific competition between shrubs in a semi-arid savanna

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Abstract Tree-on-tree competitive interactions may be more important in affecting the distribution of the tree components of savannas than inter-specific competition with grasses. The presence of intraspecific competition is expected to negatively affect inter-tree spacing, individual size distributions and plant physiology as well as survival/mortality. In this field removal experiment on *Acacia mellifera*, one of South Africa's most common encroachers on nutrient-poor soils, the growth, water relations and mortalities of shrubs where all neighbouring woody competitors were removed (target) were monitored three times during each of three growing seasons. After 3 years, the nitrogen and carbon isotopic ratios of the study plants were analysed. Target shrubs benefitted from removal of neighbours, resulting in greater growth, less water stress, a relatively small degree of canopy dieback and reduced reliance on N₂ fixation. Target shrubs grew by $25 \pm 4\%$ in height relative to $7 \pm 4\%$ for controls, with the targets suffering a maximum of <15% canopy dieback

compared to up to 60% in the controls. Severe environmental stress is known to affect neighbour interactions among shrubs and competition may constrain shrub sizes and avoid density-dependent mortality. In contrast, release from competition in our study may have allowed greater growth of target plants, increasing their total evapo-transpirational leaf surface areas and leaving them vulnerable to drought and water stress. Intra-tree competition on shallow nutrient-poor soils in savannas may thus aid the persistence of bush encroachment by regulating the sizes of individual shrubs below the threshold of drought vulnerability.

Keywords *Acacia mellifera* · Bush encroachment · Mortality · Near-neighbour removal · Water potential

Introduction

Intraspecific competition between woody plants plays a significant role in savanna structure and productivity (Smith and Grant 1986; Bonan 1991; Teague and Smit 1992), but has been less frequently cited as a factor determining the function of savannas than competition between grasses and woody vegetation (Stuart-Hill and Tainton 1989; Teague and Smit 1992; Scholes and Archer 1997). Recent work indicates that intraspecific competition between trees plays a major role in opening up encroached savannas

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and creating grassy patches in a cyclical succession (Wiegand et al. 2006). In infertile low-rainfall savannas, the effect of grasses on the performance of mature trees is considered negligible (Knoop and Walker 1985). Laterally extensive roots and a marked effect of woody plants on soil moisture (Knoop and Walker 1985; Wiegand et al. 2006; Meyer et al. 2007) may elevate the importance of inter-tree competition relative to interspecific competition with herbaceous plants in structuring the spatial distributions of trees in savannas. Competition among trees may limit or reduce their densities, sizes and spatial distribution (Smith and Walker 1983; Jeltsch et al. 2000), but positive intraspecific interactions may lead to aggregation and increased densities (Scholes and Archer 1997; Bruno et al. 2003; Miriti 2006). Semi-arid savanna vegetation dynamics are primarily driven by competition for soil moisture derived from rare but critical precipitation events (Ward 2005; Wiegand et al. 2005; Meyer et al. 2009). Rates of growth and the maximal stem heights achievable by savanna trees in semi-arid ecosystems are strongly influenced by moisture and nutrient availability (Shackleton 1997; Sankaran et al. 2008). Shackleton (2002) found that intraspecific competition, mostly within *Acacia* species, was more common than inter-specific interactions (see also Smith and Grant 1986; Wiegand et al. 2006; Meyer et al. 2007; Moustakas et al. 2008).

The presence/absence of competition between woody plant species is inferred from the spatial distribution of individuals and is associated with a reduction in size of one or both neighbours (Bonan 1991; Shackleton 2002; Meyer et al. 2007). Individual plants within a community may exploit distinct regions for resources delineated by the vertical and lateral extent of their roots (Walter 1971). When rooting zones and areas of resource acquisition by trees coincide, local competition for resources may ensue (Walter 1971; Stoll and Weiner 2000). This competition intensifies with increasing densities of neighbouring plants, leading to density-dependent tree mortality (Harper 1977; Antonovics and Levin 1980; Slatkin and Anderson 1984; Ward 2005). This process has been invoked by Wiegand et al.'s (2006) patch dynamics model which postulates *en masse* cohort recruitment resulting in intense intraspecific competition and subsequent self-thinning, which re-opens encroached patches (Wiegand et al. 2006)

and reduces tree densities (Peet and Christensen 1987; Cade and Guo 2000). Resource partitioning due to exploitation of different rooting zones among savanna tree species has been invoked to explain tree-on-tree competition avoidance (Knoop and Walker 1985). However, resource uptake by conspecific neighbouring trees with identical rooting patterns and phenological rhythms will overlap in time and space. Thus, intraspecific competition probably cannot be avoided through spatial/and or temporal niche partitioning (Goldberg and Novoplansky 1997).

We tested the hypothesis that individual shrubs not competing with neighbours experience relatively less water stress, have higher nutrient status and grow bigger (in height and canopy volume) than shrubs that are forced to compete with their neighbours. To do this, we examined the growth, mortality, water relations and isotopic composition of nitrogen and carbon in individual *Acacia mellifera* shrubs with and without neighbours in an encroached arid savanna (Kraaij and Ward 2006; Meyer et al. 2008) over three growing seasons between 2006 and 2008.

Methods

Study area

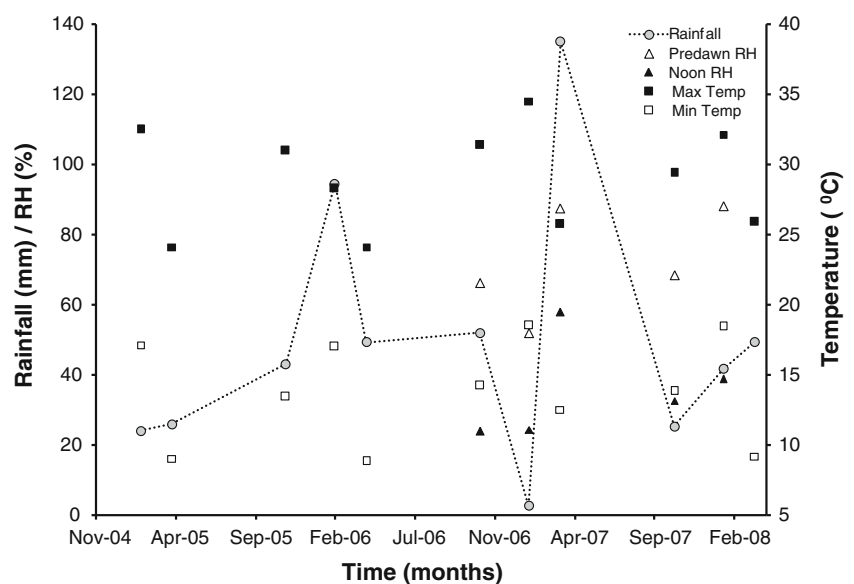
The study site was Pniel Estates in the Northern Cape province of South Africa, 35 km northwest of Kimberley (28°34'S, 24°25'E) at ±1,000 m a.s.l. This site is on the southernmost fringe of *A. mellifera* distribution in Africa. The climate is semi-arid (388 mm rainfall p.a.), dominated by variable mean summer rainfall (coefficient of variation = 39%), hot summers (32.8°C max) and cold (3.2°C min) dry winters. Frost is experienced on an average of 22 days per annum (Kraaij and Ward 2006). The study area falls within the arid savanna biome (Mucina and Rutherford 2006) and encompasses a mosaic of predominantly two main vegetation units; the Kimberley Thornveld and the Vaalbos Rocky Shrubland. The Kimberley Thornveld is found on undulating sandy plains characterised by irregular to well-developed tree cover dominated by isolated *Acacia erioloba* and *A. tortilis* trees with *A. mellifera*, *Tarchonanthus camphoratus* and *Grewia flava* predominating the shrub layer. The Vaalbos Rocky Shrubland on isolated rocky hillsides and ridges

comprises an open shrubland co-dominated by *A. mellifera* (the main encroaching species) and *T. camphoratus* L. (Mucina and Rutherford 2006). The plants at the study site were among large dolerite boulders on rocky outcrops where mean shrub height was 0.75 m (Meyer et al. 2007). Grass cover was dominated by perennial *Schmidtia pappophoroides* and *Eragrostis lehmanniana*.

Climate and weather

Long-term precipitation records covering the study period (2006–2008) from the Kimberley (28° 80 S; 24° 77 E) and Barkly West (28° 53 S; 24° 53 E) weather stations were obtained from the South African Weather Service. The Kimberley weather station (1,204 m a.s.l.) is 35 km from the study site while the Barkly West station (1,198 m a.s.l.) is 5 km from the field experimental site. On-site ambient air (dry bulb) and relative humidity (RH) were obtained every 15 min during the collection of water potential data using a sling psychrometer and accompanying psychrometric chart (S. Brannan & Sons Ltd., Cumbria, England). Precipitation at Barkly West in the past 124 years was (mean \pm SE) 380 \pm 14 mm year⁻¹. Most of the rain (44 \pm 1% of total annual precipitation) fell towards the end of the rainy season in autumn (March–April). The total annual amount (109.5 mm) in 2003 just prior to the establishment of the experiment in 2004 was the lowest annual rainfall on record.

Fig. 1 Rainfall and temperature recorded at nearby weather stations as well as on-site relative humidity (RH) during the study period



Since the start of the experiment in 2004 by Meyer et al. (2008) until the end of the present study in 2008, above average annual rainfall was recorded only once in 2006 (Fig. 1). Differences among the different stages of the growing season in ambient temperatures as well as RH were recorded (Fig. 1).

Field study

The same site and plants reported in Meyer et al. (2008) were used for the current study. Briefly, the mean lateral extent of near-surface roots of 30 randomly selected *Acacia mellifera* shrubs was determined and a distance of double the length of roots (7.5 m) was measured from each shrub. All other woody vegetation within the circumference of the measured distance from the target shrub was mechanically removed in February 2004 and the remaining stumps poisoned with Garlon 4 (Efekto, Silverton, South Africa; emulsified with diesel in a volumetric ratio of 1:50 and sprayed onto the cut surfaces) to eliminate tree–tree competition for the particular individual (target) shrubs. The current study was initiated after two complete growing seasons without intraspecific competition. *Acacia mellifera* shrubs (controls, $n = 30$) of similar heights and canopy sizes were identified, tagged and mapped in the vicinity of each shrub for which neighbours had been removed. The positions of control shrubs relative to target plants in distance, direction and

slope were varied at random. Measurements of canopy height and dimensions by Meyer et al. (2008) since March 2004 formed the baseline data for continued monitoring of shrub canopy heights and volumes for the current study (2006–2008). Occasional cutting and poisoning of re-sprouting neighbours were repeated during the study.

Shrub height and canopy volume were measured at the beginning (November), middle (February) and end (April) of each growing season. Whole tree mortalities and partial canopy dieback were also assessed from branch/twig mortalities by estimating the percentage of dead parts (following Bowers and Turner 2001). *A. mellifera* frequently grows as a multi-stemmed shrub, particularly in rocky areas. Shrub mean height (h) was determined by measuring the highest point above the ground at three different positions around the shrub. Canopy diameter and radius was estimated from the mean of the major horizontal axis (a) and the axis perpendicular to the major axis (b). The shape of *A. mellifera* shrubs approaches that of an inverted cone; thus, the formula of a cone ($V = \pi/3 [a + b/2]^2 \times h$) was used to estimate canopy volume. The growth of shrubs in height and canopy expansion over the seasons was calculated using $\log(X_2 - X_1)/t_2 - t_1$, where X_1 denotes the canopy height or volume measured by Meyer et al. (2008) in 2004 (t_1) and X_2 is the height or volume at the subsequent date (t_2) of measurement.

Plant water potential

To determine the effects of neighbour competition on plant water relations, a Scholander pressure chamber was used to measure xylem pressure potentials of both control and target shrubs. Three leafy twigs were excised with a razor blade from three separate parts of the shrub canopy and immediately inserted into the pressure chamber. Xylem pressure was measured at pre-dawn (Ψ_{PD}) and at midday (Ψ_{MD}) in November, February and April between 2006 and 2008. Shrub water potential deficit (Ψ_{DF}) was calculated from the difference $\Psi_{MD} - \Psi_{PD}$.

Nitrogen and carbon isotopes

Leaves were sampled at the end of the growing season in April 2008 and milled to a fine powder using a Culatti Type MFC micro-fine pulverising electrical

grinder (Janke and Künkel GmbH, Staufen, Germany) fitted with a 1 mm mesh. Samples were weighed ($\pm 1 \mu\text{g}$) into tin cups on a Sartorius (Sartorius, Göttingen, Germany) micro-balance and combusted in a Flash EA 1112 series elemental analyzer (Thermo Finnigan, Italy). The gases were passed to a Delta Plus XP IRMS isotope ratio mass spectrometer (Thermo electron, Germany), via a ConFlo III gas control unit (Thermo Finnigan, Germany). The in-house standards used for expressing $\delta^{15}\text{N}$ isotopes were Merck Gel (Merck KgaA, Darmstadt, Germany) and dried lentils. All the in-house standards were calibrated against International Atomic Energy Agency (IAEA) standards. Carbon isotope ratios are expressed as $\delta^{13}\text{C}$ (Ehleringer and Rundel 1989) relative to Pee-Dee Belemnite (PDB) while nitrogen isotopes are expressed as $\delta^{15}\text{N}$ (Evans 2001) relative to the natural abundance signature of N in atmospheric air.

Data analysis

Differences among between-subject factors (phases of the growing season in different years) in terms of Ψ , height and canopy size (growth) were analysed using general linear repeated measure MANOVA, with a full factorial model with Type III Sums of Squares. Linear comparisons of group means and pair-wise multiple comparisons were subjected to Bonferroni post hoc tests. The main effects were compared with Bonferroni confidence interval adjustments at a significance level (P) of 0.05.

Growth of canopy height and volume at each date of field measurement was calculated relative to the original height/sizes measured in 2004 by Meyer et al. (2008) and the results compared via repeated measures MANOVA. Repeated measures MANOVA was also used to analyse partial canopy dieback (% shrub canopy that was dead) in study plants as estimated during every field visit. A few plants died during the experiment and this resulted in missing data which created a statistical bias of temporal autocorrelation. Fractional canopy mortalities were arcsine square-root transformed to conform to ANOVA test assumptions. Whole plant mortality was evaluated using the Kaplan–Meier estimate (Kaplan and Meier 1958). Only shrubs that died during the current study were considered. Completely dead shrubs were excluded from analysis of partial canopy dieback while branch death was not factored

into the Kaplan–Meier procedure. Once-off comparisons of target and control shrubs of %N, $\delta^{15}\text{N}\%$, %C and $\delta^{13}\text{C}\%$ were analysed using one-way ANOVA. One-way ANOVA was also used to compare Ψ of target and control trees in each season.

To relate rainfall amount to Ψ , height and canopy volume, the cumulative rainfall amount over 90, 60 and 30 days preceding field recordings was regressed against the means of these parameters. The strength of correlations of Ψ and sizes to rainfall over a given period indicated whether shrub Ψ and growth were responsive to precipitation or more reactive to longer-term soil moisture conditions. Given the inherently high variability of precipitation in the study area, extreme weather conditions can give rise to rainfall amounts outside the range of normal distribution (outliers). The leverage exerted by outlier cases on the predicted value of the regression line was screened using Cook's *D* statistic (Cook 1977; Newton and Rudestam 1999).

Results

Shrub sizes and growth

Both target (18.4 cm) and control shrubs (6.6 cm) canopy heights increased significantly over the 5 years

of monitoring. Similarly, significant expansions were also found in canopy volumes (Table 1). All the plant canopies increased in height and volume over the study period despite expansion and contractions between seasons (Fig. 2). Decline in canopy height was largely noted over winter for these deciduous shrubs between the end of the wet season (April) when they lose leaves and the onset of the next (November) when the shrubs grow new leaves. For control shrubs, the first negative canopy height growth (−5.2 cm) was measured in November 2006 while it occurred a year later (November 2007) in target shrubs (−5.0 cm). There was no significant difference between target and the control shrubs in March 2004 when measured by Meyer et al. (2008). The target shrubs were significantly taller than the control plants in April 2008 (Fig. 2a).

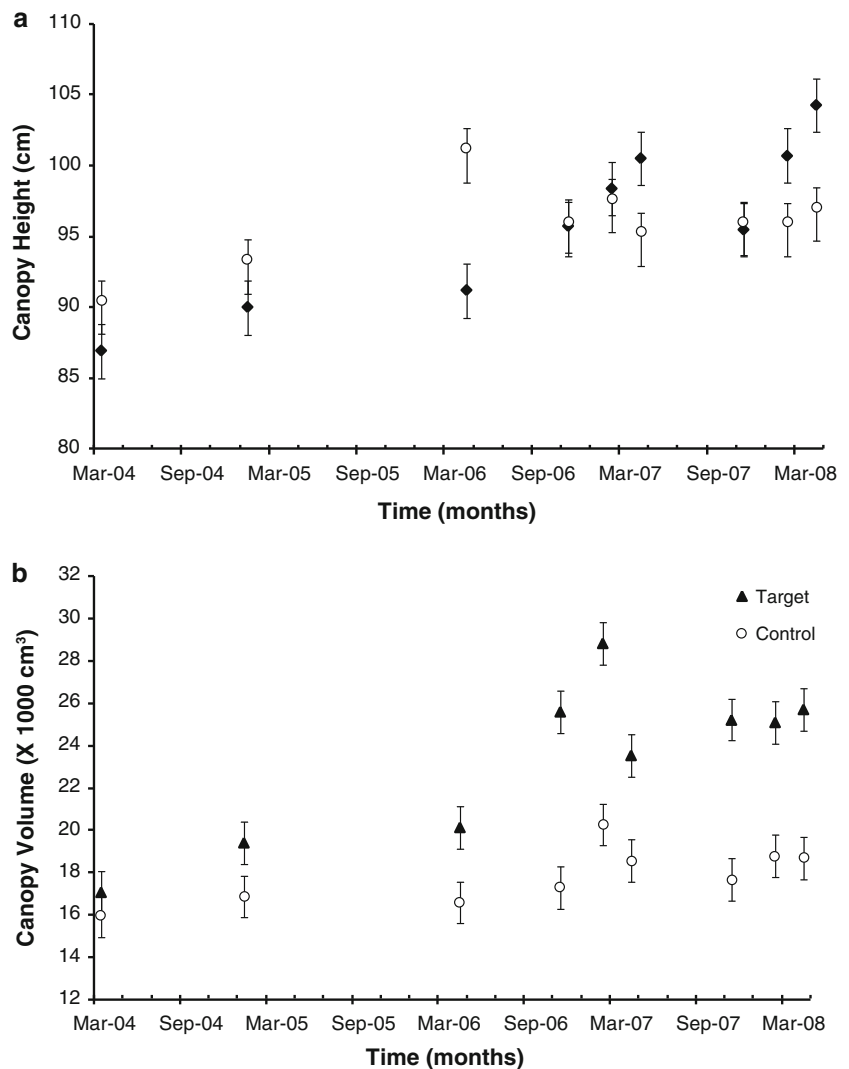
While there was significant variation among seasons in canopy height and volume, the season \times treatment interaction was not significant for height (albeit nearly significant) or volume (Table 1). Significant differences were found in the growth of shrub canopy volume but not in height. Season \times treatment interactions showed no significant effects on growth in canopy height or volume (Table 1). Target shrubs had significantly greater canopy volume expansions than control shrubs (Fig. 2b). Comparing the final (April 2008) measurements to the initial, target shrubs showed an average

Table 1 Results of repeated measures MANOVA general linear model (GLM) for monitoring of the height, volume (including data reported by Meyer et al. 2008) and partial dieback of the canopies of shrubs with and without neighbours

Source of variation (effect)	Wilks' λ	<i>F</i>	df	Error df	Significance (<i>P</i>)
Canopy height					
Seasonal canopy heights	0.584	7.73	8	44	<0.001
Season \times neighbour competition	0.263	1.97	8	44	0.074
Growth in height	0.864	1.02	7	45	0.433
Seasonal height growth \times competition	0.855	1.09	7	45	0.384
Canopy volume					
Seasonal canopy volumes	0.552	4.46	8	44	0.001
Season \times neighbour competition	0.800	1.38	8	44	0.233
Growth in volume	0.704	2.70	7	45	0.020
Seasonal volume growth \times competition	0.890	0.80	7	45	0.593
Seasonal partial canopy dieback	0.520	7.38	6	48	<0.001
Seasonal partial dieback \times competition	0.789	1.10	6	48	0.376

Differences in df result from the fact that growth could only be calculated from the second measurement onwards as well as partial dieback (branch mortality) not monitored by Meyer et al. (2008)

Fig. 2 Sizes of target and control shrubs (mean \pm SE) over time; **a** height and **b** canopy volumes. Following above average rainfall in February 2006 and November 2007, the size of target trees became significantly larger than those of control shrubs



of $25 \pm 4\%$ canopy height growth and $357 \pm 128\%$ in volume over the study period. The final height of control shrubs was $7 \pm 4\%$ greater than the initial measurements, and the volume was $164 \pm 125\%$ larger than the original measure.

Plant mortality

Fewer individual target shrubs (6 out of 30) compared to 17 of 30 control shrubs suffered partial canopy dieback in a given season ($\chi^2 = 8.53$, $df = 1$, $P = 0.003$). Individual target shrubs experienced 5–15% canopy dieback whereas most control shrubs suffered 25–60% partial canopy dieback. Control shrubs showed a

significantly higher propensity towards partial loss of canopies compared to target shrubs. There were significant seasonal variations in partial canopy dieback but no significant treatment \times season interaction (Table 1). However, 13.3% of target shrubs died (i.e., did not resprout) while no control shrub suffered complete mortality during this experiment, resulting in a significant difference between total shrub mortalities of target and control shrubs ($\chi^2 = 4.08$, $df = 1$, $P = 0.043$). Partial and whole plant dieback were especially noticeable at the onset and end of the growing season. All but one of the dead shrubs were discovered in April 2007, the other individual having died in November 2006.

Plant water potential

The most negative water potentials (both Ψ_{PD} and Ψ_{MD}), possibly indicating water stress, were measured in February 2007 by control shrubs (Fig. 3), which was also the date on which large Ψ_{DF} comparable to late season values was found in both sets of study plants (Fig. 3c). The early rainy season (November) showed the least negative Ψ_{MD} in all study plants (Fig. 3b). Significant differences were found in seasonal

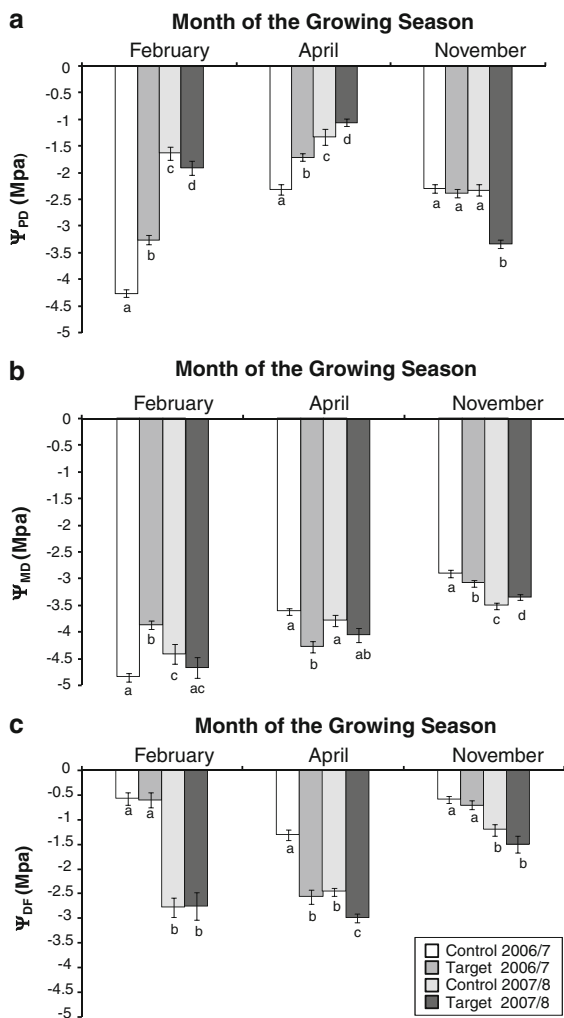


Fig. 3 Plant water potential (Ψ) (mean \pm SE) of control and target shrubs recorded in different months over the growing season between 2006 and 2008 at **a** predawn and **b** midday as well as the **c** difference between the two values. Water potentials were measured twice in each month of the growing season of February (2007/2008), April (2006/2007) and November (2006/2007)

variations of pre-dawn (Ψ_{PD}), midday (Ψ_{MD}) water potentials and the difference between the two (Ψ_{DF}). There were significant season \times treatment interactions for Ψ_{PD} , Ψ_{MD} and Ψ_{DF} (Table 2).

Control shrubs had significantly more negative Ψ_{PD} than target shrubs in all seasons, other than November and February 2008 when the values did not differ significantly (Fig. 3a). Significant differences between Ψ_{PD} of control and target shrubs were measured in April 2006 ($F_{2,54} = 33.27$, $P \leq 0.001$), February 2007 ($F_{2,56} = 71.49$, $P \leq 0.001$) and November 2007 ($F_{2,51} = 8.79$, $P = 0.005$). Thus, when soil moisture availability was limiting or temperatures were high during hot and dry rainy seasons, control shrubs experienced higher predawn water stress than target shrubs, but in seasons with favourable soil moisture availability and low minimum temperatures, there were no significant differences. November 2006 received and was preceded by, above-average autumn (April) precipitation and February 2008 benefitted from heavy early season precipitation, with low temperatures recorded in both these seasons (Fig. 1). However, when soil moisture content was high and the maximum and minimum temperatures were significantly lower than the mean, as in April 2006, target shrubs had significantly less negative Ψ_{PD} .

Midday water potential (Ψ_{MD}) values also varied in accordance with seasonal precipitation, with control shrubs having significantly more negative Ψ_{MD} in February ($P \leq 0.001$) and November 2007 ($P = 0.048$) when rainfall was below average (Fig. 3b). Target shrubs had significantly more negative Ψ_{MD} in April ($P \leq 0.001$) and November 2006 ($P = 0.049$) when precipitation was above average (Fig. 3b). The Ψ_{MD} differed significantly during April 2006 ($F_{2,54} = 28.39$, $P \leq 0.001$), February 2007 ($F_{2,56} = 76.71$, $P \leq 0.001$) and November 2007 ($F_{2,50} = 4.11$, $P = 0.048$). Thus, when soil moisture was not limiting, target trees had significantly more negative Ψ_{MD} . Midday Ψ values in April 2007 and February 2008 were not significantly different between the target and control treatments (Fig. 3b). The least negative Ψ_{PD} was registered in the late season (April) by all shrubs, possibly reflecting adequate plant water status. The late season was also the only time when significant differences were found between treatments in terms of Ψ_{DF} , with target shrubs recording larger deficits (Ψ_{DF}) than control shrubs on both occasions (Fig. 3c).

Table 2 Results of repeated measures MANOVA general Linear model (GLM) for shrub water potential (Ψ) over the course of the growing season between April 2006 and February 2008

Source of variation (effect)	Wilks' λ	F	df	Error df	Significance (P)
Predawn water potential (Ψ_{PD})					
Seasonal Ψ_{PD}	0.034	356.26	5	62.00	<0.001
Seasonal $\Psi_{PD} \times$ neighbour competition	0.164	10.58	15	171.56	<0.001
Midday water potential (Ψ_{MD})					
Seasonal Ψ_{MD}	0.196	42.53	5	52.00	<0.001
Seasonal $\Psi_{PD} \times$ neighbour competition	0.172	8.55	15	143.95	<0.001
Water potential deficit (Ψ_{DF})					
Seasonal Ψ_{DF}	0.206	40.15	5	52.00	<0.001
Seasonal $\Psi_{DF} \times$ neighbour competition	0.297	5.31	15	143.95	<0.001

Significant differences between Ψ_{DF} were found during April 2006 ($F_{2,54} = 45.93$, $P \leq 0.001$) and in April 2007 ($F_{2,53} = 7$, $P = 0.011$).

Influence of cumulative precipitation

Shrubs invested in increased height of the canopy in response to long-term rainfall trends. Positive correlations of target shrub canopy heights to cumulative precipitation (Fig. 4) occurred over 60 days ($r = 0.93$, $F_{2,5} = 31.72$, $P = 0.002$), 90 days ($r = 0.89$, $F_{2,6} = 22.47$, $P = 0.003$) and 120 days ($r = 0.80$, $F_{2,6} = 10.7$, $P = 0.017$) when exceptionally low and high precipitation amounts (one of each) were removed (Fig. 4). The canopy heights of control shrubs showed significant positive correlations with cumulative rainfall for the full range of recorded rainfall amounts over the period of 90 days ($r = 0.77$, $F_{2,7} = 10.32$, $P = 0.015$) and 120 days ($r = 0.73$, $F_{2,7} = 7.25$, $P = 0.026$). Canopy volume showed a significantly positive correlation ($r = 0.89$, $F_{2,5} = 18.79$, $P = 0.007$) to total rainfall after 60 days for both target and control shrubs (Fig. 4).

Canopy predawn water potential (Ψ_{PD}) was not correlated to the short- or long-term accumulation of rainfall, but showed a strong positive correlation to medium-term rainfall over 30 days ($r = 0.86$, $F_{2,10} = 18.15$, $P = 0.002$) and 60 days ($r = 0.94$, $F_{2,10} = 29.14$, $P = 0.001$). The predawn water potential of target shrubs showed stronger correlations to additive rainfall amounts compared to control shrubs (Fig. 4c), indicating that shrubs had a more robust response to soil moisture accumulation without neighbours. The difference between predawn and

noon water potential (Ψ_{DF}) in target shrubs showed a strong negative correlation to accumulated rainfall over the long-term of 60 days ($r = -0.93$, $F_{2,4} = 24.45$, $P = 0.008$) and 90 days ($r = -0.87$, $F_{2,4} = 12.26$, $P = 0.025$) (Fig. 4).

Tissue nitrogen and carbon and their isotopes

Target shrubs had significantly higher $\delta^{15}\text{N}\text{‰}$ mean values than control plants (Table 3), indicating a stronger dependence on biological nitrogen fixation among control plants relative to target shrubs. Target shrubs exhibited significantly higher foliar N concentrations than the control shrubs (Table 3). The low foliar N resulting from competition for N by neighbours induced nodulation and thus increased reliance on N_2 fixation by controls. No significant difference was found between the carbon isotope discrimination ($\delta^{13}\text{C}$) of target and control shrubs ($F_{2,53} = 0.078$, $P = 0.781$) 5 years after near-neighbour shrub removals. The $\delta^{13}\text{C}$ of control ($-27.2 \pm 0.2\text{‰}$) and target ($-27.1 \pm 0.1\text{‰}$) shrubs were nearly identical, possibly indicating little influence of neighbouring *A. mellifera* shrubs on each other's water use efficiency (WUE). Target shrubs had comparable ($F_{2,53} = 3$, $P = 0.089$) carbon content (%C) in their leaves ($47 \pm 0.19\%$) to control shrubs ($46.5 \pm 0.22\%$).

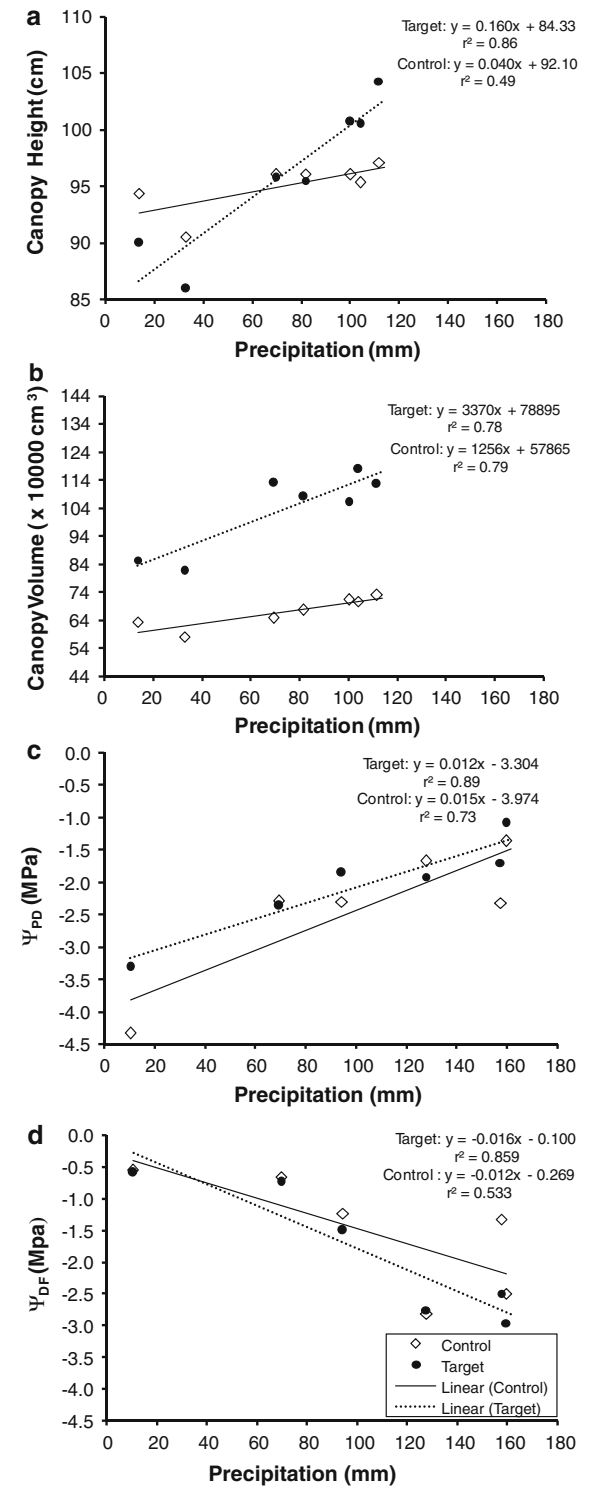
Discussion

The removal of neighbours had a marked effect on the growth and water relations of the shrubs. The increase in canopy height of target shrubs over

Fig. 4 Linear regression of control and target shrubs canopy height (a), volume (b), predawn water potential (c) and water potential deficit (d) against cumulative rainfall recorded over 60 days prior to field measurements. For sizes (height and volume), it was found that Cook’s *D* value for two outliers (i.e. exceptionally high [157.5 mm] and low [8 mm] rainfall amounts over 60 days) recorded in April 2006 and February 2007, respectively, was >1, indicating that these amounts were influential leverage points. These data points were removed and a corrected correlation performed

5 years between the first measurement in 2004 (recorded by Meyer et al. 2008) and the final measurement for this study in 2008 as well as their average growth between seasons were almost three-fold that achieved by control shrubs. While more control shrubs suffered partial canopy dieback than target shrubs, with greater percentages of the control shrub canopies being affected relative to target shrubs, a few target shrubs died whereas no control shrubs died. Control shrubs had significantly more negative predawn water potential (Ψ_{PD}) than target shrubs in dry and hot or wet and cool times of the season, but target shrub had more negative midday water potential (Ψ_{MD}) and larger differences between Ψ_{MD} and Ψ_{PD} (Ψ_{DF}) when soil moisture availability was non-limiting. Plant sizes responded positively to cumulative rainfall amounts over the long-term, whereas Ψ_{PD} was more responsive to precipitation accumulated over an intermediate period. Control shrubs had lower foliar N concentration and showed increased reliance on N_2 fixation relative to target shrubs but there was no difference in their WUE.

A marked expansion in shrub size following the above-average precipitation of 2006 was immediately followed by contraction during the subsequent dry season (i.e. prior to November 2006) for control shrubs. However, it took the exceedingly hot and dry conditions of 2007 to bring about a decline in target shrub canopy sizes a year later (November 2007). Augmented availability of soil moisture during or following above-average rainfall may bolster extensive root production and accelerated canopy growth (Zegada-Lizarazu et al. 2007). When soil moisture decreases to or below average levels, mortalities often occur, especially on underdeveloped soils (Hamerlynck and McAuliffe 2008). It is probable that a limited volume of soil and low water-retention capacity of stony underdeveloped horizons found in our study site exposed rooting zones to rapid



desiccation. A relatively high degree of soil porosity would allow rapid uptake of moisture by roots (Archer et al. 2002) and downwards percolation.

Table 3 One-way ANOVA comparisons of $\delta^{15}\text{N}$ isotopic composition and foliar tissue N concentration (mean \pm SE) of control and target shrubs at the end of the experiment in 2008

Measured parameter	Treatment		<i>F</i>	Error df	Significance (<i>P</i>)
	Control	Target			
$\delta^{15}\text{N}$ isotope (‰)	0.3 \pm 0.42	1.9 \pm 0.54	5.67	53	0.021
Foliar N concentration (%)	2.93 \pm 0.07	3.13 \pm 0.05	5.31	53	0.025

Infiltrated moisture is thus either rapidly consumed by root uptake, evaporation or percolation deeper into the soil, resulting in reduced surface soil moisture availability to plants, despite transitory subterranean storage of moisture beneath rocks (Nobel and Zutta 2007). Relatively greater increases in canopy size (Figs. 1, 2) showed that the absence of intraspecific competition enabled *A. mellifera* to take advantage of above-average precipitation. The removal of neighbouring individuals thus conferred benefits in terms of aboveground growth of target compared to control shrubs, indicating that intraspecific competition could indeed be important in semi-arid environments. Canopy size contractions during the early summer were attributable to mortality of crown branches in the dry season, possibly as a consequence of water stress resulting from low rainfall, high temperatures and low humidity in the preceding season (e.g. April 2007).

The tree removal experiment was preceded by the driest season on record (2003) and the study area persistently experienced below average precipitation for most of the study period. Such an extreme drought may possibly have caused significant dieback of both the crown branches and some roots, thus reducing the competitive interactions among shrubs. This may explain why the effect of near-neighbour removal on plant sizes and growth was not immediate, but took until 2007 to manifest itself (Fig. 2). Moreover, the drought may have resulted in low or depleted soil moisture storage, such that much of the water accessed by shrubs during the study was derived from recent precipitation as indicated by the correlation of sizes and Ψ_{PD} to cumulative rainfall. When soil moisture availability was limiting or evaporative demand was high, target shrubs had better access to soil moisture than control shrubs. This could have resulted from reduced/absent sub-surface competition for soil moisture among target plants. Water stress associated with strongly negative Ψ , as measured in

our study plants, may cause branch or whole plant mortality (Zimmermann 1983; Tyree and Sperry 1988). The protection of individual plants by intact vegetation during extreme drought (DeSteven 1991; Gill and Marks 1991; Berkowitz et al. 1995) may have facilitated the partial survival of control shrub canopies, but death of a number of target shrubs. This could be attributed to either a shielding effect of neighbours and the exposure of neighbourless shrubs to extreme conditions or shrubs benefiting from shared hydraulic lift. Target shrubs were exposed to direct sunlight, radiation and wind at canopy and ground level which may have increased evapotranspiration relative to control plants shielded by conspecifics. During seasons of non-limiting soil moisture availability, target shrubs had more negative Ψ_{MD} than the controls and this reverse trend (relative to Ψ_{PD}) partially supports the beneficial effect of neighbours. It is more likely, however, that increased growth of target shrubs predisposed them to greater sensitivity to extreme dry conditions through increased evapo-transpirational surfaces. Ansley et al. (1998) attributed fourfold higher evapo-transpirational water loss in individual honey mesquite (*Prosopis glandulosa*) trees without neighbours relative to trees at high density to either resource limitation or increased water conservation. High water loss by target shrubs experiencing minimal resource limitation during the wet season probably rendered them vulnerable to harsh conditions. Partial canopy dieback exceeding 30% of the total canopy was observed to affect discrete segments of shrub crowns in our study. Partial demise of the canopy could be a means of reducing the total photosynthetic surface area by shrubs. Shrubs with dead parts of their canopies exhibited relatively improved water relations compared to other seemingly healthy shrubs from similar treatment that suffered little or no branch mortalities. This may suggest hydraulic segmentation (Zimmermann 1983) by *A. mellifera* to

minimise water stress and ensure the survival of the individual. We note that, for the spatial scale studied as well as the temporal scale of the experiment, the influence of tree size on both growth and water potential was not significant.

Relatively smaller $\delta^{15}\text{N}\%$ values in control plants may indicate a reliance on N_2 fixation to have been induced by intraspecific competition. Previous studies have shown interspecific competition with grass to induce N_2 fixation in acacias (Cramer et al. 2007) with belowground competition for N generating such competitive responses (Cramer et al. 2010); competition from conspecifics may have a similar effect. Interestingly, a reliance on N_2 fixation by control shrubs did not lead to higher foliar N concentrations in control relative to target shrubs, but target shrubs achieved more growth. Removal of neighbours may have increased the access of target shrubs to N while competition from neighbours caused a low tissue N concentration, inducing a reliance on fixation of atmospheric N_2 by control shrubs. Cramer et al. (2009) argue that a function of water acquisition by plants is to facilitate the mass flow of nutrients through the soil. Thus, the availability of soil nutrients may influence the rate of transpiration, increasing transpiration when soil N is limited (Cramer et al. 2009). Limited soil N may have been partially responsible for negative Ψ in control shrubs with limited access to N due to intraspecific competition. Tree-on-tree competition for co-limiting N and water resources may regulate the sizes and pattern of tree aggregation in savannas.

Boulders in our site may have acted as conduits for the percolation of rainwater, while shielding the soils beneath them from evaporative losses (Nobel et al. 1992), allowing persistence of soil water (Nobel et al. 1992; Hamerlynck and McAuliffe 2008). Rocks could thus aid plant establishment through transient soil moisture and yet constrain rooting biomass via physical impediment, thus limiting plant growth and leading to small shrubs aggregating at high densities (Hamerlynck and McAuliffe 2008; Ward and Esler 2010). Physical limitations presented by rocks, shallow soil horizons and limited resources such as N probably put a threshold on the maximum size attainable and thus the extent of plant resource capture zone. Plants growing in a water-limited nutrient-poor environment show reduced leaf growth (Van Volkenburgh and Boyer 1985; Munns and

Cramer 1996) which ultimately leads to reduced plant size. The small stature of plants on rocky areas in arid environments (Schmiedel and Jurgens 2004; Ward and Esler 2010) and less robust competition among small individuals (Schenk et al. 2003) may allow for compact aggregation of individuals, as occurs during *A. mellifera* encroachment. Ward and Esler (2010) found that *A. mellifera* seedling densities were higher on rocky soils but these plants grew larger on sandy soils at the study site. Even so, a degree of tree-on-tree competition may maintain the individual plant sizes within the threshold that can be supported by the available resource pool. The removal of near-neighbour competition may in turn release an individual from the competition-imposed size limit and allow it to grow beyond such a threshold which exposes it to drought-induced mortality. The implications of our findings for bush encroachment control and management is that in shallow resource-poor soils, it may not be necessary to eliminate all plants in order to reduce shrub density. Retaining some large individuals may also benefit the soils in terms of N_2 fixation (Wiegand et al. 2005).

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