How can ecosystem engineer plants boost productivity in east Mediterranean drylands

Elena Constantinou[1], Dimitrios Sarris[1,2,3]* , Magda Psichoudaki[4], Javier Cabello[5,6] and Ioannis N. Vogiatzakis[1]

Abstract

Background Water availability is the key limiting factor for plant productivity in drylands covering ca. 40% of Earth's land surface. For such ecosystems to retain productivity and biodiversity under climatic change, it would be valuable to identify/promote keystone plant species that (i) have developed strategies to more efficiently utilize moisture resources not easily accessible and (ii) improve moisture conditions for neighboring plants. The very deep-rooted *Ziziphus lotus*, considered an ecosystem engineer, is one such example. However, it is not known which biotic traits: (a) canopy interception of moisture/rainfall, (b) hydraulic redistribution of deep ground moisture by roots, or non-biotic factors: (c) soil's volume, and (d) organic matter content, *Z. lotus* activates/modulates to play such a role. We, thus, selected dryland ecosystems where the plant dominates and measured for potential effects on the less deep-rooted *Thymbra capitata*. For assessing impacts on ecosystem productivity, we measured the spatial aggregation of ca. 3600 *T. capitata* plants. As a proxy for soil moisture availability and its spatial variability, we conducted a 7-year-long study using thymes' nighttime rehydration. Sampling extended up to 15 m away from *Z. lotus*.

Results The density of *T. capitata* plants growing up to 5 m around *Z. lotus* vs. thymes growing 10–15 m away was found significantly increased (2.5–4.5 times), while their stem/leaf moisture was ca. 10% higher at predawn compared to nightfall during the dry season. This suggests that ecosystem productivity is driven by a greater soil moisture availability around *Z. lotus* permitting more thyme daytime transpiration, in contrast to thymes growing further away. The phenomenon appeared only under dry topsoil (during the dry season; becoming stronger during dry years). Morning dew/rainfall interception from the canopy or soil depth/organic matter did not show significant effects, leaving only the hydraulic lift properties of *Z. lotus* as the most likely driver for soil moisture availability.

Conclusions The deep-rooting properties and hydraulic lift potential of *Z. lotus* may be the key in permitting it to boost ecosystem productivity. Such hydraulic plant traits require more attention as they may prove valuable in combating desertification and restoring ecosystems in arid/semiarid regions threatened by climate change.

Keywords Plant–plant interaction, Desertification, Mediterranean, Dryland, Moisture content, Deep root, *Ziziphus lotus*, Stress-gradient

Background

Water availability is the most important limiting factor for plant productivity in drylands, which cover arid and semi-arid regions, ca. 40% of Earth's land surface. Drylands are particularly affected by climate change through changing rainfall patterns and land degradation, which reduces the ability of species and people to cope with dryland conditions (Millennium Ecosystem Assessment 2005; Sarris et al. 2011; IUCN 2019). Thus, for ecosystems in such regions to retain productivity/biodiversity under climatic change, it would be valuable to identify/promote keystone plant species that (i) have developed strategies to more efficiently utilize moisture resources not easily accessible and (ii) improve

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moisture conditions for neighboring plants. Nonetheless, identifying such plants and understanding how they function is a promising but still little-explored field.

Arid and semi-arid perennial plants may develop deep root systems to reach moist soil layers and groundwater sources, and essentially function as phreatophytes (Gorai et al. 2010; Sarris et al. 2013; Fan et al. 2017). Such functioning may involve hydraulic redistribution (HR), a process where roots serve as preferential low-resistance pathways for water along soil–water potential gradients between wet and dry soil zones, and between roots and the soil matrix (Schulze et al. 1998; Hultine et al. 2004). This trait permits temporary water storage external to the plant, in the upper dry soil layers, as a way for the plant to obtain additional moisture when transpiration restarts during the daytime. In some cases, water can move both downward from the moist upper layers during wet periods (hydraulic descent) and upward from the deeper zones with access to groundwater into the middle layers (hydraulic lift; HL), if the prevailing soil water potential gradient so dictates (Lee et al. 2021). During HR, the movement of water could take place typically at nighttime or when the canopy is inactive, depending on the plant's water stress levels (Hultine et al. 2004; Scott et al. 2008).

Especially during long periods of drought, the hydraulically lifted water can be used by the neighboring plants effectively, ameliorating their performance and growth (Caldwell and Richards 1989, Dawson 1993, Horton and Hart 1998, Filella and Peñuelas 2003; Barron-Gafford et al. 2017). The uplifted water by deep-rooted species can particularly benefit shallow-rooted species (Burgess 2011), thus enhancing the survival not only of the lifting but also of the neighboring plants (Liste and White 2008; Katul and Siqueira 2010; Prieto et al. 2011; Cardon et al. 2013; Matimati et al. 2014; Sun et al. 2014). Plants growing under the hydraulic lifting plants may use such water (Prieto et al. 2011) to improve their moisture content and growth rates compared to those that do not have access to this source of water (Filella and Peñuelas 2003; Zou et al. 2005; Bogie et al. 2018). Thus, the important consequence of hydraulic lift is that a significant part of water lifted (3–60%) can be also used by other species, normally growing in the lifting trees' understory (Dawson 1993; Schoonmaker et al. 2007). This function has been found to disappear during the wet spring season and to depend on the size of the tree (and the corresponding root depth; Filella and Peñuelas 2003). Hence dry topsoil coupled with root access to deep moisture availability would be a prerequisite for HL to function. HL favors biogeochemical conditions that enhance, the otherwise poor soil organic matter decomposition process, by providing topsoil with

additional moisture (Armas et al. 2012; Torres-García et al. 2022) and facilitating plant nutrient uptake (Cardon et al. 2013). These indirect benefits of HL could have been the primary selective force in the evolution of this process, or it may simply be the result of roots not having true rectifying properties (i.e., roots are leaky to water) (Caldwell et al. 1998).

In addition to improving soil properties, some facilitating plants also influence soil aggregation, mediated by environmental variables such as soil temperature and soil moisture, but also by factors such as soil organic carbon, soil fauna, soil microorganisms, roots, and inorganic binding agents (Bronick and Lal 2005; Lehmann et al. 2017). These positive effects on soil processes may influence neighboring plant survival, establishment, and growth, determining the structure of plant communities in nurse plant systems (Bronick and Lal 2005; Lozano et al. 2020).

The difference between water uptake and water loss is known as the water balance. A negative water balance results when transpiration exceeds water uptake, the reverse corresponding to a positive water balance. During the day, intense transpiration may lead to a negative balance, whereas during the night, the deficit is fully compensated (Sonnewald 2013). However, when soils are dry, the daytime deficit is not expected to be high for isohydric plants, i.e., plants that have evolved to maintain cell turgor via the closing of stomata. In these plants, daytime moisture deficits in the immediate surroundings of fine roots are related to transpiration (Körner 2018). Therefore, plants such as thymes that respond to drought stress by stomatal closure to reduce such water loss (Tátrai et al. 2016) are not expected to experience a too-negative water balance in the daytime and thus would be found to rehydrate less from soil water at night-time.

Ziziphus lotus (L.) is an anisohydric phreatophyte (Guirado et al. 2018; Torres-García et al. 2021a, b), its dimorphic deep root may reach tens of meters in depth (Gorai et al. 2010), being able to obtain water from lower soil horizons and possibly from a free water table. Anisohydric species exhibit plasticity in their hydraulic behavior, exhibiting seasonal patterns due to the predominant role of environmental conditions in regulating soil water potential gradients (Guo et al. 2020). Their anisohydric behavior suggests great physiological plasticity, in terms of rooting depth and stomata regulation, enabling them to adapt to different water table depths (Hultine et al. 2020). *Z. lotus* could be carrying out HR by its deep roots to facilitate nutrient uptake from dry upper soil layers (Torres-García et al. 2021a). *Z. lotus* is found in the thermo-Mediterranean bio-climatic zone and even drier areas, in Spain, Italy, Cyprus, and North Africa (European Commission 2013).

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Thymbra capitata [(L.) Cav.] is a very drought-resistant plant found in the thermo-Mediterranean vegetation belt typical of garrigue or phrygana vegetation. Thymes generally are not considered very shallow-rooted shrubs (ca. 1 m rooting depth; Nielsen et al. 2014) but cannot be compared to *Z. lotus*, since *Ziziphus* roots may reach 60 m in depth (Gorai et al. 2010).

Nevertheless, these two species, as part of a positive association, may play an important role in retaining dryland ecosystem productivity. Constantinou et al. (2021) discovered that *T. capitata* may significantly increase in density and can improve its night-time rehydration in mid-summer when growing up to 5 m around *Z. lotus* compared to thymes growing 10–15 m away. Moreover, density and stem moisture for thymes growing near *Z. lotus* do not seem to be significantly affected by topography, suggesting that *Z. lotus* may have traits that act against natural drought gradients; a property that resembles that of an ecosystem engineer.

To provide insight into the functioning of *Z. lotus* as an ecosystem engineer plant and its potential role in combating desertification for dryland ecosystems this study addresses the following questions:

1. Does *Z. lotus* improve ecosystem productivity? To investigate such effects, we measured the spatial aggregation of ca. 3600 *T. capitata* plants, the less deep-rooted perennial plant with the highest population around *Z. lotus* in Cyprus (southeast Mediterranean). Our hypothesis is that the density of thymes would increase the closest to *Z. lotus* clusters.

2. Does *Z. lotus* improve neighboring plants' soil moisture availability? To address this question, we conducted a 7-year-long study using the difference between predawn and nightfall moisture content of thymes as a proxy for soil moisture availability (SMA) and assessed its spatial variability up to 15 m away from *Z. lotus* covering wet and dry seasons and years. We hypothesize that SMA would increase for thymes growing closer to *Z. lotus* clusters.

The biotic factors (a) canopy interception of moisture/rainfall and (b) hydraulic lift, as well as the non-biotic factors (c) soil's volume, and (d) soil organic matter content, have been known as key features influencing SMA. Our third question is:

3. Which of the above does *Z. lotus* activate/modulate to affect neighboring plants' SMA? If factors (a), (c), and (d) do not appear to be significant, but still (i) SMA increases for thymes close to *Z. lotus* and (ii) this appears only during the seasons when topsoil is expected to be dry, we hypothesize that hydraulic lift could be the determining trait for the functioning of *Z. lotus* in affecting SMA and in turn ecosystem productivity.

Materials and methods

Study area

The study was conducted in Cyprus, on semi-arid arborescent matorral with *Ziziphus lotus* (L.) (priority habitat type *5220) within two Natura 2000 sites; the National
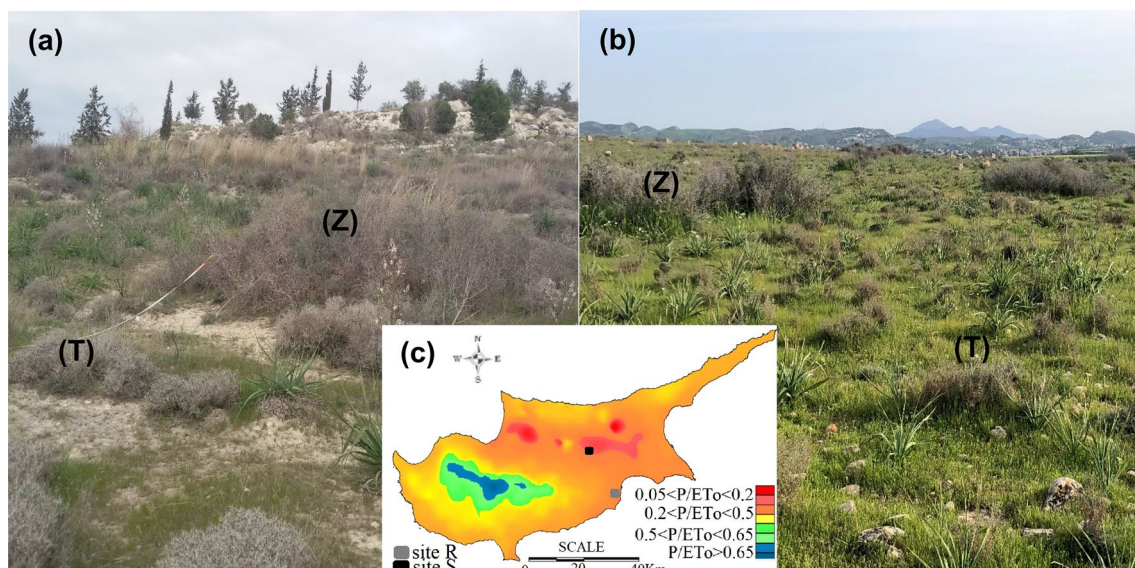

Fig. 1 **a** *Ziziphus lotus* (Z) and *Thymbra capitata* (T) within site R (National Forest Park of Rizoelia) (in mid-February 2015), **b** within site S (Alykos potamos – Agios Sozomenos) (in mid-March 2020), and **c** Location of sites R and S situated within the semiarid climatic zone of Cyprus (0.2 < P/ETo < 0.5; *P* precipitation; *ETo* reference evapotranspiration). Photos Constantinou E

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Forest Park of Rizoelia site (R; 34° 56′ 10.28″ N, 33° 34′ 23.57″ E; Fig. 1) and the Alykos potamos – Agios Sozomenos site (S; 35° 03′ 33″ N, 33° 25′ 23″ E; Fig. 1). Their climate is semiarid (annual rainfall < 400 mm; $0.2 < P/ET_o < 0.5$) with hot, dry summers from May to mid-October and mild winters from November to March (Pantelas 1996).

The experimental areas were selected as having no signs of human disturbance between the *Z. lotus* plants and no influence of any other deep-rooted plant species for more than 15 m from the selected *Z. lotus* plants. The total study area within site R was 3650 m^2 and included nine *Z. lotus* clusters. The altitude ranges from 71 to 80 m with sandy soil of gypsiric formation (Regosols-leptic Gypsisols). In site S the study area was 9800 m^2 and included 13 *Z. lotus* clusters. All clusters were randomly selected. The altitude ranges from 235 to 244 m with sandy Calcaric Regosols. Both sites are of poor organic content (< 1.4%) at the top 10 cm (de Brogniez et al. 2015).

Experimental sampling design

Starting from each *Z. lotus* cluster's crown center, three successive zones (Zone 1: 0–5 m, Zone 2: 5–10 m, and Zone 3: 10–15 m) were delimited to identify any possible effects of *Z. lotus* on *T. capitata* density and moisture content (MC) (Fig. 2). The sampling area of Zone 1 was calculated per cluster as a circular sector ($r = 5$ m radius). For the next two successive zones, the sampling area was calculated as a circular sector ($r = 10$ m and 15 m respectively) minus the previous zone's sampling area. In the case of neighboring *Z. lotus* clusters, each *T. capitata* was considered as part of the population affected by the nearest *Z. lotus*. Within each of the three successive zones, the number of *T. capitata* individuals per m^2 was estimated by counting the number of *T. capitata* plants per *Z. lotus* zone and dividing by the surface of each zone.

Since thymes (isohydric plants) respond to drought stress by stomatal closure to reduce water loss through transpiration (Tátrai et al. 2016), they are not expected to experience a very negative water balance in the daytime and thus would be found to rehydrate less from soil water at night-time. Thus, the level of rehydration of thyme stems and leaves from soil water at night-time, i.e., the difference in predawn vs. nightfall MC, could act as a proxy for the nocturnal availability of soil moisture. For measuring stem/leaf MC in *T. capitata* within the three zones around *Z. lotus*, we collected ca. 1900 samples in total, of stems with leaves, from up to 180 thymes in eight fieldwork campaigns from 2015 to 2021 that covered wet and dry seasons and years. Five campaigns were within the dry season (May, July, and September) and three were during the wet season (February and March; Table 1).

Sampling in wet and dry seasons permitted testing whether moisture gradients between topsoil and deeper soil moisture conditions could have had a different impact on the MC of *T. capitata* populations based on their proximity to *Z. lotus.* However, some years are drier than others. Comparing similar seasons between years provides another opportunity to test such effects. HL is expected to maximize when the topsoil is at its driest, but still, water accessed by deep roots is available. Thus, improved thyme night-time rehydration only close to *Z. lotus* during the dry seasons could indicate HL functioning. In turn, during wetter seasons/years, when the soil would be closer to moisture saturation, such effects could be canceled out.

The effects of air temperature and rainfall and their subsequent influence on soil moisture were also assessed. For this goal, the De Martonne Aridity Index (Pellicone et al. 2019) was calculated for the month of sampling (IDM_1) and the previous period of 3 and 6 months, including the month of sampling (IDM_3 and IDM_6). The index follows the equation: $IDM_{Nmonths} = P/(T_a + 10)$, were P is the amount of rainfall for the specific period (in millimeters) and T_α is the mean air temperature for the corresponding period (in degrees Celsius). Climatic data were provided by the Cyprus Department of Meteorology from the closest meteorological station (Larnaca International Airport for site R and Athalassa National Forest for site S). Sampling corresponded to $IDM_3 < 2.5$ for the dry season and > 4 for the wet season (Fig. 4).

Moisture content estimation in *T. capitata*

Starting from the crown of each *Z. lotus* cluster and up to the distance of 15 m, we selected 62 *T. capitata* plants, for site R and 180 for site S (Table 1), between 40–50 cm in height and 0.5–1 m in diameter. Each sampling was conducted in two phases on 2 consecutive days: the first phase immediately after sunset and the second before the dawn of the following day. From each *T. capitata* plant, a 10 cm length tissue containing stem and leaves was collected and its moisture content (MC) at nightfall was measured. The same approach was repeated at predawn, leading to a total of 1894 MC measurements from 2015 to 2021. The airtight bags containing the samples were placed in insulated boxes with ice packs until weighed. Sealed sample bags were weighed no later than 1 h after collection, using a two-decimal scale. After opening, they were placed in a furnace at 60 ℃ for 72 h and reweighed. MC, one for nightfall (MC_{nf}) and one for predawn (MC_{pd}) per thyme, was produced by subtracting the net weight of the dry sample from the net weight of the fresh sample. These were expressed as a percentage by dividing MC by the net weight of the fresh field sample. However, these values were not used independently but in relative
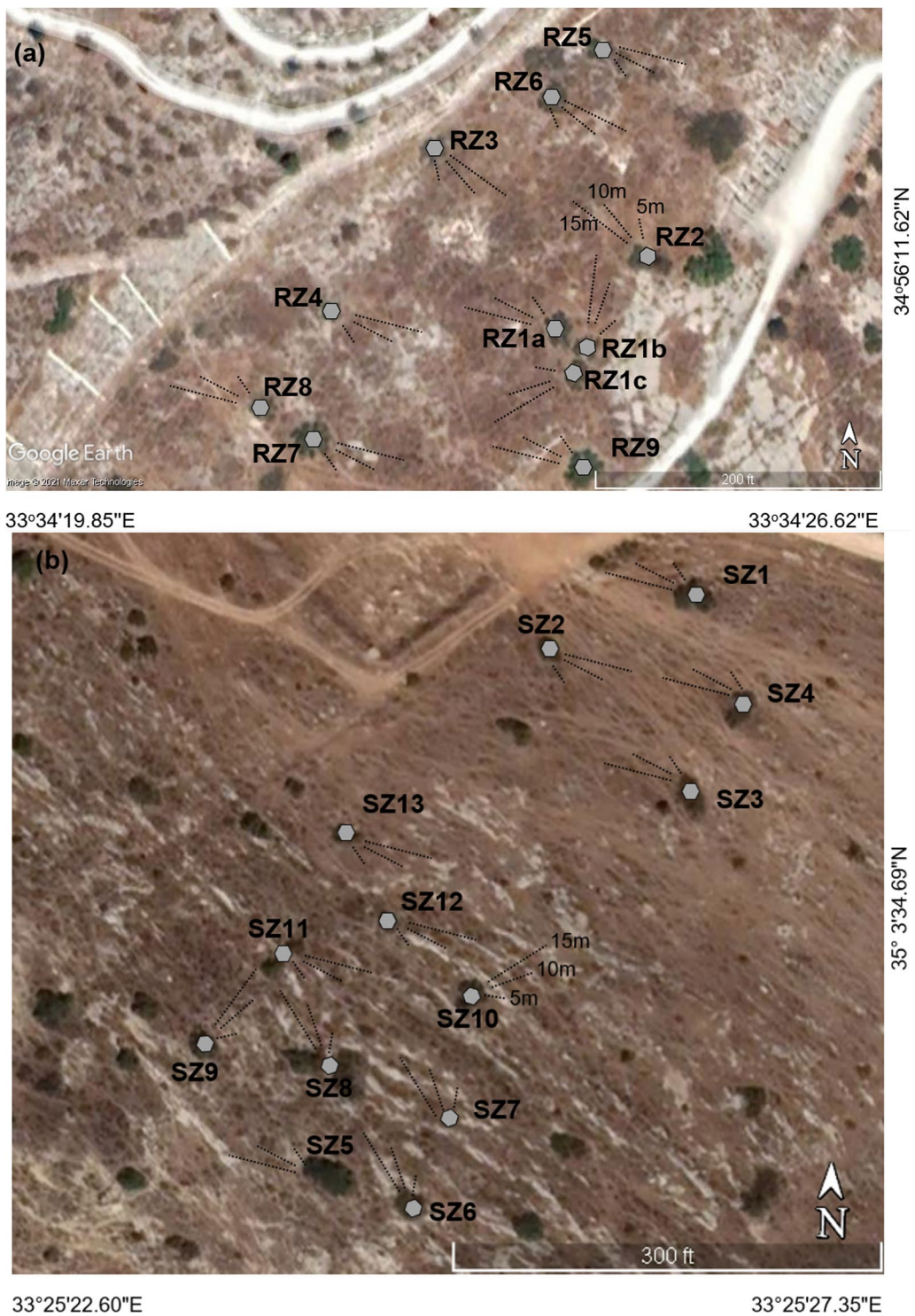
Fig. 2 Aerial photos of study areas **a** R and **b** S with the location of the *Z. lotus* clusters and the three radii used to identify the three zones (Zone 1 = 0–5 m, Zone 2 = 5–10 m, Zone 3 = 10–15 m) for measuring within them the density and moisture content of *T. capitata*

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Table 1 Spearman's Rho (r_s) from correlations between MCD of *T. capitata* and their distance from *Z. lotus* clusters ranked from the lowest to the highest p_{MCD}; $n =$ number of *T. capitata* plants

Sampling month	r_s	p_{MCD}	n	Study area
Jul 2021	− 0.679	< 0.0001	180	S
Sep 2020	− 0.618	< 0.0001	175	S
Jul 2015	− 0.813	< 0.0001	62	R
Jul 2020	− 0.624	< 0.0001	109	S
May 2020	− 0.609	< 0.0001	90	S
Feb 2016	− 0.349	0.037	36	R
Mar 2020	− 0.183	0.045	120	S
Feb 2021	− 0.117	0.125	175	S

Sampling during the dry season is in bold

terms to avoid limitations as noted by Turner (1981) and Jones (2007).

Instead, the moisture content difference (MCD) of each thyme, was calculated using the equation: $MCD = (MC_{pd}) - (MC_{nf})$. Under lack of nighttime transpiration plant tissues are typically rehydrated during night-time (Dawson et al. 2007). This new index represents the degree by which night-time rehydration occurs for thyme tissues. A positive MCD value would suggest that transpiration is active during daytime and that plant tissue MC losses, due to stomata transpiration, are replenished during night-time. This indicates adequate soil moisture availability. An MCD of close to zero would suggest that stomata remain closed during daytime to minimize transpiration losses, which in turn suggests low soil moisture availability.

Soil depth, organic carbon, and atmospheric moisture impacts on soil

Improved soil moisture around *Z. lotus* may be the result of deeper soil, higher soil organic matter, or/ and more rainfall and morning dew interception from the plant's canopy. To determine any differences in soil depth between zones that could influence soil moisture availability, the soil depth for 90 *T. capitata* was measured (ca. 30 measurements per zone) in site S using an Edelman soil sampler.

As a proxy for differences in soil organic matter between zones, the dissolvable organic carbon (DOC; mg/L) content in zones 1 and 3 in area S was measured using a Total Organic Carbon (TOC) analyzer (TOC analyzer Aurora Model 1030, OI Analytical, Inc.) for 100 thymes included in the MC estimation methodology (1 soil sample per thyme; 50 samples per zone). Before TOC analysis every five samples were pooled together producing 10 TOC measurements per zone (20 TOC samples in total). Each soil sample contained 10 cm of topsoil, collected with a metallic tube, from five different locations in each zone. The pooled samples were homogenized using a shaker for 30 min. Then 10 g from the homogenized sample was dissolved in 40 mL of $CaCl_2 \cdot 2H_2O$ (2.94 g in 2 L) and filtered through Whatman 42 filter paper. Samples were stored in the freezer until they were processed.

For monitoring surface soil moisture input from rainfall and morning dew, nine EC5 Soil Moisture Smart Sensors connected to two H21-002 HOBO Micro Station Data Loggers (ONSET) were installed in site S under two thymes and a *Z. lotus* plant (RZ4; Fig. 2a). The first thyme was in Zone 1 about 2 m away from the canopy of RZ4 and the second in Zone 3 about 15 m away from the nearest *Z. lotus*. At each *T. capitata*, two sensors were placed at a depth of 10 cm and two at a depth of 50 cm next to the canopy and within the thyme rhizosphere. An additional sensor was placed 5 cm deep under the canopy of RZ4. Soil moisture (in m^3/m^3) was recorded every hour beginning from the 25th of January 2020 for 1 year.

Statistical analysis

Statistical analysis was carried out using the IBM SPSS program v. 25.0. All data were analyzed for normal distribution with the Kolmogorov–Smirnov test. For data not found to be normally distributed either the Kruskal–Wallis non-parametric test was applied for differences among data groups (followed by the Dunn–Bonferroni post hoc test) or the non-parametric Spearman's Rho when correlation analysis was performed. For data found to be normally distributed the one-way ANOVA test was performed.

Results

Thymbra capitata density variability

In a total of 1377 *T. capitata* plants, Zone 1 produced the highest density for *T. capitata* with 0.44 plants per m^2 (Standard Error; SE = 0.08), in the experimental area of site R, followed by Zone 2 (0.25 plants per m^2; SE = 0.03) and Zone 3 (0.17 plants per m^2; SE = 0.03). The corresponding medians were 0.36, 0.23, and 0.18 (Fig. 3a). In the study area of site S, in a total of 2186 *T. capitata* plants, the highest density of *T. capitata* was recorded in Zone 1, with 0.57 plants per m^2 (SE = 0.09), followed by Zone 2 (0.23 plants per m^2; SE = 0.03) and Zone 3 (0.13 plants per m^2; SE = 0.04). The medians were 0.63, 0.26, and 0.09 per zone respectively (Fig. 3b). The Kruskal–Wallis test identified statistically significant differences between the thyme densities of Zones 1 and 3 in both sites ($p < 0.01$ for R and $p < 0.0001$ for S).
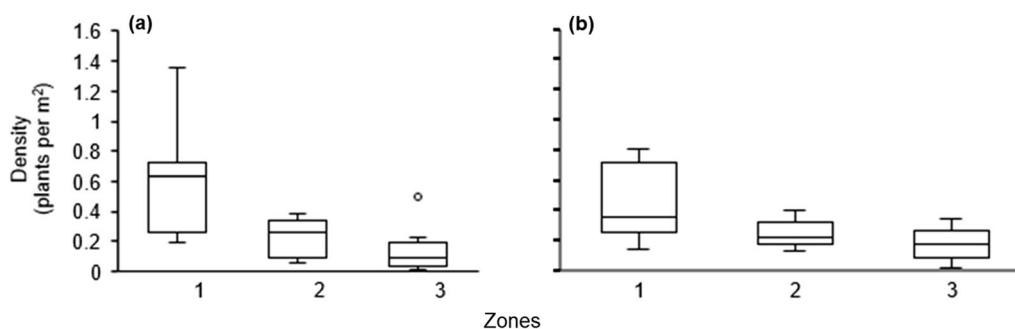
Fig. 3 The density (plants/m^2) of *T. capitata* around *Z. lotus* per zone in sites **a** R and **b** S. The horizontal line within each box represents the median. Statistically, significant differences exist between Zones 1 and Zone 3 in both sites at $p < 0.01$ for R and $p < 0.0001$ for S

Moisture content differences in *T. capitata*

The Spearman's rank correlation between thymes' MCD and their distance from *Z. lotus* in each sampling period produced a strong negative correlation ($p_{MCD} < 0.0001$) for thymes sampled during the dry season months, in both study areas (Fig. 4). Regression analysis produced similar results. For the wet season months, correlations were much weaker $p_{MCD} > 0.01$ or not significant at all in both sites (Table 1). Note that mild winters in Cyprus (as also in neighboring Israel) do not produce full *Z. lotus* canopy defoliation. The full p_{MCD} values, from all months of sampling that are shown in Table 1, were found to be significantly correlated with IDM$_1$, IDM$_3$, or even better with IDM$_6$ (Table 2). This suggests that the driest the months prior to sampling, the strongest was the MCD for the thymes closer to *Z. lotus* clusters and that differences in climatic dryness not only within a year but also between years appear have an effect on MCD. Furthermore, these results suggest that the more MCD departs from zero the more stomata remain open during the daytime as a result of more soil moisture being available, based on our original hypothesis.

The statistical analysis for possible soil depth differences in site S illustrated that soil depth did not differ across the three zones ($p = 0.462$). The mean soil depths for Zones 1–3 were 15.03 cm (SE = 0.68), 14.30 cm (SE = 0.72), and 15.5 cm (SE = 0.62) respectively. The one-way ANOVA revealed that there were no statistically significant differences in DOC content between Zones 1 and 3 [$F_{(1,18)} = 3.134$, $p = 0.094$]. The mean DOC content for Zone 1 was 7.56 mg/L (SE = 2.39) and for Zone 3 was 17.75 mg/L (SE = 1.39).

The comparison of the soil moisture sensors recordings of site R to Larnaca Airport Station weather data confirmed that rainfall events produced an increase in soil moisture under the RZ4 canopy, and within 2 h the increase was recorded by all four sensors placed at 10 cm, without soil moisture recordings being higher for the closer to *Z. lotus* sensors. The increase was also recorded by the four sensors at 50 cm but after several hours. On the other hand, morning dew events recorded at the Meteorological station did not produce any soil moisture increase under the *Z. lotus* canopy nor in any of the sensors placed on the thymes.

Discussion

Our findings clearly document that thyme population densities are significantly greater up to 5 m away from dominant *Z. lotus* plants under the natural spatial distribution established within the semiarid plant communities investigated in Cyprus (Fig. 3). The *Z. lotus* habitat (Priority habitat type *5220) is considered the climax vegetation stage in these low productivity systems, suggesting that it may have taken even centuries for natural vegetation succession to produce such an aggregation.

Constantinou et al. (2021) proposed that *Z. lotus* may be classified as an ecosystem engineer and that the plant may possess traits that act against natural drought gradients. Our 7-year-long study has identified that *Z. lotus* has a positive impact on thyme stem/leaf moisture content availability, which in turn may be the key to explaining the increased densities of thymes around dominant *Ziziphus* plants (Fig. 4). Additionally, the shortest the distance *T. capitata* grew from *Z. lotus*, the higher was the moisture content difference (MCD) in *T. capitata* in the dry season in both study areas (Table 1). In fact, the driest the year, the more pronounced the phenomenon appeared (Table 2). Considering that MCD measurements can act as a proxy for soil moisture availability, we identified more water in the soil exploited by the rhizosphere of *T. capitata* close to *Z. lotus* during the dry season and in dry years not more than 5 m away from dominant *Ziziphus* plants. Thymes that are better watered can open stomata and transpire in the daytime, reduce moisture content by nightfall and replenish their
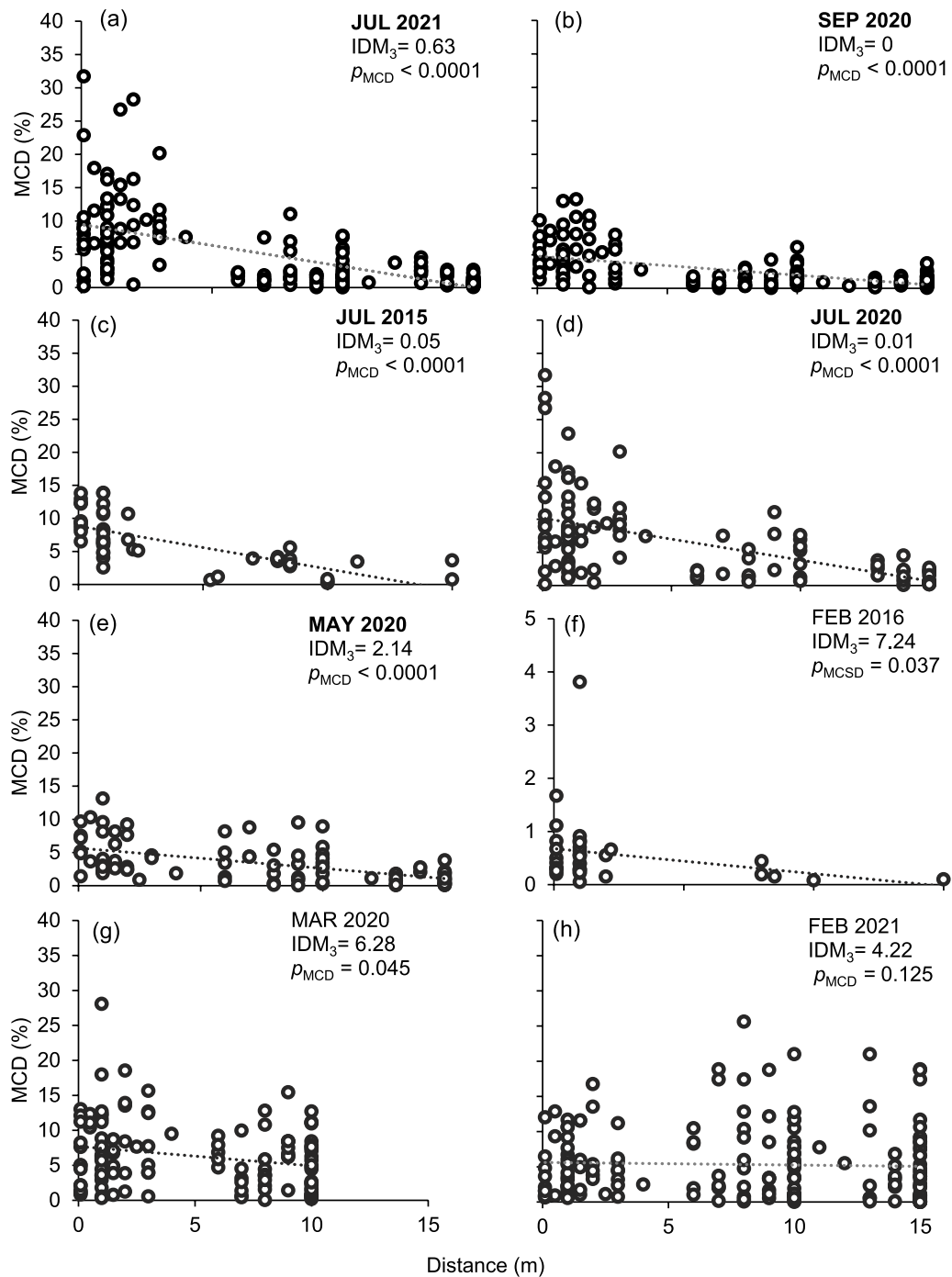
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Fig. 4 Linear regression between moisture content differences (MCD) in stems of *T. capitata* and their distance from the closest *Z. lotus* ranked from the lowest **a** to the highest **h** p_{MCD}. IDM_3 = the De Martone Aridity Index for the previous period of 3 months, including the month of sampling. Dry season months of sampling are in bold. For full statistics see Table 1. Note that the scale for MCD in **f** differs and the Zone 3 data for March 2020 are missing

cell turgor pressure (rehydrate tissues) by dawn. Thus, their MCD is expected to increase. Thymes that do not have such moisture pools available, retain stomata closed for longer periods in the daytime and keep transpiration to minimum levels. Accordingly, no significant differences occur between nightfall and predawn stem/leaf moisture content (MCD close to zero).

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Table 2 The Spearman's Rho (r_s) from the correlation between p_{MCD} of Table 1 and the IDM of the month of sampling (IDM_1) as well as of the previous period of 3 and 6 months (including the month of sampling, IDM_3, and IDM_6)

	IDM_1	IDM_3	IDM_6
r_s	0.736	0.738	0.786
p	0.038	0.037	0.021
n	8	8	8

Ziziphus lotus may possess multiple ecological functions leading to improved soil moisture in its proximity. Our findings allow us to determine the most probable ones.

(A) Soil was not found to be deeper in 5-m proximity from *Z. lotus* compared to 15-m away. Thus, it is not likely that the plant creates deeper soils around it by capturing, wind-swept soil particles through its canopy as has been found for other species (Flores and Jurado 2003).

(B) The potential impact of rainfall and morning dew intercepted by the canopy on soil moisture availability of *Ziziphus* was investigated using nine soil moisture sensors over a year. Every recorded rainfall event from the closest meteorological station (distance of 8.5 km), produced a soil moisture increase as recorded by all nine sensors. Following rainfall events, soil moisture levels were not recorded to be the highest by the sensors closer to *Z. lotus*, nor did meteorologically documented incidents of morning dew produce noticeable soil moisture recordings in any of the sensors. Thus, it is not likely that the plant's canopy, as the dominant plant structure within its ecosystem, intercepts more rainfall and morning dew compared to bare soil further away, which then becomes available to neighboring thymes. Soil moisture has been reported to be higher under some plant species' canopy compared to bare ground areas (Maestre and Cortina 2003). However, other studies showed that these effects are not general (Maestre et al. 2002; Cuesta et al. 2010). Note that thymes in this study were not under the immediate influence of *Z. lotus* canopy, which makes any impact of rainfall interception of *Ziziphus* on thymes less likely. Future analysis could also cover any torrential rainfall effects (Dorman et al. 2015).

(C) It has been shown that plant litter carbon and carbon extracts from *Z. lotus* roots into soil biota and from there into the soil may increase soil organic matter, which in turn may improve its water-holding capacity (Minasny and McBratney 2018). Although this function cannot be ruled out from influencing our systems, the DOC analysis did not indicate that dissolvable soil carbon was higher for thymes closer to *Ziziphus*. However, a more in-depth soil analysis that may include measuring among others, soils water-holding capacity, would be useful for future verification.

(D) Thyme MCD measurements vs. plant distance from *Z. lotus* (Fig. 4) revealed that the closest thymes grew to *Z. lotus* the highest was their ability to rehydrate at nighttime ($p_{MCD} < 0.0001$), particularly during the dry season in both study areas. For the wet season months, correlations were much weaker $p_{MCD} > 0.01$ or not significant at all (Table 1). Furthermore, the driest the year ($IDM_3 < 2.5$), the strongest the effect that the above phenomenon exercised (Table 2). Thus, it is when the moisture contrast between topsoil vs. deeper ground is expected to be the highest within the year or in-between years (i.e., conditions that favor HL) that thymes close to *Z. lotus* benefit from improved moisture content. This, in turn, may explain the significantly higher thyme population densities around the facilitating plant as HL water would reduce plant moisture stress, sustain more vigorous microbial populations, and improve nutrient availability. Stable isotope analysis could further shed light on the phenomenon as has been the case with other species performing "bio-irrigation" through hydraulic redistribution (Bogie et al. 2018).

Hydraulically lifted water during the dry season and particularly in dry years is a phenomenon from which neighboring plants benefit (McMichael and Lascano 2010). In the long Mediterranean dry season, topsoil becomes dry but still, moisture from the wet season may exist in the deeper ground, a condition which favors the occurrence of hydraulic lift (Richards and Caldwell 1987). In dry years when still deeper ground moisture is available, we would again expect the soil moisture difference between topsoil and deeper ground to be strong, with very low water potentials to occur in soil layers outside the upper rhizosphere. Such conditions favor hydraulically lifted water to move osmotically from the deeper ground towards the outside of the fine roots and into the upper soil layers. Neighboring plants with roots exploiting these soils may make use of such water likely with assistance from mycorrhiza networks (Egerton-Warburton et al. 2007; Pickles and Simard 2017). Thymes further away from the plant performing hydraulic lift (HL) would not be able to exploit such a resource. HL has been indirectly (Tewksbury and Lloyd 2001), as well as directly (Liste and White 2008) linked

to the ability of plants to increase ecosystem productivity. Such examples are *Quercus suber* (Kurz-Besson et al. 2006), *Acacia tortilis* (Ludwig et al. 2003), four woody species of the Brazilian Cerrado (Scholz et al. 2002), three Amazonian trees (Oliveira et al. 2005) as well as the Sahel native shrub pearl millet (*Pennisetum glaucum*) in drought years (Bogie et al. 2018). Thus, the role of *Z. lotus* as an ecosystem engineer could very well involve such functioning.

Anisohydric phreatophytic species, such as *Z. lotus*, are known for their plasticity in their hydraulic behavior (Sun et al. 2014; Guo et al. 2020). *Z. lotus* has a very deep rooting potential (Gorai et al. 2010) and has been suggested to conduct HR by its deep roots to facilitate nutrient uptake from dry upper soil layers (Torres-García et al. 2021a). Therefore, improved moisture availability may be the key, in the semi-arid conditions investigated, to the higher density of thyme plants when growing close to *Z. lotus*. This may explain how the plant counterbalances the negative effects of south-facing aspects on thyme plant distribution (Constantinou et al. 2021) and is in support of facilitation being the main force driving community structure and function (Callaway et al. 2002).

The ecological role of late-successional species has been demonstrated in arid environments (Padilla et al. 2009) since the maintenance of ecosystem functions is a top conservation priority (Balvanera et al. 2001). HR is a key process in drylands that not only provides moisture to generally dry soil but also facilitates the acquisition of nutrients by plants (Cardon et al. 2013). Therefore, identifying species, such as *Z. lotus*, which maintain or influence such ecosystem functions is a wise conservation approach and provides an excellent potential for dryland afforestation within their native range, minimizing the risk of biological invasions (Mizrahi and Nerd 1996; Padilla and Pugnaire 2006). Thus, our findings can support future restoration efforts, to expand habitat type *5220, which is now severely restricted in Europe and of poor conservation status, and contribute towards changing the attitude of farmers and policymakers that see *Z. lotus* as an agricultural pest.

How *Z. lotus* benefits from higher thyme densities in its proximity remains a question since this could increase competition for resources. However, in conditions where soil evaporation pressure is high because of high solar radiation, denser thyme communities may favor *Z. lotus* as well, by reducing topsoil temperatures that can exceed 60 °C in the summertime at 34° latitude. Thyme canopies can reduce these temperatures by even ca. 20 °C, improving moisture conditions (Matsi and Sarris, unpublished observations), while making very

conservative use of soil moisture (Moradi et al. 2014). This minimizes the risk of losing water to evaporation for the HL species as well. Sheltering from the detrimental effects of high solar radiation also permits higher seedling establishment rates (Príncipe et al. 2019). Therefore, these two species, as part of a positive association, appear to play an important role in maintaining key ecosystem functions of their habitat as may be the case for other ecosystem engineering species and their facilitating plant communities. Thus this paper, provides an excellent example and the methodological tools to expand such research. The MCD method we applied would benefit from further evaluation by comparison with the standard instrumental moisture content assessment approaches (Turner 1981; Jones 2007); although this could produce limitations in large-scale field sampling campaigns at night-time since the latter is more time consuming. Nonetheless, it is important to advance our understanding of hydraulic plant traits for improving dryland ecosystem productivity to the benefit of rural human populations that depend on their services. This may be key in the battle against desertification since drylands are home to more than two billion people and are the source of a large proportion of the food and fibre used around the world (IUCN 2019).

Conclusions

Our findings provide evidence that the moisture content of *T. capitata* and its density significantly increase around *Z. lotus*, as a most likely result of the hydraulic lift properties of the latter. Hydraulic lift may be one of the key plant functions in explaining the spatial aggregation of shrubs around ecosystem engineering plants in drylands requiring, however, not only direct but also novel indirect methodological designs, as provided in this paper, for its large-scale investigation. Such hydraulic plant traits require more attention as they may prove valuable in combating desertification and restoring ecosystems in arid/semiarid regions threatened by climate change to the benefit of rural human populations that depend on dryland ecosystem services.

Abbreviations

R	National Forest Park of Rizoelia
S	Alykos potamos – Agios Sozomenos
P	Precipitation
ET_o	Reference evapotranspiration
IDM	De Martonne Aridity Index
MC	Moisture content
MCD	Moisture content difference
TOC	Total organic carbon
SMA	Soil moisture availability
HR	Hydraulic redistribution
HL	Hydraulic lift

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication

Not applicable.

Competing interests

The authors declare no conflict of interest or competing interests.

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References

Armas C, Kim JH, Bleby TM, Jackson RB (2012) The effect of hydraulic lift on organic matter decomposition, soil nitrogen cycling, and nitrogen acquisition by a grass species. Oecologia 168(1):11–22. https://doi.org/10.1007/s00442-011-2065-2

Balvanera P, Daily GC, Ehrlich PR, Ricketts TH, Bailey SA, Kark S, Kremen C, Pereira H (2001) Conserving biodiversity and ecosystem services. Science 291:2047–2047. https://doi.org/10.1126/science.291.5511.2047

Barron-Gafford GA, Sanchez-Cañete EP, Minor RL, Hendryx SM, Lee E, Sutter LF, Tran N, Parra E, Colella T, Murphy PC, Hamerlynck EP, Kumar P, Scott RL (2017) Impacts of hydraulic redistribution on grass–tree competition vs facilitation in a semi-arid savanna. New Phytol 215:1451–1461. https://doi.org/10.1111/nph.14693

Bogie NA, Bayala R, Diedhiou I, Conklin MH, Fogel ML, Dick RP, Ghezzehei TA (2018) Hydraulic redistribution by native Sahelian shrubs: bioirrigation to resist in-season drought. Front Environ Sci 6:98. https://doi.org/10.3389/fenvs.2018.00098

Bronick CJ, Lal R (2005) Manuring and rotation effects on soil organic carbon concentration for different aggregate size fractions on two soils in northeastern Ohio, USA. Soil Tillage Res 81(2):239–252. https://doi.org/10.1016/j.still.2004.09.011

Burgess SSO (2011) Can hydraulic redistribution put bread on our table? Plant Soil 341:25–29. https://doi.org/10.1007/s11104-010-0638-1

Caldwell MM, Richards JH (1989) Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 79(1):1–5. https://doi.org/10.1007/BF00378231

Caldwell MM, Dawson TE, Richards JH (1998) Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113(2):151–161. https://doi.org/10.1007/s004420050363

Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R et al (2002) Positive interactions among alpine plants increase with stress. Nature 417(6891):844–848. https://doi.org/10.1038/nature00812

Cardon ZG, Stark JM, Herron PM, Rasmussen JA (2013) Sagebrush carrying out hydraulic lift enhances surface soil nitrogen cycling and nitrogen uptake into inflorescences. Proc Natl Acad Sci USA 110(47):18988–18993. https://doi.org/10.1073/pnas1311314110

Constantinou E, Sarris D, Vogiatzakis IN (2021) The possible role of *Ziziphus lotus* as an ecosystem engineer in semiarid landscapes. J Arid Environ 195:104614. https://doi.org/10.1016/j.jaridenv2021104614

Cuesta B, Villar-Salvador P, Puertolas J, Rey Benayas JM, Michalet R (2010) Facilitation of *Quercus ilex* in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs. J Ecol 98(3):687–696. https://doi.org/10.1111/j1365-2745201001655x

Dawson TE (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. Oecologia 95:565–574. https://doi.org/10.1007/BF00317442

Dawson TE, Burgess SS, Tu KP, Oliveira RS, Santiago LS, Fisher JB, Ambrose AR (2007) Nighttime transpiration in woody plants from contrasting ecosystems. Tree Physiol 27(4):561–575. https://doi.org/10.1093/treephys/274561

de Brogniez D, Ballabio C, Stevens A, Jones RJA, Montanarella L, van Wesemael B (2015) A map of the topsoil organic carbon content of Europe generated by a generalized additive model. Eur J Soil Sci 66:21–134. https://doi.org/10.1111/ejss.12193

Dorman M, Perevolotsky A, Sarris D, Svoray T (2015) Amount vs temporal pattern: on the importance of intra-annual climatic conditions on tree growth in a dry environment. J Arid Environ 118:65–68. https://doi.org/10.1016/jjaridenv201503002

Egerton-Warburton LM, Querejeta JI, Allen MF (2007) Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. J Exp Bot 58(6):1473–1483. https://doi.org/10.1093/jxb/erm009

European Commission (2013) Interpretation manual of European Union habitats version EUR 28. European Commission, Brussels. https://eunis.eea.europa.eu/references/2435. Accessed 1 Dec 2022

Fan Y, Miguez-Macho G, Jobbágy EG, Jackson RB, Otero-Casal C (2017) Hydrologic regulation of plant rooting depth. Proc Natl Acad Sci USA 114(40):10572–10577. https://doi.org/10.1073/pnas1712381114

Filella I, Peñuelas J (2003) Indications of hydraulic lift by *Pinus halepensis* and its effects on the water relations of neighbour shrubs. Biol Plant 47:209–214. https://doi.org/10.1023/B:BIOP.0000022253.08474.fd

Flores J, Jurado E (2003) Are nurse–protégé interactions more common among plants from arid environments? J Veg Sci 14(6):911–916. https://doi.org/10.1111/j1654-11032003tb02225x

Gorai M, Maraghni M, Neffati M (2010) Relationship between phenological traits and water potential patterns of the wild jujube *Ziziphus lotus* (L.) Lam in southern Tunisia. Plant Ecol Divers 3(3):273–280. https://doi.org/10.1080/175508742010500337

Guirado E, Alcaraz-Segura D, Rigol-Sánchez JP, Gisbert J, Martínez-Moreno FJ, Galindo-Zaldívar J, González-Castillo L, Cabello J (2018) Remote sensing-derived fractures and shrub patterns to identify groundwater dependence. Ecohydrology 11(6):1933. https://doi.org/10.1002/eco1933

Guo JS, Hultine KR, Koch GW, Kropp H, Ogle K (2020) Temporal shifts in iso/anisohydry revealed from daily observations of plant water potential in a dominant desert shrub. New Phytol 225(2):713–726. https://doi.org/10.1111/nph16196

Horton JL, Hart SC (1998) Hydraulic lift: a potentially important ecosystem process. Trends Ecol Evol 13(6):232–235. https://doi.org/10.1016/s0169-5347(98)01328-7

Hultine KR, Scott RL, Cable WL, Goodrich DC, Williams DG (2004) Hydraulic redistribution by a dominant warm-desert phreatophyte: seasonal

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patterns and response to precipitation pulses. Funct Ecol 18(4):530–538. https://doi.org/10.1111/j0269-8463200400867x

Hultine KR, Froend R, Blasini D, Bush SE, Karlinski M, Koepke DF (2020) Hydraulic traits that buffer deep-rooted plants from changes in hydrology and climate. Hydrol Process 34(2):209–222. https://doi.org/10.1002/hyp13587

IUCN (2019) Drylands and climate change. Issues brief. International Union for Conservation of Nature and Natural Resources. Available via iucn. org. https://www.iucn.org/resources/issues-brief/drylands-and-climate-change. Accessed 2 Dec 2022

Jones HG (2007) Monitoring plant and soil water status: established and novel methods revisited and their relevance to studies of drought tolerance. J Exp Bot 58(2):119–130. https://doi.org/10.1093/jxb/erl118

Katul GG, Siqueira MB (2010) Biotic and abiotic factors act in coordination to amplify hydraulic redistribution and lift. New Phytol 187(1):3–6. https://doi.org/10.1111/j.1469-8137.2010.03306.x

Körner C (2018) Concepts in empirical plant ecology. Plant Ecol Divers 11(4):405–428. https://doi.org/10.1080/1755087420181540021

Kurz-Besson C, Otieno D, Lobo do Vale R, Siegwolf R, Schmidt M, Herd A, Nogueira C, David TS, David JS, Tenhunen J, Pereira JS, Chaves M (2006) Hydraulic lift in cork oak trees in a savannah-type Mediterranean ecosystem and its contribution to the local water balance. Plant Soil 282:361–378. https://doi.org/10.1007/s11104-006-0005-4

Lee E, Kumar P, Knowles JF, Minor RL, Tran N, Barron-Gafford GA, Scott RL (2021) Convergent hydraulic redistribution and groundwater access supported facilitative dependency between trees and grasses in a semi-arid environment. Water Resour Res 57(6):e2020WR028103. https://doi.org/10.1029/2020WR028103

Lehmann A, Zheng W, Rillig MC (2017) Soil biota contributions to soil aggregation. Nat Ecol Evol 1(12):1828–1835. https://doi.org/10.1038/s41559-017-0344-y

Liste HH, White JC (2008) Plant hydraulic lift of soil water—implications for crop production and land restoration. Plant Soil 313:1–17. https://doi.org/10.1007/s11104-008-9696-z

Lozano YM, Hortal S, Armas C et al (2020) Complementarity in nurse plant systems: soil drives community composition while microclimate enhances productivity and diversity. Plant Soil 450:385–396. https://doi.org/10.1007/s11104-020-04503-6

Ludwig F, Dawson TE, de Kroon H et al (2003) Hydraulic lift in *Acacia tortilis* trees on an East African savanna. Oecologia 134:293–300. https://doi.org/10.1007/s00442-002-1119-x

Maestre FT, Cortina J (2003) Small-scale spatial variation in soil CO_2 efflux in a Mediterranean semiarid steppe. Appl Soil Ecol 23(3):199–209. https://doi.org/10.1016/S0929-1393(03)00050-7

Maestre FT, Bautista S, Cortina J, Díaz G, Honrubia M, Vallejo R (2002) Microsite and mycorrhizal inoculum effects on the establishment of *Quercus coccifera* in a semi-arid degraded steppe. Ecol Eng 19(4):289–295. https://doi.org/10.1016/S0925-8574(02)00097-6

Matimati I, Verboom AG, Cramer MD (2014) Do hydraulic redistribution and nocturnal transpiration facilitate nutrient acquisition in *Aspalathus linearis*? Oecologia 175:1129–1142. https://doi.org/10.1007/s00442-014-2987-6

McMichael BL, Lascano RJ (2010) Evaluation of hydraulic lift in cotton (*Gossypium hirsutum* L.) germplasm. Environ Exp Bot 68(1):26–30. https://doi.org/10.1016/j.envexpbot200910002

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: desertification synthesis. World Resources Institute, Washington DC

Minasny B, McBratney AB (2018) Limited effect of organic matter on soil available water capacity. Eur J Soil Sci 69(1):39–47. https://doi.org/10.1111/ejss12475

Mizrahi Y, Nerd A (1996) New crops as a possible solution for the troubled Israeli export market. In: Progress in new crops: proceedings of the third national symposium Indianapolis Indiana USA. American Society for Horticultural Science, pp 37–45. https://www.cabdirect.org/cabdirect/abstract/19981808000. Accessed 1 Dec 2022

Moradi P, Ford-Lloyd B, Pritchard J (2014) Plant-water responses of different medicinal plant thyme (*Thymus* spp.) species to drought stress condition. Aust J Crop Sci 8(5):666–673

Nielsen JA, Frew RD, Whigham PA, Callaway RM, Dickinson KJM (2014) Thyme invasion and soil properties in the Central Otago region of New Zealand. Geoderma Reg 1:48–58. https://doi.org/10.1016/j.geodrs.2014.08.002

Oliveira RS, Dawson TE, Burgess SSO, Nepstad DC (2005) Hydraulic redistribution in three Amazonian trees. Oecologia 145:354–363. https://doi.org/10.1007/s00442-005-0108-2

Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. Front Ecol Environ 4(4):196–202. https://doi.org/10.1890/1540-9295(2006)004[0196:TRONPI]20CO;2

Padilla FM, Ortega R, Sánchez J, Pugnaire FI (2009) Rethinking species selection for restoration of arid shrublands. Basic Appl Ecol 10(7):640–647. https://doi.org/10.1016/jbaae200903003

Pantelas V (1996) The Bioclima and Phytosociology in Cyprus. Report in Department of Forests, Ministry of Agriculture, Natural Resources and Environment. Nicosia, Cyprus

Pellicone G, Caloiero T, Guagliardi I (2019) The De Martonne aridity index in Calabria (Southern Italy). J Maps 15(2):788–796. https://doi.org/10.1080/1744564720191673840

Pickles BJ, Simard SW (2017) Mycorrhizal networks and forest resilience to drought. In: Mycorrhizal mediation of soil. Elsevier, pp 319–339. https://doi.org/10.1016/B978-0-12-804312-700018-8

Prieto I, Padilla FM, Armas C, Pugnaire FI (2011) The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. Perspect Plant Ecol Evol Syst 13(3):181–187. https://doi.org/10.1016/j.ppees.2011.05.002

Príncipe A, Matos P, Sarris D, Gaiola G, do Rosário L et al (2019) In Mediterranean drylands microclimate affects more tree seedlings than adult trees. Ecol Indic 106:105476. https://doi.org/10.1016/j.ecolind.2019.105476

Richards JH, Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73(4):486–489. https://doi.org/10.1007/BF00379405

Sarris D, Christodoulakis D, Körner C (2011) Impact of recent climatic change on growth of low elevation eastern Mediterranean forest trees. Clim Change 106(2):203–223. https://doi.org/10.1007/s10584-010-9901-y

Sarris D, Siegwolf R, Körner C (2013) Inter- and intra-annual stable carbon and oxygen isotope signals in response to drought in Mediterranean pines. Agric For Meteorol 168:59–68. https://doi.org/10.1016/jagrformet201208007

Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC (2002) Hydraulic redistribution of soil water by neotropical savanna trees. Tree Physiol 22:603–612. https://doi.org/10.1093/treephys/229603

Schoonmaker AL, Teste FP, Simard SW et al (2007) Tree proximity, soil pathways and common mycorrhizal networks: their influence on the utilization of redistributed water by understory seedlings. Oecologia 154:455–466. https://doi.org/10.1007/s00442-007-0852-6

Schulze ED, Caldwell M, Canadell J et al (1998) Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands. Oecologia 115:460–462. https://doi.org/10.1007/s004420050541

Scott RL, Cable WL, Hultine KR (2008) The ecohydrologic significance of hydraulic redistribution in a semiarid savanna. Water Resour Res 44:W02440. https://doi.org/10.1029/2007WR006149

Sonnewald U (2013) Physiology of metabolism. In: Strasburger's plant sciences. Springer, Berlin. https://doi.org/10.1007/978-3-642-15518-5_5

Sun SJ, Meng P, Zhang JS, Wan X (2014) Hydraulic lift by *Juglans regia* relates to nutrient status in the intercropped shallow-root crop plant. Plant Soil 374(1–2):629–641. https://doi.org/10.1007/s11104-013-1888-5

Tátrai ZA, Sanoubar R, Pluhár Z, Mancarella S, Orsini F, Gianquinto G (2016) Morphological and physiological plant responses to drought stress in *Thymus citriodorus*. Int J Agron 2016:8. https://doi.org/10.1155/2016/4165750

Tewksbury J, Lloyd J (2001) Positive interactions under nurse-plants: spatial scale stress gradients and benefactor size. Oecologia 127:425–434. https://doi.org/10.1007/s004420000614

Torres-García MT, Salinas-Bonillo MJ, Gázquez-Sánchez F, Fernández-Cortés A, Querejeta JL, Cabello J (2021a) Squandering water in drylands: the water use strategy of the phreatophyte *Ziziphus lotus* (L.) Lam in a groundwater dependent ecosystem. Am J Bot 108(2):1–13. https://doi.org/10.1002/ajb21606

Torres-García MT, Salinas-Bonillo MJ, Cleverly JR et al (2021b) A multiple-trait analysis of ecohydrological acclimatisation in a dryland phreatophytic shrub. Oecologia 196:1179–1193. https://doi.org/10.1007/s00442-021-04993-w

Constantinou *et al. Ecological Processes*   (2023) 12:30

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Torres-García MT, Oyonarte C, Cabello J, Guirado E, Rodríguez-Lozano B, Salinas-Bonillo MJ (2022) The potential of groundwater-dependent ecosystems to enhance soil biological activity and soil fertility in drylands. Sci Total Environ 826:154111. https://doi.org/10.1016/jscitotenv2022154111

Turner NC (1981) Techniques and experimental approaches for the measurement of plant water status. Plant Soil 58:339–366. https://doi.org/10.1007/BF02180062

Zou CB, Barnes PW, Archer S et al (2005) Soil moisture redistribution as a mechanism of facilitation in savanna tree–shrub clusters. Oecologia 145:32–40. https://doi.org/10.1007/s00442-005-0110-8

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