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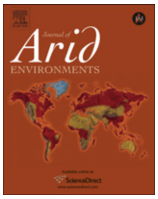

Do *Acacia* and *Tamarix* trees compete for water in the Negev desert?

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ABSTRACT

We investigated the spatial distribution of the three *Acacia* and two *Tamarix* tree species and related the spatial distribution of these two genera to their ^{18}O value, i.e. their ^{18}O/^{16}O isotopic ratio in the Negev desert, Israel. At the regional spatial scale, there was a significant difference in the overall distributions of these two genera, although there was considerable overlap. At the 1 km^2 scale, there was no deviation from homogeneity. At a finer scale, no deviation from a random distribution was found in three ephemeral rivers between the two largest trees in these two genera, *Acacia raddiana* and *Tamarix nilotica*. We found that *Tamarix* used deep water from aquifers while *Acacia* trees used an alternate source, most likely surface water. Spatial segregation of *Tamarix* and *Acacia* occurs at the large spatial scale but not at the small scale, perhaps because of the high tolerance of *Tamarix* species for salinity and the low tolerance of *Acacia* species for saline conditions. It appears that the trees are not spatially segregated on the small scale because they use different water sources.

1. Introduction

Acacia and *Tamarix* (saltcedar or tamarisk) are the only two tree genera in the Negev desert in Israel. Both genera are restricted to ephemeral river beds (known as wadis, a term from the Arabic; Ward et al., 1993) and both are important sources of biodiversity for many plants and animals (Münzbergova and Ward, 2002; Ward and Rohner, 1997). The populations of *Acacia* are declining throughout the Negev (Rohner and Ward, 1999; Ward and Rohner, 1997). In particular, roads that alter floodwater movement affect *Acacia* survival, implying that these taxa use surface water and have more shallow root systems than was previously assumed (Ward and Rohner, 1997). Furthermore, it has been shown that, on average, five additional species of plants decline in abundance as a result of the decrease in *Acacia* abundance, emphasizing the “keystone” role that *Acacia* plays in these ecosystems (Münzbergova and Ward, 2002).

In contrast, there is no evidence that *Tamarix* is in decline in the Negev or other deserts, and the genus is considered an aggressively invasive woody plant in several areas of the world. For example, *Tamarix* spread rapidly in the western USA, from an estimated 4000 ha in 1920 to over 500 000 ha in the mid-1960s, becoming established in floodplains, riparian areas, wetlands and lake margins (Stohlgren et al., 1998). This rapid increase was associated with the regulation of streamflows following construction of large dams and water diversion projects in the western USA (Everitt, 1998). *Tamarix* rapidly establishes on moist, open substrates in the absence of interspecific competitors, and can quickly become dominant, preventing establishment of other species (Sher et al., 2002). In North American ecosystems, the same conditions facilitate establishment of native dominants such as cottonwoods (*Populus* spp.) and willows (*Salix* spp.), but *Tamarix* is only likely to become invasive in the absence of these other species, due to slower above-ground growth of its seedlings (Sher and Marshall, 2003; Sher et al., 2000). *Tamarix* infestations are also associated with declining water tables (Weeks et al., 1987), channelization

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though increased sedimentation (Blackburn et al., 1982), increased soil salinity (Smith et al., 1998), and wildfires (Busch and Smith, 1995). Such conditions favor *Tamarix* over native trees (Shafroth et al., 2002). While regional *Tamarix* distributions completely overlap with several native tree species, it is unusual to observe them as co-dominants in the same stand (Shafroth et al., 2002).

Tamarix is being studied extensively in North America, but its ecology is less well understood in other regions, such as in Israel. While *Tamarix rammosissima* and *Tamarix chinensis* (and their hybrids) are the primary species in North America, *Tamarix aphylla* is a growing problem in Israel, overlapping in range with the native *Tamarix* species, *Tamarix nilotica* (Waisel, 1960). *T. aphylla* is also a noxious riparian weed in arid central Australia where it has negative impacts comparable to those caused by *Tamarix* in the southwestern USA (Griffin et al., 1989).

Tamarix in Israel appear to overlap in habitat type with *Acacia*. However, there has been little research to test the potential interaction or competition between *Tamarix* and *Acacia*. Understanding patterns of distribution in these genera relative to one another can provide information regarding subtle differences in habitat preference and whether *Tamarix* may affect the establishment and survival of declining *Acacia* species. Field observations suggest that *Tamarix* and *Acacia* species may not be randomly distributed with respect to one another. Using observational data, we tested the hypothesis that species' ranges are completely overlapping, and whether at smaller scales they may be partitioning the habitat.

Both *Tamarix* and *Acacia* can occur in very arid habitats (as low as <25 mm precipitation/year), and so are presumed to develop deep tap roots to use groundwater (i.e. they are phreatophytic) (Halevy and Orshan, 1972; Turner, 1974). The presence of and ability to exploit a deep, permanent water source, such as groundwater, makes it possible for plants to survive for long periods without rain (Shrestha et al., 2003; Ward and Rohner, 1997), even when keeping stomata open and extending growth (Gardner, 1983). *Tamarix* has been shown to be facultatively phreatophytic in the United States, utilizing both saturated and unsaturated zones (Smith et al., 1998). Halevy and Orshan (1972) considered the genus *Acacia* to be obligately phreatophytic based on distribution patterns. However, rooting depths and water use patterns of *Tamarix* and *Acacia* have not been experimentally investigated in the Middle East and therefore it cannot be assumed that they depend on groundwater. Alternatively, these trees may be simply using the periodic rains and floodwater that infrequently occur in large pulses (Ward and Rohner, 1997).

The water source (surface or groundwater) on which these trees depend is potentially affected by several environmental factors. These factors include competition, proximity to a water pumping station (indicating that groundwater is close to the surface), and time of year (i.e. degree of drought). We sought to identify patterns of water use by the two largest trees in these genera, *Acacia raddiana* and *T. nilotica*, to determine the degree to which these species may be competing for water, and to test the hypothesis that both species use groundwater. Water sources used by a tree can be identified using water hydrogen and oxygen isotope analysis (Dawson and Ehleringer, 1991). Groundwater has a distinct isotope ratio that necessarily differs from that of surface water sources, because the latter is subject to evaporation, which changes the isotope ratio (Yakir and Sternberg, 2000). Twigs of trees contain water in the xylem whose isotope ratio can be analyzed to identify the tree's water source.

If *Acacia* and *Tamarix* do in fact overlap in general range, analysis of the distribution of individuals at finer scales can give us some indication of the probability that these two genera interact or partition the environment. For those species that are found in close proximity, water isotope ratio analysis can shed light on potential competition for this highly limiting resource, and elucidate whether rooting zones are likely to be similar or not.

2. Methods

2.1. Spatial distributions

We investigated distributions of *Tamarix* and *Acacia* on a total of three different general spatial scales: regional (10 general areas representing broad geographic ranges within Israel), local (461 specific locations that are watersheds or municipal areas), and individual (342 trees within three wadis). Regional and local analysis considered distributions of the two genera as well as other species, while investigation of the distribution of individuals focused on the two most common species, *A. raddiana* Savi and *T. nilotica* (Ehrenb.) Bunge. Our small-scale analysis also allowed for investigations of distributions at various scales at the individual level (i.e. trees within wadis).

To investigate regional and local distributions of all *Tamarix* and *Acacia* species in Israel, we used ROTEM accounts, which are data kept by the National Herbarium in Jerusalem, Israel. In addition to the latitudinal and longitudinal data, ROTEM accounts list general areas and specific locations. General areas were categories in ROTEM accounts that included regions such as "Upper Jordan Valley" and "Southern Negev". Specific locations were typically names of ephemeral rivers or wadis (such as "Nahal Shezaf"; "nahal" = Hebrew for ephemeral river) or sub-regions (such as "Northern Beer Sheva"). ROTEM accounts record presence and absence of plant species by location; absence indicates that the entire specific location has been surveyed sufficiently to know with great confidence that a species is absent within this area. For the accounts we obtained from 1973 through 1998, we obtained 340 records of the distribution of *Tamarix* and 535 records of *Acacia*. These included 461 specific locations within 10 general areas where five species of *Acacia* and *Tamarix* (*A. tortilis* Hayne, *A. raddiana* Savi, *Acacia gerrardii* Benth., *T. nilotica* (Ehrenb.) Bunge, *T. aphylla* (L.) Karsten) were recorded. We used these records to investigate the distribution of the genera *Acacia* and *Tamarix* genera within the general areas, the distribution among the five species within the general areas, and the distribution of the two genera within the specific locations. We also examined the meso-scale spatial relationships of specific locations at the 1 km^2 scale. The hypothesis of random distribution was tested using χ^2 analysis of presence versus absence of each species or genera for each area surveyed. We also examined the meso-scale spatial relationships at the 1 km^2 scale.

At the individual scale, in three wadis with both *A. raddiana* and *T. nilotica* present, we investigated the hypothesis that trees of the two species are distributed randomly with respect to each other within wadis. These two species were chosen because they are the most widespread, most likely to co-occur, the largest trees within their genera, and more likely to compete for water resources.

In March 2000, we mapped the location of 27 *A. raddiana* and 105 *T. nilotica* trees within a section of Nahal Tsichor (30°15′N, 35°00′E) approximately 500 m in length. Similarly, in January 2001, we measured 50 *A. raddiana* and 51 *T. nilotica* trees within a 700 m section of Nahal Shizaf (30°42′N, 35°15′E) and 59 *A. raddiana* and 50 *T. nilotica* trees within a 800 m section of Nahal Karkeshet (30°38′N, 35°10′E).

Tamarix individuals may exist as a clump of ramets that originate from a single tap root system. Thus, each grouping of stems was considered a genet and was counted as a single tree. *Tamarix* will produce roots from buried or submerged stems or stem fragments; thus the presence of roots originating from a stem could not be used to identify individuals (Merkel and Hopkins, 1957). No vegetative reproduction occurs in *Acacia* so each stem could be considered to be a separate individual (Ward and Rohner, 1997).

Tree distributions were analyzed using a derivative of the scale-dependent ‘ring statistic’ (Wiegand et al., 1999; Wiegand et al., 2000). The ring statistic $O_{AB}(r)$ is a second order statistic giving the frequency/probability of finding a plant of type B (e.g. *T. nilotica*) at distance r from a plant of type A (e.g. *A. raddiana*). Thus, the ring statistic is a scale-dependent measure. Measurement of $O_{AB}(r)$ involves the placement of rings of radius $r \pm \delta r/2$ around individuals of type A and counting the number of individuals of type B intersected by the ring (in the sense of annulus, not circle). In this way, from the position of each individual of type A, the density of individuals of type B was determined for a range of discrete distances r from the location of that individual. Finally, the density profiles observed from all individuals of type A were averaged, resulting in the statistic $O_{AB}(r)$. For ease of implementation we did not use smooth rings, but overlaid the study area with a grid of cells and used rings consisting of cells whose center is located at a distance of $r \pm \delta r/2$ from the center of the cell containing an individual of type A. Thus, we chose $r = 0$ m, 10 m, 20 m, 30 m up to 150 m ($\delta r = 10$ m). More detailed descriptions of the ring statistic are given in Wiegand et al. (2000) and Wiegand and Moloney (2004). The latter includes a detailed account of the edge correction applied. In the present study, this is of specific importance because of the elongated shape of the wadis.

We tested for significant deviation from randomness using constrained randomization, meaning that the location of individuals of type A were fixed while the locations of individuals of type B were randomized within the wadi. This tests the degree of spatial association of plants of type B with plants of type A, given the underlying pattern of plants of type A. Based on the highest and lowest values of $O_{AB}(r)$ of 99 randomized patterns, following the recommendations of Wiegand and Moloney (2004), we created confidence envelopes for spatial pattern. Any crossing of the lower or upper limit of the interval was considered a significant deviation from randomness. Analyses were performed for both A = *A. raddiana*, B = *T. nilotica* and A = *T. nilotica* and B = *A. raddiana*. In an additional analysis, we applied random labeling, meaning that the number of trees per species and the locations of all trees were fixed but the species identity across trees was randomized.

2.2. Oxygen isotopes

We collected twigs from *A. raddiana* and *T. nilotica* trees from 14 water pumping station locations where groundwater samples could be taken and compared with the water found in the xylem of the trees in April (spring) 1999 and again in October (late summer) 1999. During April, the surface water was available to the trees in the form of rain and floodwater, whereas October was the end of the summer drought season. Different isotope signatures were obtained from shallow surface water and deep groundwater. In April, one twig was collected from the *A. raddiana* and *T. nilotica* trees closest to each of the 14 pumping stations, from which water was also collected and analyzed for ^{18}O. In October, an additional two replicates for each species were taken from six of the locations. Twigs were selected within a range of approximately 1.5–2.5 cm diameter. Immediately after cutting a section approximately 5 cm long, each twig was placed in test tubes with airtight stoppers, which were then reinforced with parafilm. These tubes were then sealed in plastic bags and placed in a cooler while in the field to prevent water loss until they could be transferred to a freezer before analysis. Distance to pumping station and nearest neighbor (NND) was also recorded for each sample.

Water was distilled from the previously unopened sample tubes under vacuum and the δ^{18}O value of 0.5 ml aliquots was determined by equilibrium with CO_2 (Epstein and Mayeda, 1953). Ratio of ^{18}O to ^{16}O was measured on CO_2 in a Finnigan MAT250 mass spectrometer and are expressed in the δ notation (in ‰):

$$\delta x = [R(\text{sample}) - R(\text{standard})]/R(\text{standard}) * 1000$$

where x is ^{18}O, R is ^{18}O/^{16}O, and the standard is Vienna Standard Mean Ocean Water (also known as V-SMOW). Precision of the isotopic analysis was better than 0.3‰ for oxygen isotopes (De Niro and Epstein, 1979). The δ^{18}O value of this water depends on the δ^{18}O of the water taken up by the plant and on subsequent enrichment imposed by evapotranspiration (Ehleringer and Dawson, 1992).

Quantitative analysis of the water samples involved the comparison between tree xylem water and associated pumping station water samples. Similarity within an error range suggests the use of groundwater by that tree (Phillips and Gregg, 2001). Values that fall above this 1:1 line indicate a proportionally greater amount of ^{18}O in the tree’s water. Since ^{16}O is disproportionately lost in evaporation, such values could indicate either an independent water source or groundwater that has been subject to evaporation at the surface, directly from the tree (in hot weather), or from the sample tube (experimenter error). Values that fall below this 1:1 line indicate an entirely different water source, indicating either rain or floodwater as a source.

3. Results

3.1. Spatial distributions

At the regional scale, *Tamarix* and *Acacia* were found at a significant number of locations in the same general areas, except for Eilat (EL) where no observations of *Tamarix* were recorded. A χ^2 test of presence versus absence of *Acacia* and *Tamarix* according to region found no significant differences between the species in their distributions when the Eilat (EL) site was excluded, suggesting that distributions of the two genera were overlapping and generally random at this largest scale. Within general areas, *Acacia* was typically present in more locations than *Tamarix* ($\chi^2 = 116.15$, $p < 0.001$) although, in the northern Negev (NZ), there were more *Tamarix* locations than *Acacia* locations. Among the *Acacia* species, *A. raddiana* was the species most often observed, and among *Tamarix*, *T. nilotica* was the most common (Appendix 1, electronic version only). Where both genera occurred, relative proportions to each other remained generally constant across sites, with only the exception of *T. nilotica* being more abundant than *A. raddiana* in the northern Negev.

At the local scale, *Acacia* and *Tamarix* were not randomly distributed ($\chi^2 = 31.45$, $p < 0.001$, $df = 1$). *Acacia* and *Tamarix* species were found at 271 and 190 specific locations, respectively, but only 48 of 461 locations were common to both *Acacia* and *Tamarix* species. *A. raddiana* and *T. nilotica* occurred together most frequently (28 times), *A. tortilis* and *T. nilotica* occurred together on 11 occasions, 5 sites were occupied by *A. raddiana* and *T. aphylla*, and 4 sites were jointly occupied by *A. tortilis* and *T. aphylla*. Two sites were occupied by three species, *A. raddiana*, *T. nilotica* and *T. aphylla*. No joint occurrences of *A. gerrardii* and any *Tamarix* species occurred. A test of homogeneity between *Acacia* and *Tamarix* species was not significant ($\chi^2 = 0.897$, $p = 0.343$).

For the spatial analysis of specific *T. nilotica* and *A. raddiana* individuals in three wadis, *A. raddiana* trees were found to be randomly distributed with respect to *T. nilotica* trees on all scales considered (Fig. 1) and vice versa (i.e. *T. nilotica* with respect to *A. raddiana*; results not shown). Minor crossings of the confidence

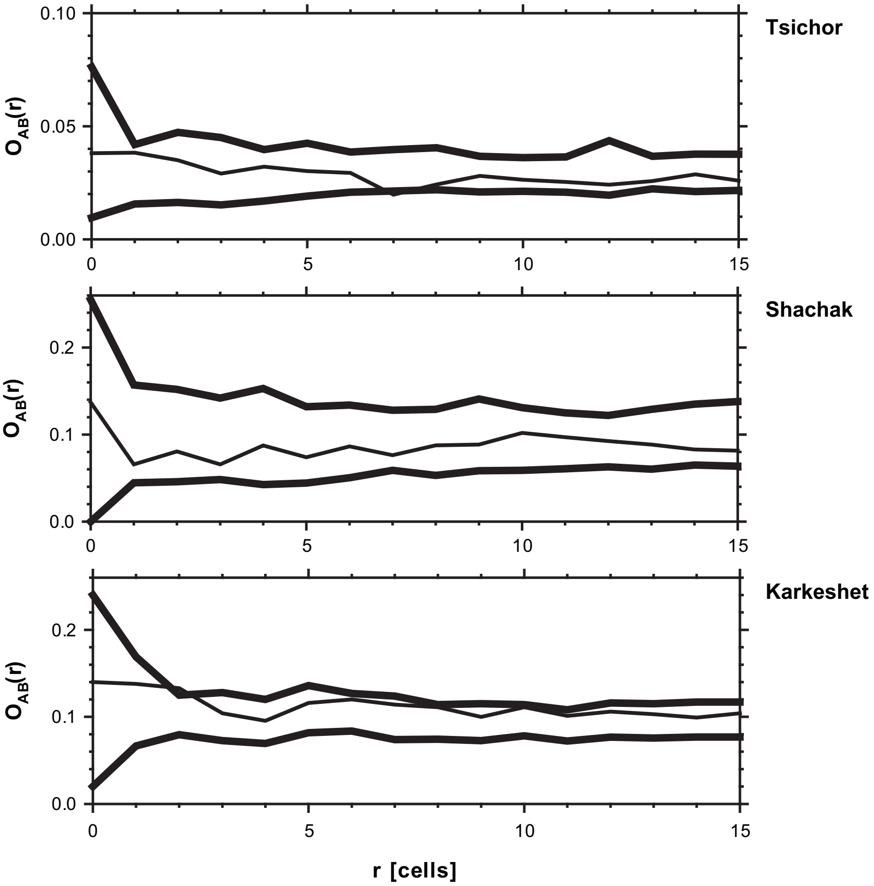

Fig. 1. Second order spatial analysis of the spatial distribution of *Acacia* trees relative to the spatial distribution of *Tamarix* trees in Nahal Tsichor, Nahal Shachak, and Nahal Karkeshet (from top to bottom). Light line: observed pattern, heavy lines: upper and lower confidence limits estimated with 99 randomizations of the *Acacia* locations. Here, $O_{AB}(r)$ measures the probability of finding an *Acacia* at distance r from a *Tamarix* tree. Distance is measured in units of cells 10 m in length.

limits would most likely disappear under larger sample sizes. Randomness was also found when considering non-homogeneities in the spatial tree distributions (=random labelling).

3.2. Oxygen isotopes

Oxygen isotope signatures of *T. nilotica* were consistently close to those of their associated aquifer water (i.e. close to the 1:1 line of identical ratios), whereas *A. raddiana* had isotope signatures that were both greater and less than those of the aquifers (Fig. 2). Seasonal comparisons for *A. raddiana* suggest that at most locations, spring and summer values do not differ. Resampling of specific individuals revealed that the only dramatic change was an *A. raddiana* individual that had been well above the 1:1 line in spring (showing floodwater use, due to greater evaporation) indicating greater use of groundwater (i.e. moved closer to the 1:1 line) in summer (Fig. 3).

T. nilotica had generally unchanged isotope values in summer (i.e. still using groundwater), but some trees' isotope values became less negative. General trends were in this direction, indicating evaporative loss of ^{16}O in the water (Fig. 4). This may indicate more mixed use of surface and groundwater, but this is unlikely because there is little to no surface water present at that time. Alternatively, this loss could have occurred in the twigs before sampling, due to high temperatures that would cause loss through the bark, or after sampling as experimental error in the field or laboratory (three of five are virtually identical). No significant patterns (range in $p = 0.26$–0.98) were found between nearest neighbor distance and isotope value (range in $r^2 = 8 \times 10^{-5}$ to 0.28), or between distance to pumping station and isotope value (range in $r^2 = 8 \times 10^{-3}$ to 0.35) in spring and summer.

4. Discussion

Our results suggest that although there is a clear potential for competition between *Tamarix* and *Acacia* due to overlapping ranges in Israel, they are unlikely to do so as a result of differing

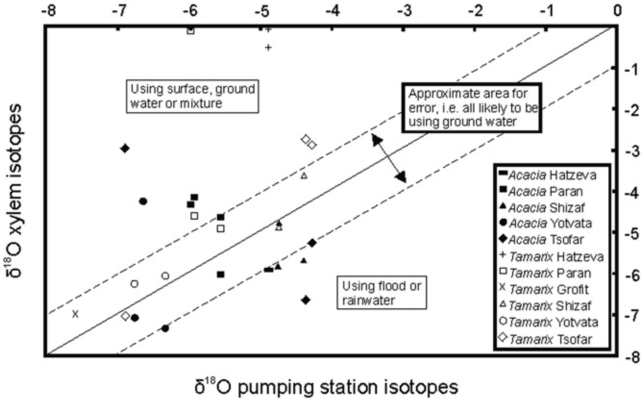

Fig. 2. Spring $\delta^{18}O$ values isotope values for *A. raddiana* and *T. nilotica* growing in the Arava against local pumping station $\delta^{18}O$ isotope ratios. Values within the error range around the 1:1 line indicate strong similarity of isotope ratios and therefore the probability that the trees are using pumping station water. Values above the 1:1 line indicate use of surface, groundwater or a mixture of the two. Values below the 1:1 line indicate use of flood or rainwater.

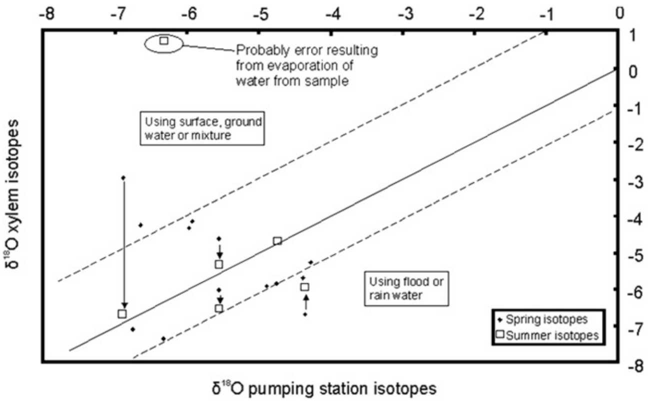

Fig. 3. Comparison of spring and summer xylem δ^{18}O isotope values (for re-sampled *A. raddiana* trees). Arrows indicate direction that values changed from spring, when there is ample surface water to summer values, when there is no surface water. Note that in some cases, filled diamonds do not have a corresponding open square because of problems with evaporation of the samples.

distributions within these ranges and the use of different water sources. Although partitioning of wadis could indicate competitive exclusion during establishment (as witnessed in the USA between *Tamarix* and other co-occurring woody species), it appears more likely that differences between locations in soil properties or timing of resource availability is responsible. If these two genera (and species within the genera) have even slightly different preferences for safe sites for germination or growth, we might expect them to be non-randomly distributed within their general range. Where these conditions overlap, we see limited co-occurrence, most commonly in *T. nilotica* and *A. raddiana.* Even so, these species are unlikely to be competing for water because their isotope signatures are not the same, suggesting that the *Tamarix* is more likely to use groundwater than the *Acacia*. Thus, in this harsh environment, these two tree genera have little interaction.

Salinity tolerance is likely to be one of the differences in environmental preferences driving the infrequently overlapping local distributions. We did not measure salinity tolerance in this study. However, other studies have shown that *Tamarix* species are more tolerant of saline conditions (Duncan, 1994), while *Acacia* species are very sensitive to high salinity. Salinity interferes with nitrogen acquisition and utilization, particularly if *Acacia* species fix nitrogen (Zahran, 2004). Saline conditions influence the various steps of nitrogen metabolism, such as uptake, reduction and protein synthesis (Frechill et al., 2001). Salinity further affects nitrate uptake at two levels: by direct competition of chloride with nitrate and at the membrane level and/or the membrane proteins by changing plasmalemma integrity (Cramer et al., 1985).

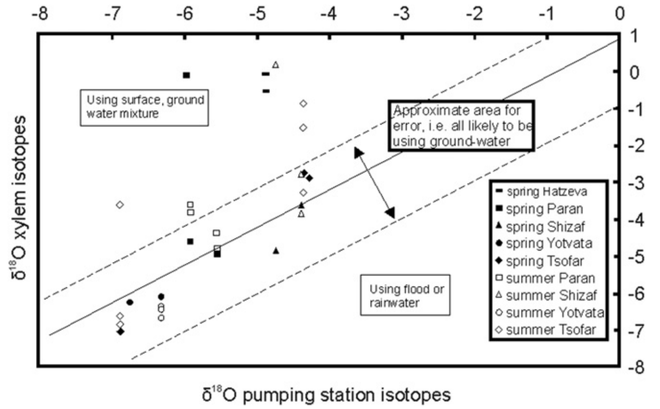

Fig. 4. Spring (filled) and summer (open) xylem δ^{18}O isotope values for *T. nilotica* in the Arava. Values above the 1:1 line indicate use of surface, groundwater or a mixture of the two. Values below the 1:1 line indicate use of flood or rainwater. Spring and summer values generally remain the same; i.e. clustered around the 1:1 line, indicating groundwater use. When different, summer values were greater than spring values, indicating evaporative loss, most likely after uptake from the groundwater (e.g. transpiration or experimenter error), because no surface water is present in summer.

Even slight increases in soil salinity may be enough to exclude *Acacia* and favor *Tamarix*. However, additional environmental factors must play a role in those wadis where *Acacia* is dominant, including the Eilat region, where many *Acacia* but no *Tamarix* were recorded. Although *Tamarix* is known to have wide environmental tolerances, *T. rammosissima* have been found to do poorly in persistently shallow water-tables (≤10 cm) (Sher and Marshall, 2003), whereas this study also suggests that these conditions may favor *Acacia. Tamarix* is also likely to be shade-intolerant. Studies in the USA have shown *Tamarix* seedlings to be poor competitors against other woody species (Sher et al., 2000; Sher et al., 2002), although it appears unlikely from this study that *Tamarix* would compete for water with *Acacia* species. When water is not limiting, *Tamarix* could be overgrown by faster growing species.

This is not the first demonstration that streamside trees do not necessarily access stream water (Dawson and Ehleringer, 1991). However, to our knowledge, this is the first use of water isotope analysis to indicate evidence of resource partitioning between species with overlapping ranges. These results support previous suggestions that *A. raddiana* is restricted to wadis with shallow water-tables due to shallow root systems, and that road-building can affect *Acacia* survival by diverting surface water on which it depends (Ward and Rohner, 1997).

Tamarix appears to be more dependent on groundwater than *Acacia*, which would explain why *Tamarix* species appear to be less affected by human alterations of floodwater movements (DW, pers. obs.), although it may therefore be sensitive to changes in the water table. Nonetheless, isotope analysis shows that competition for water does not exist because even when the two species co-occur, they are likely to access different soil depths, with *Acacia* species primarily using surface water during the winter (from floods) and *Tamarix* species using groundwater from aquifers throughout the year. Thus, in Israel, *Tamarix* is unlikely to be a threat to the increasingly rare *Acacia*, even where the potentially invasive species may be flourishing.

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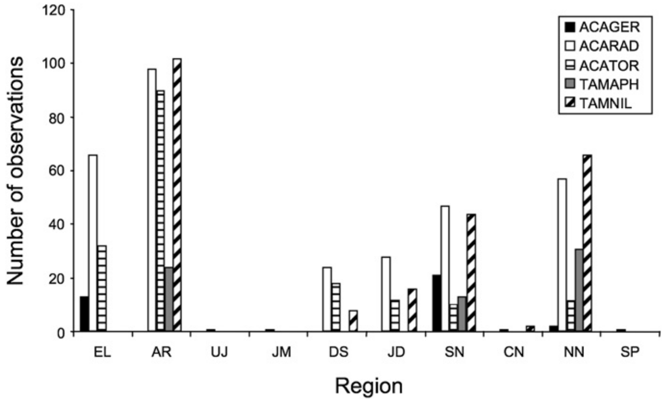
Appendix 1

Regional distribution of *Acacia* and *Tamarix* species. EL = Eilat, AR = Arava (=Syrian-African Rift Valley), UJ = Upper Jordan Valley, JM = Judean Mountains, DS = Dead Sea, JD = Judean Desert, SN = Southern Negev, CN = Central Negev, NN = Northern Negev, SP = Samarian Plains. The species we recorded were: ACAGER = *A. gerrardii*, ACARAD = *A. raddiana*, ACATOR = *A. tortilis*, TAMAPH = *T. aphylla*, TAMNIL = *T. nilotica*.



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