

Acacia trees as keystone species in Negev desert ecosystems

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Abstract. The only trees in most of the Negev desert are 3 native *Acacia* species. We tested the hypothesis that they act as keystone species as a result of the improved soil conditions under their canopies. Furthermore, because many *Acacia* populations suffer high levels of mortality due to water stress, we tested whether trees in high mortality populations had diminished effects on plant species and soil quality under their canopies. We show that plant species diversity beneath the tree canopies is higher than in the surrounding areas. There was also a clearly identifiable suite of species with higher occurrence under the trees. Plant species composition differed significantly between high and low mortality sites. However, there was higher species diversity in high mortality sites and under trees with higher water stress. Soil nutrient content was higher under the trees than in the open areas, especially under larger trees and trees with higher water status. The results indicate that there is a combination of positive and negative effects of *Acacia* trees on the under-canopy environment, which may include positive effects of higher soil nutrients and a negative influence of higher soil salinity.

Keywords: Nurse plant; Soil nutrient; Water stress.

Abbreviations: MANCOVA = Multiple Analysis of Covariance; PAR = Photosynthetically active radiation; PCA = Principal Components Analysis.

Nomenclature: Feinbrun-Dothan et al. (1991).

Introduction

Large isolated trees are considered key organisms in arid and semi-arid environments. Their importance as nurse plants and as sources of shade and food for animals has been described by a number of authors (e.g. Belsky et al. 1989; Dean et al. 1999). Their effects on the environment beneath their canopies include the reduction in the extremes of environmental temperatures (Valiente-Banuet & Ezcurra 1991; Suzan et al. 1996), provision of suitable amounts of photosynthetically active radiation (PAR) to understorey plants (Smith et al. 1987), enhancement of soil fertility (increased nitrogen, organic carbon, phosphorus and microbial biomass) (Charley & West 1975; Franco & Nobel 1989; Nobel 1989; Franco-Pizana et al. 1996), increased soil moisture (Belsky 1994) and protection against predators (McAuliffe 1984; Suzan et al. 1996). The function of deep-rooted perennials in hydraulic lift was shown by Caldwell et al. (1991). The effects of these trees on the vegetation is commonly described in terms of higher above-ground productivity (Belsky et al. 1989; Belsky 1994), facilitation of seedling establishment (Franco & Nobel 1989; Franco-Pizana et al. 1996) and higher species diversity (Suzan et al. 1996; Raffaele & Veblen 1998). Trees may also have negative effects on understorey vegetation via below-ground competition, which could reduce the amounts of nutrients and water available (Parker & Muller 1982; Monk & Gabrielson 1985).

The native *Acacia* tree species *A. raddiana*, *A. tortilis* (see Rohner & Ward 1997 for a taxonomic note) and *A. pachyceras* (Danin 1998) are the only trees found in the Negev desert; they constitute a major ecological feature in southern Israel (Danin 1983). While several studies have evaluated the effects of *A. tortilis* on soil quality and understorey vegetation in mesic areas of Africa (McNaughton 1983; Belsky et al. 1989; Alstad & Vetaas 1994; Nyberg & Högberg 1995), no studies of the importance of any of these species have been conducted in desert ecosystems. We test the

hypothesis that *Acacia* trees are keystone species in Negev desert ecosystems and increase plant species diversity under their canopies through increased soil quality (primarily), shade and hydraulic lift.

There is widespread concern regarding the mortality of *Acacia* trees in the Negev desert, Israel (Ashkenazi 1995; Ward & Rohner 1997; Ben David-Novak & Schick 1998; Wiegand et al. 1999). Mortality varies widely, and may reach as high as 61% in populations of adult trees (Ward & Rohner 1997). This mortality is linked to water stress induced by anthropogenic factors, such as aquifer pumping and poor road-building practices (Ward & Rohner 1997; Bowie & Ward in press; Shrestha et al. in press). Ward & Rohner (1997) showed that there were 5 fewer species of perennial plants in *Acacia* populations suffering high mortality than in low mortality populations. This result points both to the keystone role of *Acacia* trees and the sensitivity of this role to *Acacia* water stress. Thus, we also tested the hypothesis that water stress diminishes the benefit that these trees confer on species growing under them.

The aims of the study were to determine the effects of *Acacia* trees on plant community composition and soil quality under the canopy compared to the open spaces among the trees. Furthermore, we wished to determine how these effects are dependent on water stress and tree size. Finally, we tested whether the trees confer improved growing conditions on *Ochradenus baccatus*, a species frequently found growing in association with *Acacia* trees.

Methods

Comparisons of plant communities under trees and in the open

To compare the ability of the different *Acacia* species to affect plant species composition under them, we measured plant species composition (using the McAuliffe (1990) log-series survey method) in 13 sites and soil quality in 6 of these sites that contained 1 or 2 of the 3 *Acacia* species. Where possible, we chose sites where more than 1 *Acacia* species was found to minimize possible confounding effects caused by differences among sites. At each of these sites, we recorded plant species composition under 5 trees per species and in a paired plot randomly chosen from an area adjacent to each tree but not under the canopy of any species (= open plot). Three soil samples per plot were taken in 3 pairs of plots at each selected site. The following sites were used (Fig. 1):

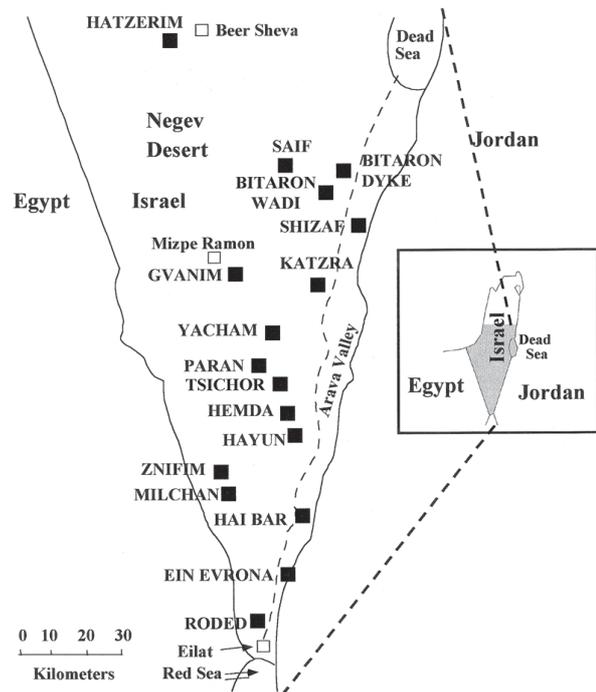


Fig. 1. Map of the Negev desert, ■ = study sites; □ = cities or towns; ---- = edges of the Syrian-Africa (Arava) rift valley.

Gvanim 30° 35' N 34° 54' E	<i>A. raddiana</i> , <i>A. pachyceras</i>
Tsichor 30° 14' N 35° 00' E	<i>A. raddiana</i> , <i>A. pachyceras</i>
Milchan 29° 55' N 34° 54' E	<i>A. pachyceras</i>
Znifim 29° 56' N 34° 52' E	<i>A. pachyceras</i>
Hayun 30° 12' N 35° 01' E	<i>A. pachyceras</i>
Hemda 30° 14' N 35° 02' E	<i>A. pachyceras</i>
Paran 30° 19' N 34° 58' E	<i>A. raddiana</i>
Hai Bar Yotvata 29° 52' N 35° 02' E	<i>A. raddiana</i> , <i>A. tortilis</i>
Katzra 30° 33' N 35° 09' E	<i>A. raddiana</i> , <i>A. tortilis</i>
Shizaf 30° 45' N 35° 25' E	<i>A. raddiana</i> , <i>A. tortilis</i>
Yacham 30° 22' N 34° 59' E	<i>A. raddiana</i>
Ein Evrona 29° 40' N 35° 00' E	<i>A. tortilis</i>
Bitaron Dyke 30° 50' N 35° 15' E	<i>A. tortilis</i>

All sites, with the exception of Hai Bar, are in ephemeral riverbeds ('wadi') because this is where most *Acacia* trees are found.

The same sampling scheme was used in 3 *Acacia raddiana* dominated sites with the highest mortality and 5 sites with the lowest mortality from sites surveyed by Ward & Rohner (1997). The high mortality sites were: Saif (30° 52' N 35° 09' E, mortality = 61%), Shizaf (36%) and Roded (29° 35' N 34° 56' E, 58%) (Stern et al. 1986). Low mortality sites were Bitaron Wadi (30° 50' N 35° 13' E, 27%), Bitaron Dyke (30%), Katzra (18%) and Hai Bar Yotvata (26%). In each site, 3 trees with the highest and 3 trees with the lowest water status (measured by pre-dawn water potential using a Scholander pressure chamber; Scholander et al. 1965) were surveyed. These trees were chosen out of a set of 25 trees per site surveyed by Shrestha et al. (in press).

Relationship between plant species composition and Acacia mortality

In a previous survey of mortality (Ward & Rohner 1997), plant species composition and percent canopy cover under *Acacia* trees in each of 40 populations across the Negev desert were recorded. The data were used in this study to examine the relationship between plant species composition and percentage *Acacia* mortality in that population.

Association of Ochradenus baccatus with Acacia trees

To study the association of *O. baccatus* with *Acacia* trees, 297 plants were recorded in Saif, Bitaron Dyke and Roded. The size and position of the plant (under *Acacia* or in open areas between trees) were recorded. Relative water content of *O. baccatus* was measured in August 1999. We used fresh stem tips, because leaves are not always present in this stem-assimilating plant, and followed the methodology of Koide et al. (1996).

Soil quality

Soil samples were taken from a depth of 0–20 cm. To assess soil quality, the following parameters were measured:

1. pH, in a water solution.
2. Soil salinity, measured as electrical conductivity.
3. Saturation and field water-holding capacity (Veiheya & Hendrickson 1931). Saturation and field capacities were strongly positively correlated ($r = 0.93$, $F = 1358.2$; $P < 0.001$, error d.f. = 196); consequently, only saturation capacity was used in the tests.
4. Nitrogen, measured as the ammonium content in the soil extracts as advised in Binkley & Vitousek (1989). Alternative methods of extraction – anaerobic incubation, ensuring loss of nitrate through denitrification and boiling, liberating the ammonium from soil compounds, were examined. A paired *t*-test showed that these methods produce comparable results ($t = 1388$, $P = 0.18$, error d.f. = 14). Boiling for 25 minutes in 4M KCl was chosen for its simplicity and replicability. To measure the ammonium content in the resulting soil extract, the manual indophenol blue method was used, as described in Stock (1983).
5. Phosphorus, measured with the ascorbic acid method described in Kuo (1996). Alternative methods of extraction were used – in water and in 0.01M CaCl₂. Because the water extraction method provided significantly higher values ($t = -9.713$, $P < 0.001$, error d.f. = 8), it was chosen for all the samples.
6. Organic carbon, measured with the Walkley-Black method described in Nelson & Sommers (1982).

To assess the suitability of the soils for plant growth, a bio-assay was used. *Ephedra aphylla*, a plant often associated with *Acacia* trees, seeds were planted in soil collected for the soil measurements listed above. Ten seeds were planted in each soil sample in a 3.3-l pot. The number of individuals and total root and shoot dry mass were recorded after a month.

Statistical analyses

We performed paired *t*-tests for comparison of plant species diversity parameters for under trees vs. open plots. Nested ANOVA and nested ANCOVA (covariate = tree size) were used for comparisons of species effects among sites and for under:open comparisons within sites. To protect the comparison-wise error when comparing many parameters, we used MANOVA to calculate the overall probabilities of differences among groups. To test the overall effect of soil quality, we conducted a Principal Components Analysis (PCA) (Wilkinson 1992) and calculated the first principal component of all soil parameters listed above. Differences among plots/species in PC1 were then tested using nested ANCOVA.

Fuzzy set ordination

We used fuzzy set ordination to relate plant community composition to the percentage mortality of *A. raddiana* populations. Unlike other ordination techniques, fuzzy set ordination requires *a priori* selection of parameters to be examined. We defined the set of plots of high mortality by linearly scaling the mortality values for each plot between 0 and 1. These values are known as actual mortality values. We then computed the Morisita-Horn index of similarity (Magurran 1991) for plant community composition between all pairs of plots. Following Roberts (1986), we then calculated membership of plots in the set of plots similar to high mortality plots as the weighted average of each plot's similarity to every other plot (using the Morisita-Horn index), where the memberships of the other plots in the set of high mortality plots serve as the weights. These values are considered to be the apparent mortality values. We regressed the apparent mortality values on the actual mortality values. Should mortality affect plant community composition, there will be a significant correlation between apparent and actual mortality values. Because these values are not normally distributed, we tested the significance of this correlation using a randomization test (using the computer program, RESAMPLING STATS; Simon 1995) and performed 1000 runs to calculate the *P*-value.

Comparison of plant species

To calculate species differences between 'under canopy' and 'open' plots, percentage frequency and percentage cover of species were calculated for these data subsets. Their difference (= % frequency/cover for the under plots – % frequency/cover for the open plots) served as a measure of the strength of association with the under-tree relative to the open plots. These data were not statistically tested, but provide a picture of the distribution of plant species within the localities. The same procedure was used to compare plots from high and low mortality sites.

Results

Plant species composition and soil quality under trees and in the open

Paired *t*-tests (error d.f. = 53) of under tree vs. open plots chosen randomly in the neighbourhood of under-canopy plots were significant for Shannon-Wiener species diversity ($t = 3.602$, $P < 0.001$, evenness (Magurran 1991) ($t = 2.755$, $P = 0.008$, and species richness ($t = 6.0$, $P < 0.0001$) (Fig. 2). In contrast, when we compared under-canopy plots with plots in areas of high plant cover in drainage lines in the open there were no significant differences in any of these 3 parameters (range in $t = 0.15$ – 1.441 , range in $P = 0.15$ – 0.87 , error d.f. = 89).

The comparison of species among plots showed 22 species restricted to under the canopy and 15 species to the open areas. All these species occurred at low frequency and percentage cover. The comparison of under-canopy vs. open frequencies and cover values showed that the first 4 species were typical of under-canopy plots and the next 5 species were typical of randomly-selected open areas (note: first number in parentheses after species

name = percentage change in frequency and 2nd number shows change in cover in under canopy plots relative to open areas):

Lycium shawii (+ 6.1%, + 3.4%)
Asteriscus graveolens (+ 4.4%, + 6.6%)
Ochradenus baccatus (+ 3.8%, + 26.8%)
Atriplex halimus (+ 3.8%, + 10.3%)

Gymnocarpus decandrum (– 6.6%, – 11.0%)
Commicarpus verticillatus (– 5.5%, – 23.4%)
Hammada scoparia (– 4.4%, – 9.6%)
Zygophyllum dumosum (– 4.4%, – 5.3%)
Retama reatam (– 6%, – 27.0%).

A MANOVA on all soil parameters for all plots indicated a significant difference between plots under the trees and open areas (Wilks' $\lambda = 0.25$, $P < 0.001$, d.f. = 108, 906). There were significant differences in pH, saturation capacity, soil salinity and nitrogen (range in $F = 1.7$ – 14.4 , range in $P = 0.008$ – 0.04 , error d.f. = 162). For *A. raddiana* only, there was a significant difference in soil phosphorus ($F = 7.46$, $P = 0.006$, error d.f. = 306). There were no significant differences in organic carbon ($F = 0.9$, $P = 0.51$, error d.f. = 162).

A PCA was performed to create an overall measure of soil quality for each plot (Axis 1: Eigenvalue = 1.96, 39.2% of variance explained; Axis 2: Eigenvalue = 1.18, 23.5% of variance explained). The ANOVA of the under vs. open comparison of PC1 was significant ($F = 9.98$, $P = 0.001$, error d.f. = 520), indicating a higher amount of nutrients and lower pH in the under-canopy plots. Soil samples for the under-canopy plots were collected at distances of 1, 2 and 3 m from the trunk in one of the cardinal directions. Neither the distance (Wilks' $\lambda = 0.97$, $P = 0.96$, d.f. = 10, 310) nor the direction (Wilks' $\lambda = 0.87$, $P = 0.11$, d.f. = 15, 425) was significant.

In an ANOVA of bio-assay results, there were significant differences in the under-open comparison in the number of *Ephedra* seedlings ($F = 3.96$, $P = 0.04$, error d.f. = 215), with a higher number of seedlings in the

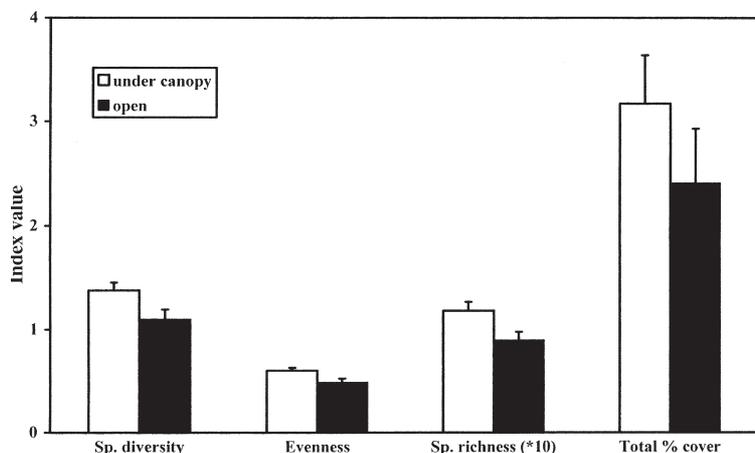


Fig. 2. Mean (\pm s.e.) species diversity, evenness, species richness and total % cover of all plant species in plots under the canopies of *A. raddiana* trees and in the open. All differences between under canopy and open, except for total % cover, are significant. Note that species richness values have been divided by 10.

Table 1. Differences in soil quality (pH, saturation capacity (%), salinity (mS), P ($\mu\text{g g}^{-1}$), N ($\mu\text{g g}^{-1}$), organic carbon (%), tree size (m^3), species richness and diversity under the tree *Acacia* species and in the adjacent open plots. * in the first column = significant differences between understorey and open plots in soil parameters. Last column indicates the significance of differences among species, all the tests having d.f. = 96, for soil parameters.

Species Plot position	<i>A. raddiana</i>		<i>A. pachyceras</i>		<i>A. tortilis</i>		Differences among species
	under	open	under	open	under	open	
pH*	7.56 ± 0.02	7.62 ± 0.03	7.43 ± 0.04	7.56 ± 0.02	7.56 ± 0.03	7.59 ± 0.03	*
Saturation capacity*	28.36 ± 0.98	29.45 ± 1.15	30.60 ± 1.36	30.52 ± 0.91	28.29 ± 0.87	26.96 ± 0.83	n.s.
Salinity*	3.13 ± 1.34	2.22 ± 0.79	2.00 ± 0.79	0.76 ± 0.09	5.15 ± 1.56	2.67 ± 0.79	n.s.
P	11.07 ± 0.93	10.20 ± 0.85	13.96 ± 2.51	19.98 ± 3.12	17.46 ± 2.21	11.85 ± 2.20	n.s.
N*	5.01 ± 0.46	4.49 ± 0.44	5.29 ± 0.44	4.46 ± 0.47	5.34 ± 0.78	4.40 ± 0.56	n.s.
Organic carbon	0.31 ± 0.03	0.20 ± 0.02	0.31 ± 0.03	0.22 ± 0.03	0.41 ± 0.05	0.41 ± 0.05	n.s.
Tree size	8.74 ± 0.86		11.45 ± 1.61		6.24 ± 0.71*		
Species diversity	1.65 ± 0.06		1.74 ± 0.09		1.42 ± 0.10*		
Species richness	14.00 ± 0.89		16.17 ± 1.46		10.76 ± 1.22		*

under-canopy soils. None of the other parameters measured was significant. In a multiple regression analysis, we found that there was a significant negative correlation between the number of *Ephedra* seedlings and soil salinity (standardized β -coefficient = -0.61 , $t = -11.64$, $P < 0.001$, error d.f. = 215) and a positive correlation with soil saturation capacity ($\beta = 0.12$, $t = 2.34$, $P = 0.02$, error d.f. = 215).

The comparison of soil parameters under the trees between a heavily grazed and ungrazed area in Hai Bar indicates a significant effect of large herbivores using the *Acacia* trees as resting spots on all soil parameters measured (range in $F = 12.57$ -6320, $P < 0.001$, error d.f. = 34). For all parameters, except pH, the mean value in the grazed area was higher than that in the ungrazed area.

Differences in effects on plant species composition and soil quality among *Acacia* species

There was a significant difference in plant species richness and species diversity in the under-canopy plots among *Acacia* species (Table 1). Although the *Acacia* species differ in size (Table 1), there was no significant effect of tree size on species richness ($F = 1.29$, $P = 0.25$, error d.f. = 86), species diversity ($F = 0.06$, $P = 0.80$, error d.f. = 86) or evenness.

The MANCOVA comparison of soil parameters, using tree size as a covariate, was significant (Wilks' $\lambda = 0.74$, $P = 0.006$, d.f. = 12, 180). There was a significant difference in soil pH among species. The effect of the covariate was also significant ($F = 5.89$, $P = 0.017$). This result indicates that there is both an effect of species and tree size on soil pH. None of the other variables or covariates was significant. All results are presented in Table 1.

A PCA for obtaining an overall measure of soil quality for each plot had an eigenvalue = 2.71 and 38.7% of variance explained along axis 1 and an eigenvalue = 1.26 and 17.9% of variance explained along axis 2. The ANCOVA (tree size = covariate) comparing species was not significant ($F = 1.25$, $P = 0.29$, error d.f. = 95).

Effects of *A. raddiana* on *O. baccatus*

O. baccatus plants growing under *A. raddiana* canopies (mean \pm s.e. canopy volume = $9.85 \pm 1.45 \text{ m}^3$) were significantly larger ($F = 21.4$, $P < 0.001$, error d.f. = 290) than those growing in open areas (mean \pm s.e. = $6.11 \pm 0.76 \text{ m}^3$). Data on total cover of *A. raddiana* trees were only available for Saif. The comparison of observed (57.5%) and expected (28.0%) values at this site indicates a non-random occurrence of *O. baccatus* beneath the *A. raddiana* canopies ($\chi^2 = 43.17$, $P = 0.001$). The comparison of relative water content of *O. baccatus* plants growing under canopies and in the open was not significant ($P = 0.27$, randomization test).

Relationships between under-canopy plant species composition and *Acacia* mortality

There were no significant correlations (error d.f. = 18) between percentage *Acacia* mortality and species diversity ($F = 0.441$, $P = 0.515$), species richness ($F = 0.829$, $P = 0.375$) and percentage cover ($F = 0.454$, $P = 0.509$).

The relationship between plant species composition under *Acacia* tree canopies and *Acacia* mortality was tested using fuzzy sets ordination (Roberts 1986). There was a significant positive correlation between the apparent and actual mortality ($r = 0.75$, $P > 0.001$; randomization test) (Fig. 3), indicating that plant community composition under trees is affected by mortality. The most frequent species were *O. baccatus* (60% of plots), *Zilla spinosa* (57.5%) and *Fagonia arabica* (55%). The species with the highest mean percentage covers for the entire data set were *L. shawii*, *O. baccatus* and *Retama reatam*.

The ANOVA comparing high and low mortality sites indicated significant differences in species diversity (mean \pm s.e. high mortality = 1.606 ± 0.096 , low mortality = 1.259 ± 0.098 , $F = 4.94$, $P = 0.03$, error d.f. = 53), but not in evenness ($F = 0.31$, $P = 0.57$, error d.f. = 53) or species richness ($F = 3.75$, $P = 0.058$, error d.f. = 53).

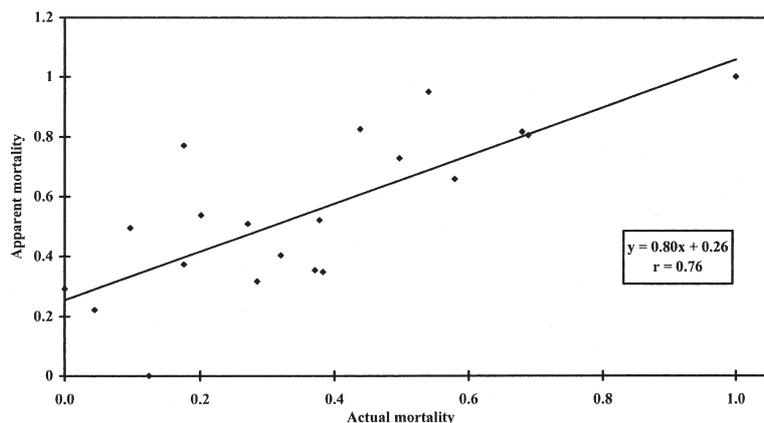


Fig. 3. Relationship between actual and apparent mortality, calculated from the similarity in plant species composition between plots using fuzzy sets ordination.

To test the effect of the water status of the *Acacia* on understorey plants, we calculated the difference between under and open species diversity for each pair of plots and regressed this value against pre-dawn water potential (a reliable index of water status). The regression was not significant ($F = 0.36$, $P = 0.55$, error d.f. = 52). Thus, the water status of an *Acacia* did not affect its ability to maintain plant diversity under the canopy.

The results of a multiple regression examining the effects of soil quality, tree water status and *Acacia* canopy volume on species diversity, evenness and species richness (Table 2) indicate strong negative effects of high salinity on species richness and species diversity. The most important factor affecting evenness was soil nitrogen, indicating that dominance increases when soil nitrogen is high.

The comparison of vegetation under the canopy of *Acacia* trees in the high and low mortality sites (corrected for the unequal number of sites) showed that 18 species were restricted to the low and 13 to the high mortality sites. The high-low frequency and total cover difference comparison showed *O. baccatus* (−7.5%, −14.4%) and *L. shawii* (−5%, −4.6%) to be species associated with low mortality *Acacia* populations and *Z. spinosa* (+6%, +1.1%) and *Reichardtia tingitana* (+8%, +1.0%) as species more common in the high mortality populations.

A PCA for obtaining an overall measure of soil quality for each plot had an eigenvalue = 2.03 and 40.6% of variance explained along axis 1 and an eigenvalue = 1.27 and 25.3% of variance explained along axis 2. The regression between *Acacia* pre-dawn water potential and the soil quality beneath the trees (expressed as PCA axis 1 values) was tested for significance. Because of heterogeneity of variance, a randomization test was used. There was a significant correlation between these parameters ($r = -0.34$, $P < 0.001$) (Fig. 4), indicating that soil quality under trees increases with increasing tree water status.

Multiple regressions, with tree water status and tree

size as independent variables, showed significant positive correlations for saturation capacity, nitrogen and salinity and significant negative correlation for soil pH (range in $F = 6.71$ – 13.06 , all $P < 0.001$, error d.f. = 159). There was a significant negative correlation between soil pH and the water status of the tree and tree size ($r^2 = 0.11$; water status: $\beta = -0.25$, $t = -3.17$, $P = 0.001$; tree size: $\beta = -0.16$, $t = -2.06$, $P = 0.001$). The larger absolute value of β (standardized) coefficient for water status indicates

Table 2. Multiple regression summary for 3 dependent variables: **a.** Species diversity; $r^2 = 0.34$, $F_{7,154} = 11.297$, $P < 0.001$; **b.** Evenness. $r^2 = 0.12$, $F_{7,154} = 2.941$, $P < 0.006$; **c.** Species richness. $r^2 = 0.41$, $F_{7,154} = 15.108$, $P < 0.001$.

Note that the greater the absolute value of the β -coefficient (standardized), the greater the influence of that variable on the dependent variable (significant variables only).

Independent Variable	β -coefficient	t	P
a. Species diversity			
pH	0.155	2.076	0.040
Saturation capacity	0.108	1.414	0.159
Phosphorus	−0.020	−0.284	0.776
Nitrogen	−0.140	−1.687	0.094
Salinity	−0.413	−5.298	< 0.001
Tree size	0.092	1.292	0.198
Water status	0.098	1.333	0.184
b. Evenness			
pH	−0.123	−1.417	0.159
Saturation capacity	0.181	2.057	0.041
Phosphorus	0.100	1.261	0.209
Nitrogen	−0.325	−3.381	0.001
Salinity	0.175	1.948	0.053
Tree size	0.059	0.711	0.478
Water status	0.225	2.657	0.009
c. Species richness			
pH	0.013	0.190	0.850
Saturation capacity	0.216	2.992	0.003
Phosphorus	0.059	0.908	0.365
Nitrogen	−0.216	−2.747	0.007
Salinity	−0.355	−4.813	< 0.001
Tree size	0.150	2.220	0.028
Water status	0.340	4.894	< 0.001

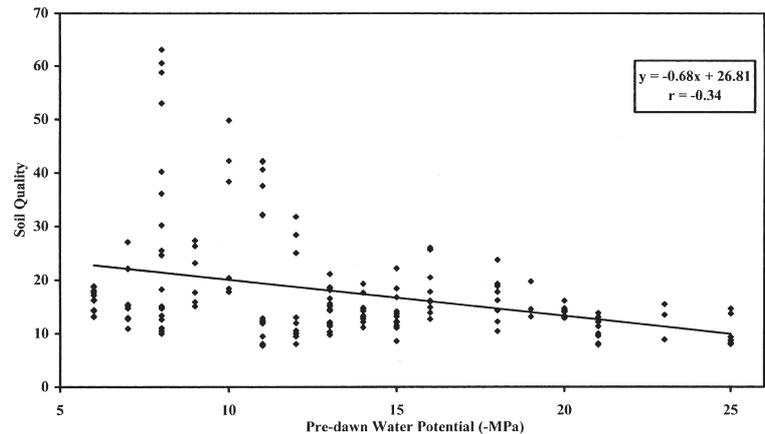


Fig. 4. Relationship between 'soil quality' beneath *A. raddiana* (expressed as coordinate values along PCA axis 1 calculated over all soil parameters) and pre-dawn water potentials (measured in winter (Jan-Feb) 1999).

that it has a greater effect on soil pH than tree size. There was a significant positive correlation between water status and tree size and nitrogen ($r^2 = 0.14$; water status: $\beta = 0.21$, $t = 2.79$, $P = 0.005$; tree size: $\beta = 0.26$, $t = 3.43$, $P < 0.001$) and salinity ($r^2 = 0.11$; water status: $\beta = 0.17$, $t = 2.22$, $P = 0.03$; tree size: $\beta = 0.24$, $t = 3.08$, $P = 0.02$). There was a significant positive correlation between soil saturation capacity and water status but not tree size ($r^2 = 0.08$; water status: $\beta = 0.26$, $t = 3.28$, $P = 0.001$; tree size: $\beta = 0.06$, $t = 0.73$, $P = 0.46$).

Discussion

Differences in plant species composition under Acacia trees and in the open areas between trees

Our results, comparing the under and randomly-selected open plots in terms of species richness and species diversity, show a positive effect of *Acacia* trees on these parameters. However, places of comparable diversity to that under the *Acacia* trees may be found within the wadis, especially in the channels, which have higher levels of underground water. We were able to identify groups of species with higher occurrence in either under-canopy or open plots (cf. Belsky et al. 1989). All species found to be restricted to a single type of plot were very rare and their presence might be a matter of chance. *Ochradenus baccatus* and *Lycium shawii* are species that are commonly associated with *Acacia* trees, where they can achieve very high cover values (especially in low mortality sites). *O. baccatus* grew better under *Acacia* canopies, which may be facilitated by its alternative climbing habit (cf. Zahran & Willis 1992), but it did not contain more water there. This result suggests that it is increased soil quality and not increased soil moisture (induced by hydraulic lift and/or increased shade) that enhances the growth of *O. baccatus* under *Acacia* canopies.

Differences in plant species composition between A. raddiana with different water status

The under-open difference in species diversity and richness was not greater in trees with high water status. This result, together with the result for the comparison of high and low mortality sites, contradicted our expectation that *Acacia* trees in better condition will support higher species diversity beneath their canopies. This might be explained by the balance between the positive effect of the *Acacia* trees (higher soil saturation capacity, ensuring greater soil water retention, and a greater amount of soil nitrogen) and the negative effects of enhanced under-canopy soil salinity. The importance of negative effects of salinity on species diversity has been shown by Evenari et al. (1982). Their results were supported by our bio-assay data, which showed a significant negative correlation between the number of *Ephedra* seedlings and soil salinity. The significant under-open difference in the number of *Ephedra* seedlings and the non-significant difference for individual biomass is congruent with the findings of Barnes & Archer (1996), who recorded the importance of environmental modification by nurse plants for seedling establishment, but not for the growth of plants. However, contrary to our findings, a number of studies record higher productivity of plants grown in soils collected under tree canopies compared to those from the open areas (e.g. Tiedemann & Klemmedson 1973; Callaway et al. 1991).

Another explanation for the higher species diversity in high mortality populations and under more water-stressed trees might be competition for water between the *Acacia* tree and understorey vegetation, which becomes more important in larger trees with higher water status. This effect, and the negative effect of shading, was demonstrated by Franco & Nobel (1989) in the relationship between the nurse plant *Hilaria rigida* and the dependent *Ferocactus acanthodes*.

The results of the multiple regression of species diversity indices against soil and tree parameters showed nitrogen concentration to be the second-most important negative factor influencing species diversity. The concentration of soil nitrogen was positively correlated with salinity, which might be one explanation for the negative correlation between nitrogen and species diversity in our data set (salinity was higher under the trees). On the other hand, following Grime (1979), one might expect an increase in the establishment of one or few dominant species in the environment with increasing amount of nitrogen, which leads to a decline in species diversity.

Influence of Acacia trees on the soil quality under their canopies

The overall PCA of soil parameters showed that there were higher amounts of nutrients in soils under the canopy of the *Acacia* trees when compared to the open areas among the trees. Interestingly, there were significant differences in soil quality between *Acacia* understorey and high plant cover areas in wadi channels, yet there were no significant differences in plant parameters in this comparison. This result indicates that while moist areas in wadi channels may support as much plant diversity as under the trees, the *Acacia* trees have a unique role in improving soil quality that is independent of soil moisture effects. The comparison of each soil parameter showed decreased pH values under the canopies, with a mean decrease of 0.03 units (max. difference of 0.13 units for *A. pachyceras*). This result is consistent with that of Nyberg & Högberg (1995) who recorded a decrease on pH of 0.21 units under the canopy of *A. tortilis*. The increased amount of soil nitrogen (mean difference of 6.3 mg g⁻¹) under trees in our study lends support to the influence of legumes on this important nutrient, as recorded in Barnes & Archer (1996). The ability to fix nitrogen in *A. tortilis* was recorded by Assefa & Kleiner (1998) and for *A. raddiana* by Ndoye et al. (1995). Nitrogen concentrations under *Acacia* trees in our study correspond with those found by Belsky et al. (1993) in low-rainfall savannas in Africa under the canopies of *A. tortilis* and *Adansonia digitata*. The increased water-holding capacity (mean difference of 1.18%) of under-canopy soils in our study is in agreement with the findings of Paulsen (1953). The increased salinity (all 3 *Acacia* species) and levels of phosphorus (*A. raddiana* only) in under-canopy soils are in agreement with the findings of Turner et al. (1966) in studies of saguaro cactus (*Carnegiea gigantea*) and Franco-Pizana et al. (1995) in *Prosopis glandulosa*. The lower salinity in the open areas may be an effect of greater flushing of

salts in the open areas of the wadis during the winter floods. Under *Acacia* trees, the soil stability afforded by the trees' roots may reduce salt flushing. The existence of a gradient of soil nutrients from the base of trunk to the edge of the canopy, as reported by Bernhard-Reversat (1982) and Franco-Pizana et al. (1995), was not found in our study.

The comparison between the size of trees, their pre-dawn water potentials and soil parameters showed different soil quality (higher nitrogen content and salinity and lower pH) beneath the canopy of larger trees and trees with higher water status. This is in agreement with Alstad & Vetaas (1994), who found higher amounts of nitrogen and organic carbon and lower pH under larger *A. tortilis* trees in one of their two study sites. In our study, greater water-holding capacity was found under trees with higher water status only. These results indicate that there is a higher level of soil modification by larger trees and trees with higher water status.

The comparison of a heavily grazed and an ungrazed area indicated important effects of large herbivores (see also Rohner & Ward 1999), which use the *Acacia* trees as resting areas, on all soil parameters measured. Faecal deposition is the mechanism of increase in nutrient content and salinity and decrease of pH in soils in the heavily-grazed area. Thus, in addition to the significant negative effects of these herbivores on the survival, growth and defences and their positive effects on dispersal and germination of *Acacia* trees (Rohner & Ward 1997, 1999), there is also an important effect of faecal deposition. This result is consistent with those of Dean et al. (1999), who stressed the importance of nutrient input to the under-canopy soils of *A. erioloba* from the faeces of birds and mammals in the Kalahari desert.

Another possible mechanism of increased soil nutrient build-up under tree canopies includes nutrient transport from soils by the tree root system, and their release to the under-canopy environment through the litter (Belsky et al. 1989). The importance of nitrogen input due to nitrogen-fixing root symbionts is unlikely because studies comparing nitrogen amounts in soils beneath the canopy of trees with and without N-fixing bacteria did not demonstrate differences between them (Belsky et al. 1989; Belsky 1994). The long-term accumulation of nutrients at the trunk base through stem flow and bark sloughing is another explanation for nutrient enrichment (Kellman 1979; Belsky et al. 1993).

Conclusions

Our study showed that plant species diversity and soil nutrient content beneath the tree canopies is higher than in the surrounding areas of their ecosystems. Soil nutrient content is also higher under larger trees and trees with higher water status than under smaller trees and trees with low water status, while there was no difference for plant species diversity. This finding pointed to the negative influences of higher salinity under the *Acacia* trees on species diversity, which may diminish the positive effects of higher nutrient content in the under-canopy soils. In agreement with Dean et al. (1999), we confirmed the importance of *Acacia* trees for maintaining spatial heterogeneity by creating nutrient-enriched patches in the nutrient-poor desert environment, leading to higher species diversity in the region. The results of this study support those of Ward & Rohner (1997) and Rohner & Ward (1999) showing that *Acacia* trees are keystone species in Negev desert ecosystems. Furthermore, consistent with these studies, we have shown that anthropogenic disturbance of these ecosystems has serious negative effects on the populations of certain plant species that grow in close association with the trees, and on soil quality in the ecosystems as a whole.

Acknowledgements. The authors thank Iris Schmidt and Juma Jinoon for assistance in the field. ZM was a MASHAV fellow of the Israeli Ministry of Foreign Affairs during the period of this study. Financial assistance was received from Keren Keyemet L'Israel (to DW), the Israeli Ministry of Science, the German Ministry of Environmental Affairs DISUM grant No. 00046A (to DW) and the Ramon Science Center. The Ramon Science Center is funded by the Israeli Ministry of Science and the Local Council of Mizpe Ramon. This is contribution No. 136 of the Ramon Science Center and no. 353 of the Mitrani Department for Desert Ecology.

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Received 15 November 1999;
 Revision received 6 September 2000;
 Final revision received 3 December 2001;
 Accepted 24 January 2002.
 Coordinating Editor: J. Franklin.