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HIGHLIGHTED STUDENT RESEARCH

The role of dew in Negev Desert plants

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Abstract We investigated the possible use of dew as a water source for three desert plant species native to the Negev Desert: an annual *Salsola inermis*, and two perennials *Artemisia sieberi* and *Haloxylon scoparium,* with different rooting depths of 15, 30 and 90 cm, respectively. We quantified dew-water inputs and used stable isotope analyses to determine the proportion of dew as compared to the proportion of soil water each species utilized. Dew was isotopically enriched (δD values ranged from −25 to 5 ‰), relative to rainfall with δD values that ranged from −40 to −20 ‰ and relative to soil water with δD values that ranged from −65 to −35 ‰. Using a two-source isotope mixing model, we found that *S. inermis, A. sieberi* and *H. scoparium* used, on average, 56, 63 and 46 % of their water from dewfall, respectively. Our results suggest that dew-water utilization by Negev Desert plants is highly significant ecologically and thus may be more common than previously thought. In light of future predicted climate change, it may be increasingly important for plants of the Negev Desert to make use of dew as a water resource as it may play an important role in their ability to cope with the associated hydrological constraints predicted for the Negev region.

Keywords Water · Stable isotopes · Climate change · Drought tolerance · Aridity

Communicated by David Tissue.

Highlighted student paper: Our results indicated that certain desert plant species, especially shallow-rooted species, depend on dew. This study is the first, to our knowledge, to show directly that several desert species utilize dew as a water source and sheds new light on the intricate balance between plants and their surroundings, especially in ecosystems in which water is limited. In light of predicted desertification and climate change, the use of dew as a water resource by plants may serve an important role in plants in general and specifically in arid and semi-arid regions worldwide.

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Introduction

Dew is often cited as a "common" or "significant" source of water in many of the world's deserts (Baier 1966; Kidron et al. 2002; Kidron 2005; Monteith 1963), and in some cases, the total accumulation of dew as measured on artificial wind-protected surfaces may reach over 30 % of the total annual water input on any given day (Agam 2005). Garratt and Segal (1988) estimated that dewfall rates on a plant's canopy can reach 0.09 mm h^{-1}. Especially in desert environments, the importance of dew as a water source for plants lies in its reliability as a water source input throughout the year as compared to the unpredictability of rainfall (Beysens 1995, Malek et al. 1999, Zangvil 1996). There is, however, an ongoing controversy as to the importance of dew for ecosystem water balance, in general, and for plants

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within arid ecosystems, in particular (Stone 1963). For such plants, dew, as a water source, may play a pivotal role in defining overall plant water status and may, in fact, shape the drought-response strategy or level of drought tolerance for a wide range of species.

The importance of dew for plants may be especially acute in water-limited environments, such as the Negev Desert of Israel. The Negev region comprises arid ecosystems and receives rain only in the winter (October–March), similar to the northern part of the Sahara (Griffiths 1972). An average of ~200 days with measurable dew formation has been reported in the Negev highlands (400–600 m a.s.l.), with an accumulated total of approximately 40 mm of water, over 30 % of the annual hydrological input (Agam and Berliner 2006; Burgess and Dawson 2004; Evenari et al. 1971; Kappen et al. 1979; Kidron 1999; Zangvil 1996). For this reason, plant biologists have conjectured for many years that dew, like fog and cloud water in other ecosystems, may be an important water source in the Negev highlands. With increased aridity expected for many regions of the globe under climate change, the importance of dew may be amplified in a broad range of different ecosystems worldwide and especially in arid regions, which also appear to be increasing in size (Rahimi et al. 2013). Such changes could significantly increase the vulnerability of plant species to the already chronic water deficits experienced in arid ecosystems, such as in the Negev Desert.

Because water availability is a major factor influencing plant growth and survival in most terrestrial ecosystems, and particularly in arid and semi-arid areas, plant adaptations to limited water availability and drought are essential for maintaining plant productivity and for sustainable and efficient use of water globally (Anderson et al. 1999; Merquiol et al. 2002). The degree of water-use efficiency (WUE), i.e., the ratio of the amount of CO_2 assimilated to the amount of water lost from plants, is one important feature that may determine how well a desert plant performs under water limitation (Bacon 2004). The trade-off between traits controlling carbon fixation and traits decreasing water loss is influenced by the integration of carbon metabolism and water use within the plant. Ben-Asher et al. (2010) found that the cost of this trade-off was reduced by the presence of dew—creating higher WUE in plants that were located in arid regions with heavy dewfall.

It is widely accepted that efficient root water uptake is also an important adaptation to water deficits (Rewald et al. 2011), especially under acute drought and/or saline conditions (Hill et al. 2013; Shelef et al. 2010). The maintenance of viable and functional roots is essential for water uptake. Interestingly, in many desert plants, such as *Artemisia sieberi* and *Salsola inermis*, it is common that the largest fraction of the total root mass is found in the top 10–20 cm of the soil profile (Eissenstat and Van Rees 1994; Fahey and Hughes 1994).

The hydrogen (δ^2H) and oxygen stable isotope composition (δ^{18}O) of rain, fog and also dew water have been used to trace which of these water sources plants might be using (Dawson et al. 2002). Through isotopic labeling within the plant (Wen et al. 2012), dew was found to flow downward from the plant canopy, and then back upward from the soil where it was later used in transpiration. For example, Breshears et al. (2008) used δ^{18}O water and water-potential analysis to demonstrate that water could be absorbed through the foliage of *Juniperus* spp. in the arid deserts of New Mexico, USA. They used isotope-labeled water to show that wetted shoots exhibited higher concentrations of δ^{18}O isotopes than control non-wetted shoots. Continuing these types of studies on dew utilization by desert plants could resolve the enigma of dew significance in the total water balance.

The overall goal of this study was to determine the role of dew for Negev Desert plants, focusing on three common Negev Desert plant species: two dominant perennial species—*A. sieberi* and *Haloxylon scoparium*—and one annual—*S. inermis*. Specifically, our aim was to quantify the relative contribution of dew to the total water balance of the different plant species. We hypothesized that the isotopic compositions of dew, soil water, and rain would be sufficiently different so that each of these water sources could be traced from their input source into the plants. The differences measured among plant species would allow us to estimate the proportional use of these water resources in situ. Finally, we hypothesized that an annual desert plant would rely more on dew as a water source compared to perennial plant species.

Materials and methods

To identify the quantity of water used and the locality of water extraction (uptake) for the study species, we employed several complementary techniques: plant and soil sampling, quantification of dew and isotopic analyses of water sources, plants and soils.

Study site and plants

The three desert species represent a dominant majority of the total plant richness of the high Negev region. We sampled and grew plants at Sede Boqer in the Negev (34°46′E 30°51′N; 460 m a.s.l.). Two are dominant perennial shrubs, *Artemisia sieberi* Besser (Asteraceae) and *Haloxylon scoparium* Pomel (Chenopodiaceae), and one is an annual plant, *Salsola inermis* Forssk (Chenopodiaceae). *S. inermis* is commonly found in saline desert habitats throughout arid Israel. It germinates in the autumn and flourishes in the summer between June and October when rain water is not available in the Negev. *A. sieberi* is a perennial shrub that has two leaf formations, one in winter and one in summer, differentiated in their morphology (Feinbrun-Dothan and Danin 1991). *H. scoparium* is a perennial woody shrub found in sandy environments and shrub steppes. It is a halophyte originating from Irano-Turanian and Saharo-Arabian ecosystems.

Rooting depth

In order to quantify the root depth of the three species under investigation, we located five plant specimens of each species in situ located in the Sede Boqer campus. The plants were completely excavated, with the full root system, from the soil. Water was applied to the area around the plant in order to moisten the soil, thereby easing the excavation and decreasing the likelihood of ruining the root system. The plants were laid out flat. The length of the roots was measured from the base of the trunk to the end of the root system.

Quantifying potential dew

A Hiltner dew balance (scale) was placed in a meteorological station at the Sede Boqer campus, with no obstruction that could prevent false dew collection. This same Hiltner dew balance was used for several years in the Negev Desert (Zangvil 1996; Zangvil and Druian 1980) and continuously recorded dew deposition. The balance continuously weighs an artificial condensation plate that hangs just above the soil surface.

Measurements using this balance were taken continuously for 1 year, during 2011. To improve its accuracy, it was connected to a data logger (Compact Self-Contained Micrologger CR23X; Campbell Scientific, USA). We kept the load cell temperature at an even level during nighttime by using a simple thermostat to eliminate a temperature effect. The data collected from this device are very convenient to obtain, yet still only provide a qualitative estimate of dew input compared to dewfall that would occur naturally because the material properties of the condensation plate are very different from those of the soil surface or of plant leaves. Also, (1) the plate hangs just above the soil surface with an air gap, thus effectively isolating it from the soil; (2) the plate is made from thin plastic, a very different type of material from those composing soil and plant leaves; and (3) the dew condensing on the plate accumulates on its surface, while dew formed on natural surfaces may infiltrate into the soil or the plant. Therefore, we consider the data obtained from mass changes using the Hiltner dew balance as quantitative measures of "potential dew," or the capacity of the air above the soil surface to provide condensate (liquid water); this capacity is largely determined by atmospheric conditions (Ninari and Berliner 2002).

In addition to the Hiltner balance, dew was also collected adjacent to plants in the field. Pre-weighed Kim wipes (Kimtech Science, Kimberly Clark Global Sales, GA) were placed outside in the evening, then collected and sealed in glass vials, with three replicates per day. These collections were made over a 2-month period twice a week. The weight was recorded, and then the samples were dried for 24 h at 65 °C and weighed again for dry weight. The difference represented the amount of dew collected near plants. Plant relative water content was also measured following Rachmilevitch et al. (2006). The dew that had accumulated on the Kim wipes was correlated to the relative water content of the plants to see if there was an association between dew accumulation and plant absorption.

Isotope analysis

Isotope abundance in our water samples was determined with mass spectrometry. Natural abundance stable isotope composition is calculated as:

$$\delta^{XX}E = \left({}^{XX}R_{\text{sample}}/{}^{XX}R_{\text{standard}} - 1\right) \times 1000\ ‰;$$

where E is the element of interest, H or O in this research; XX is the mass of the rarest and heaviest stable isotope for that element (^{2}H or ^{18}O for water); and R is the ratio of the abundances of the isotopes under investigation (e.g., $^{2}H/H$ or $^{18}O/^{16}O$). Due to the very small absolute differences resulting in the samples and the standard (in our case Vienna standard mean ocean water), the ratio is multiplied by 1,000 to express the isotope ratio in per mil (‰) or parts-per-thousand notation. The resulting difference or delta (δ) value is the amount of rarest to commonest (heavy to light) isotopes in the sample being analyzed. Positive values indicate that the sample has more heavy isotopes present than the standard, whereas negative values indicate that the samples contain lighter isotopes than the standard (Dawson and Simonin 2011).

Dew and stem samples (replicates of $n = 3$) from *S. inermis, A. sieberi* and *H. scoparium* were collected twice a week just before sunrise at the study site from March to July 2011. Stems were cut (5 cm), and leaves were removed from them to eliminate photosynthetic material; the stems were then placed in tubes, sealed immediately and stored at 4 °C until analyzed at the Center for Stable Isotope Biogeochemistry at UC Berkeley for isotope composition (see below).

Soil samples (replicates of $n = 3$) were collected at depths between 10 and 30 cm belowground under each plant species from March to July 2011. These samples were also stored at 4 °C until taken to the UC Berkeley isotope lab for isotope analysis. Water was extracted from all of the samples using cryogenic vacuum distillation (Ehleringer et al. 2000). The isotope ratio of each water sample was determined by three methods: combusting approximately 2 μL of water in the presence of hot (800 °C) Cr using the H/Device for hydrogen isotope (δ^2H) composition; with CO_2–H_2O equilibration for oxygen isotope (δ^{18}O) composition, both interfaced to a Finnigan MAT Delta-plusXL isotope ratio mass spectrometer (IRMS) (Bremen, Germany) (for plant samples); and using isotope ratio infrared spectroscopy (IRIS) (West et al. 2010) only for the pure dew samples. Long-term external precision for IRMS was 0.18 ‰ for δ^2H, 0.12 ‰ for δ^{18}O using IRMS and 0.22–0.33 ‰ for both isotopes using IRIS.

Isotope mixing model

Dew water use by each plant species was determined using a simple two-source mixing model after Phillips and Greg (2001) as:

$$f = (\delta^{18}O_{xylem} - \delta^{18}O_{deepsoil})/(\delta^{18}O_{dew} - \delta^{18}O_{deepsoil})$$

where "xylem" is the plant water isotope composition, "dew" is the dew water isotope composition, and "deep-soil" is the isotope composition of soil water around plant roots derived from precipitation inputs but not from dew inputs. In this case, if *f* is greater than one, it means that dew water is the dominant water source used by the plant, and when *f* is less than 0, water comes exclusively from the soil (precipitation derived). Values ranging from 0 to 1 indicate a mixture of sources between dew and soil.

Statistical analysis

For statistical tests, JMP 7.0.1 (SAS Institute, Cary, NC) was used. Statistical analyses were performed on data sets between the root lengths of all three species and compared to the amount of dew used by the plants; Spearman's ρ was used for correlation analysis. The significance level applied was $P < 0.05$.

Results

Rooting depth

The maximal rooting depth of the three study species varied from very shallow to deep (Table 1). *S. inermis* had the shallowest roots reaching a maximum depth of 15–20 cm. This was 40 % shallower than *A. sieberi* and 75 % shallower than *H. scoparium*. Of the two perennial species studied, *A. sieberi* had roots reaching only 25–35 cm into the soil profile, while *H. scoparium* had the deepest roots, averaging 60–90 cm in depth.

Dew collection

Figure 1 shows dew inputs (when above 0.002 mm) that were recorded during the wet and dry seasons of 2011. Along with our dew collection, we also gathered rainfall inputs during 2011 from the weather station located at the Sede Boqer campus.

Figure 1 shows the year-long dew collection record in 2011; dew amounts increased around rain events. While dew was measured year round, our data indicate that significant dewfall events occurred about 200 days per year (55 % of all days). There were very few days when levels reached 15 mm or greater.

Dew accumulation and relative water content

The correlation between the amounts of dew that accumulated on plant leaves and a plant's relative water content (Fig. 2a–c) showed that with greater dewfall and resultant water accumulation on leaf surfaces, there was more moisture absorbed by the plants. We found this in all three species; *A. sieberi* (Fig. 2b) showed a slope in the relationship of 0.63, while *H. scoparium* (Fig. 2c) had a slope of 0.79. The slope for *S. inermis* was 0.64, but reached a higher level of dew accumulation (0.8 g, maximum; Fig. 2a) compared with the *A. sieberi*, which accumulated a maximum of 0.47 g, and *H. scoparium*, which accumulated approximately 0.3 g of dew on the leaves, in a single dew event. *S. inermis* had an R^2 of 0.56 ($P < 0.00001$), a 48 % higher correlation than that of *A. sieberi*, which had an R^2 of 0.29 ($P < 0.00002$). *H. scoparium* had the lowest correlation ($P < 0.00035$) between dew accumulated and water absorbed by the plant. The analysis of *S. inermis* showed that any amount of dew that had accumulated on the leaves seemed to be absorbed by the plant leaves due to the high correlation between relative water content and dew accumulation. The accumulation of dew on the leaves is apparent but needs to be further investigated to find its actual significant influence.

Table 1 The average root depth of the three study species, *Artemisia sieberi*, *Haloxylon scoparium* and *Salsola inermis*, in Sede Boqer, December 2012 (SE, $n = 5$)

Species	Average root depth (cm)	Percent dew used[a]
Salsola inermis	15.4 ± 1.02	48–63
Artemisia sieberi	34 ± 3.34	55–71
Haloxylon scoparium	90 ± 6.6	38–55

[a] Percentage of the extracted water from each plant species that was derived from dew based on isotope mixing model (see text)

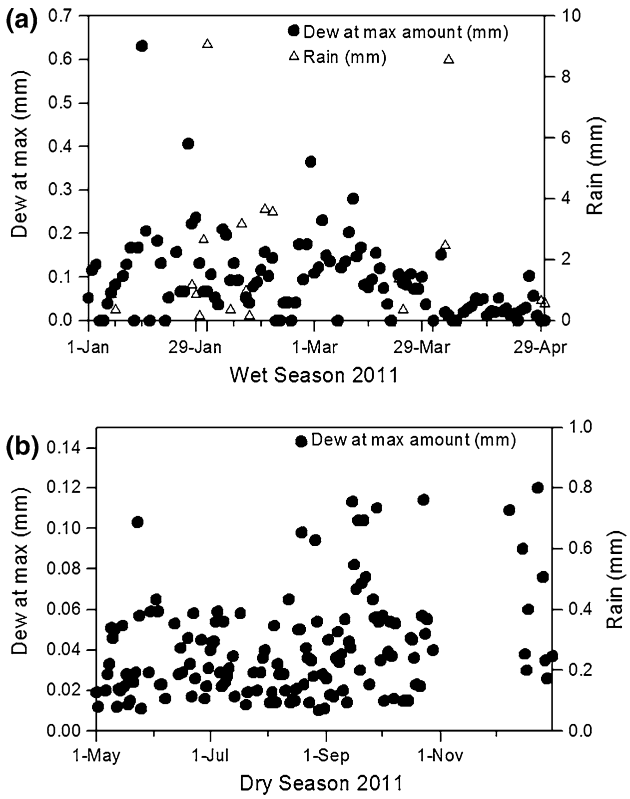

Fig. 1 Dew and rain precipitation in the Sede Boqer region for January 2011–January 2012. **a** Wet and **b** dry seasons; there is no rain in the latter. Dew at maximum was the highest amount of dew collected overnight on a calibrated and temperature-resistant Hiltner scale. Rain was collected from a meteorological site next to the Hiltner system

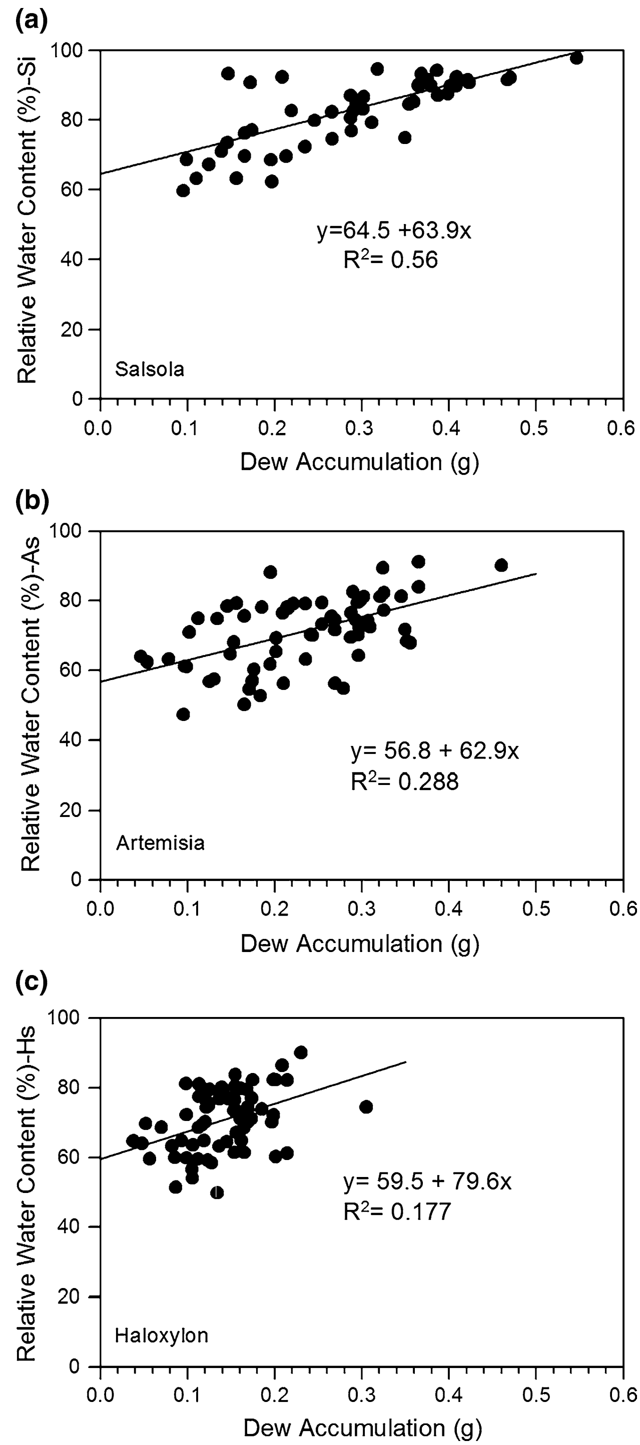

Fig. 2 **a** Correlation between dew accumulation and relative water content of *Salsola inermis* (*SI*; $n = 40$), **b** correlation between dew accumulation and relative water content of *Artemisia sieberi* (*AS*; $n = 40$), **c** correlation between dew accumulation and relative water content of *Haloxylon scoparium* (*HS*; $n = 40$). Dew accumulated on all the plants and relative water content is plotted on a scatter plot for the days dew was collected

Isotopic composition and meteoric water lines

The relationship between δ^2H and δ^{18}O of rainfall locally collected—the local Eastern Mediterranean meteoric water line described by Gat (1987) ($\delta^2H = 20.7 + 8 \times \delta^{18}O$)—did not exactly match what we found here due to the different locations; therefore, we used our local rain collection samples, soil water samples and locally collected dew samples, all plotted in Fig. 3a. In Fig. 3b, we have left the lines but not the symbols from Fig. 3a (from the rain, dew and soil water sources) in this figure we have now added our plant water data so that the plants can be viewed in relation to the water source lines. Using the approach described in Goldsmith et al. (2012), that provides a graphical model showing the relationship between the water source lines (in their case the local meteoric line from rainfall samples and the soil water evaporation line) our results show that the plant waters lie above both the rain water (local meteoric)

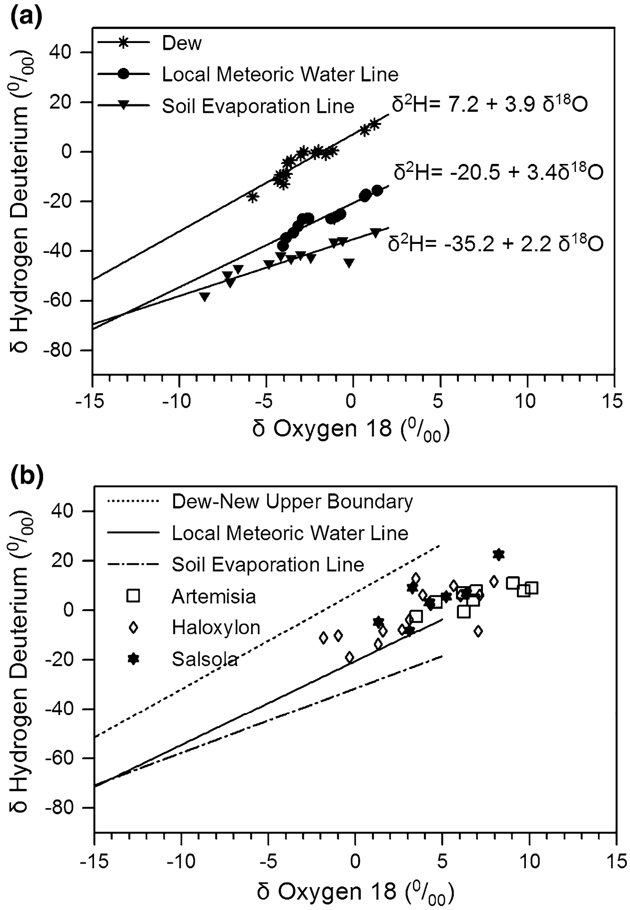

Fig. 3 **a**, **b** Local meteoric water line, dew and soil evaporation of hydrogen (δ^2H) and oxygen stable isotope composition (δ^{18}O). Water isotope samples of dew rain and soil were collected between March 2012 and August 2012. The local meteoric line ($\delta^2\text{H} = -20 + 3.5 \times \delta^{18}\text{O}$), the dew line ($\delta^2\text{H} = 7.2 + 3.9 \times \delta^{18}\text{O}$), and the soil evaporation line ($\delta^2\text{H} = -35.2 + 2.2 \times \delta^{18}\text{O}$)

and soil evaporation lines and close to the dew water line. This provides support for our interpretation that a significant fraction of a plant's water is derived from the dew, represented by the "upper" boundary (dew) for the water source lines. The relationships between the δ^2H and δ^{18}O of dew, plant stem water, soil water, and local precipitation are also plotted in Fig. 4a–c. *S. inermis* (Fig. 4a) had an isotope composition that suggested it was using surface soil moisture that originated from dew water deposition but was subsequently influenced (enriched) by surface evaporation. The isotope composition of plant water that we obtained for both *A. sieberi* (Fig. 4b) and *H. scoparium* (Fig. 4c), as well as from the soil water sampled from around each of these plant species, differs significantly from the isotope values of our dew samples, as well as of dew water

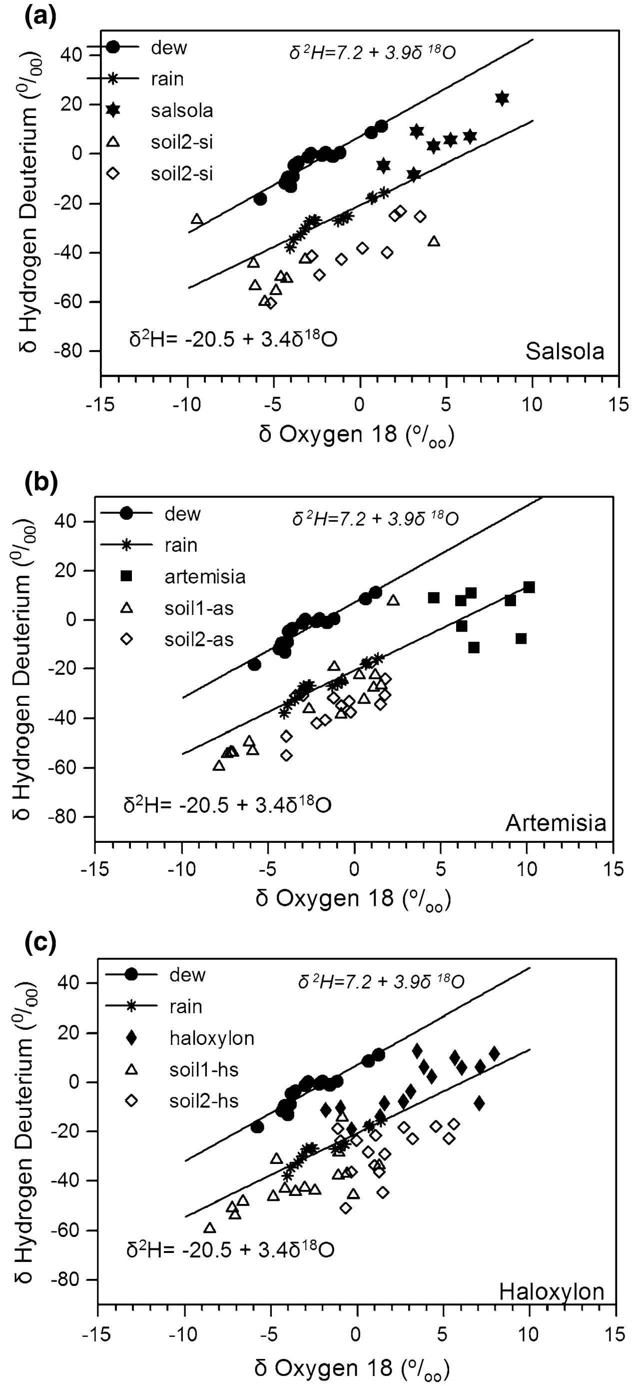

Fig. 4 Correlation between δ^2H and δ^{18}O in dual isotope space. Water isotope samples of dew, plant stems and soil were collected between March 2012 and August 2012. The plant stems, soil1 at 15-cm (shallow), soil2 at 30-cm (deep) depths and dew were all collected on the same date and from the same location; rain samples were collected from Sede Boqer (plant and soil samples $n = 30$, dew and rain samples, $n = 10$). **a** δ^2H and δ^{18}O of *S. inermis*, **b** correlation between δ^2H and δ^{18}O of *A. sieberi*, **c** correlation between δ^2H and δ^{18}O of *H. scoparium*. For abbreviations, see Fig. 2

that had been deposited and later (after sunrise) influenced by evaporation. Soil water isotope values also plot, relative to our local meteoric water line, in a manner that suggests that they were influenced by evaporation. The higher (more positive) isotope values shown indicate that all of our study plants used a mixture of water sources with *S. inermis* showing the greatest bias toward the use of dew water. In contrast, *A. sieberi* and *H. scoparium* used mostly water derived from deeper in the soil along with a mixture of dew.

Mixing-model results

Using the isotope data from the plant and source waters, we employed a two-source linear mixing model to determine the proportional use of different water sources (dew or soil water not from dew) used by each plant species. The model output shows that *S. inermis* used between 48–63 % of water derived from dewfall inputs, while *A. sieberi* used between 55–71 % of water derived from dewfall inputs (Table 1). *H. scoparium* used a combination of dew water and some soil water, with dew water constituting between 38–55 % of the water within the plant.

Isotopic composition throughout the season

The stable water isotope compositions of dew, plant water, and soil extracted from 15- and 30-cm depths were plotted throughout the entire period of the investigation against δ^2H and δ^{18}O. From this plot, we see that the dew water and stem water of the *S. inermis* followed the same line (Fig. 5a, d); soil water from around this plant species was the least similar to the dew water. Water extracted from *A. sieberi* (Fig. 5b, e) overlaps with both dew and soil water, while water extracted from *H. scoparium* (Fig. 5c, f) shows the greatest overlap with soil water and little overlap with dew water. These time-series plots of isotope composition corroborate our calculations using the mixing model, with implications for different amounts of the different water sources used by each of the three plants.

Correlation between root length, dew accumulation and dew usage

A Spearman's ρ analysis revealed a significant correlation between root lengths and dew accumulation in the plant species *S. inermis* (Spearman's $\rho = 0.46$) and *A. sieberi* (Spearman's $\rho = 0.56$), but no correlation for *H. scoparium* (Spearman's $\rho = -0.4$) (Table 2). All three species showed a correlation between their root length and the percent of dew they each used; *S. inermis* (Spearman's $\rho = 0.6$) displayed the highest correlation between root depth and dew usage, while *A. sieberi* (Spearman's $\rho = 0.1$) displayed the least; *H. scoparium* (Spearman's $\rho = 0.4$) also showed a correlation.

Discussion

Our results show that dew-water utilization exists in all three Negev Desert plant species that we investigated, providing the first direct evidence that plants utilize dew as a water resource in the Negev Desert. Not unlike previous studies that have explored summer rainwater utilization (Ehleringer and Dawson 1992), fog water acquisition (Dawson 1998), and cloud water/mist use (Goldsmith 2013; Berry and Smith 2013; Gotsch et al. 2014a, b), in the absence of a summer rain period, it appears that the plants we investigated use significant fractions of non-rain-derived sources of water (e.g., fog, mist, dew). Past research on the influence of dew has focused on non-vascular plants (Lange et al. 2007), and our data show that dew is a frequent water input and advantageous for the physiology of these species. Perhaps the best-known examples of the influence of dew come from investigations of the so-called resurrection plants and from studies of cyanobacteria and lichens (Agam and Berliner 2006; Harel et al. 2004; Kidron 2000); the results presented here show that vascular plants in these arid and dew-prone ecosystems also utilize dew as a water resource. The current study clearly demonstrates that dew is an important water source for desert plant species. This finding may also have implications for other vascular plant species of this flora.

Though dew is considered to make a relatively small contribution to the overall input of water sources to any ecosystem, in high deserts, like the Negev, that can be severely water limited, dew appears to be an essential resource for the continued functioning and possibly the survival of, particularly, shallow-rooted annuals or resurrection plants like lichens, mosses and some fern species. A study on desert lichens showed that dew water enhanced photosynthesis in the early morning hours but did not have the same effect in the vascular plant *H. scoparium* (Lange et al. 1986). However, in other studies of non-vascular plants, dew water use does appear to have a positive influence on the carbon balance during the early morning hours. For example, heavy dew was found to cause a positive daily carbon balance for some desert mosses (Csintalan et al. 2000).

Our isotope data provide further evidence that dew water for Negev Desert plants is an important water source. For example, the δ^2H data for plant stem water lies along the evaporation line between rainfall and dew water, suggesting that plants use a mixture of these two water sources (the end members along the mixing line). Also, the δ^2H data show that the stem water of *S. inermis*, the annual species, has a stem-water isotope composition most similar to that of dew water, and quite different from the soil water isotope

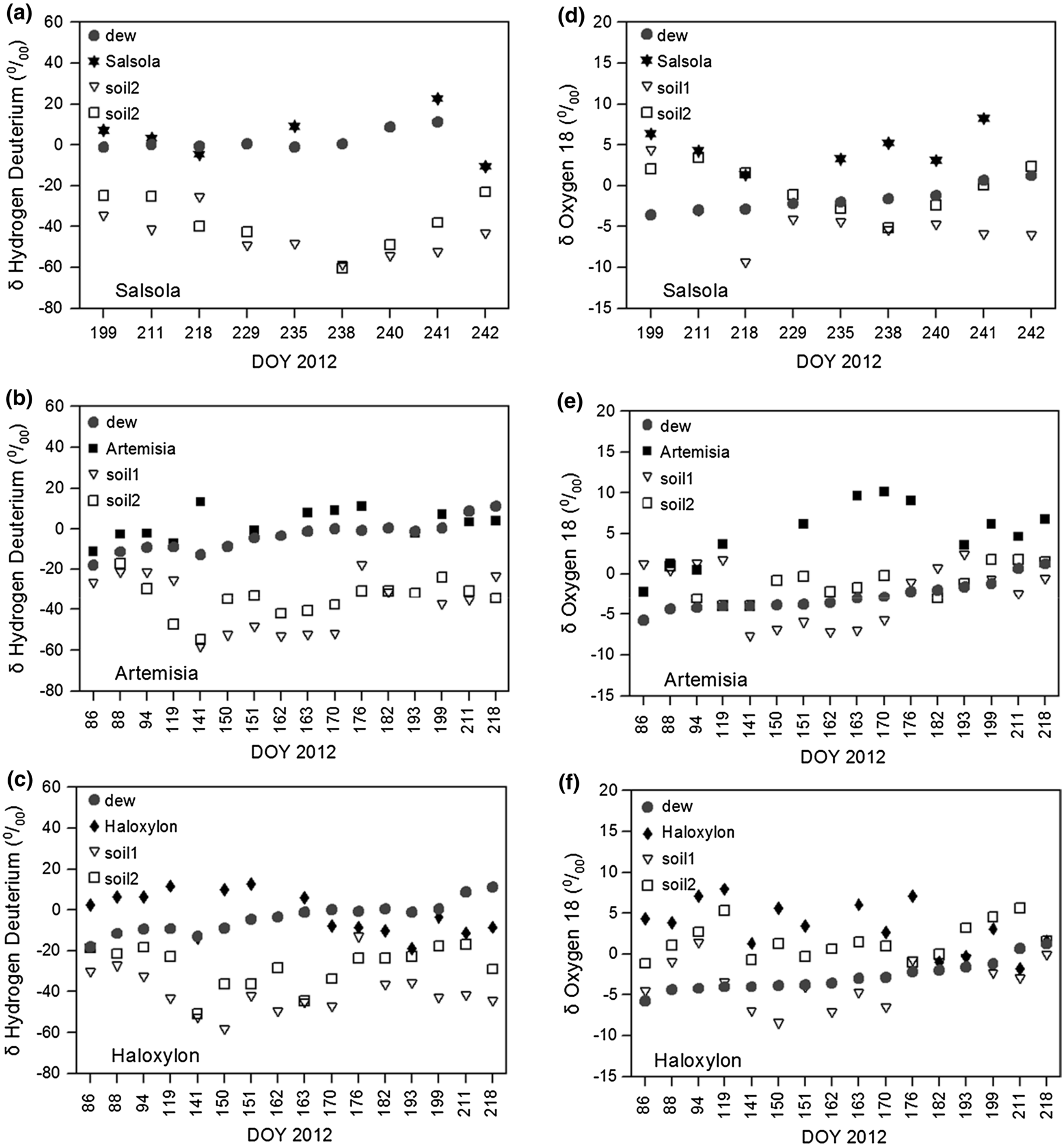

Fig. 5 δ^2H and δ^{18}O from March to August 2012 of stems, shallow soil1 (15-cm depth) and deep soil2 (30-cm depth) from the same date and location in Sede Boqer; **a** δ^2H of *S. inermis* (plant and soil samples, $n = 30$; dew samples, $n = 10$); **b** δ^2H of *A. sieberi* (plant and soil samples, $n = 55$; dew samples, $n = 20$); **c** δ^2H of *H. scoparium* (plant and soil samples, $n = 55$; dew samples, $n = 20$); **d** δ^{18}O of *S. inermis* (plant and soil samples, $n = 30$; dew samples, $n = 10$); **e** δ^{18}O of *A. sieberi* (plant and soil samples, $n = 55$; dew samples, $n = 20$); **f** δ^{18}O of *H. scoparium* (plant and soil samples, $n = 55$; dew samples; $n = 20$)

values. In contrast, *H. scoparium* and *A. sieberi*, the perennial species, showed a more mixed stem-water isotope ratio with a bias towards the soil–water source although they still used dew at a high percentage as well.

For *S. inermis* and *A. sieberi*, there was a statistically significant correlation between dew-water use, plant relative water content, and root length, with the shallowest rooted species possessing the highest use of dewfall inputs.

Table 2 Percentage of dew water for each plant species and its correlation to root length

Species	% Dew usage to root length (Spearman's ρ)	Relative water content to root length (Spearman's ρ)	Dew accumulation to root length (Spearman's ρ)
S. inermis	0.61	0.21	0.46
A. sieberi	0.1	0.46	0.56
H. scoparium	0.4	0.2	−0.4

Spearman's ρ non-parametric test

In contrast, *H. scoparium* seemed to only use dew when soil water was in short supply; this also likely occurred because its leaves possess smooth scales that cannot absorb and collect the dew. The importance of the dew that accumulated on the plant from the blotting paper and the amount of dew overnight in the relative water content results is represented by the slopes in Fig. 2a–c, in that the higher R^2 in *S. inermis* shows the higher absorption of dew by the plant when there was more dew present, while *H. scoparium* had a 68 % lower correlation than *S. inermis*, and we see that it is clearly using less dew even when dew is present in the atmosphere and on the leaf surface.

Ecological implications

The ability of desert plant species to utilize dew water and not depend solely on stored soil water derived from precipitation may permit them to grow and survive in areas that they otherwise might not. Under severe water limitation brought about by increased drought, a plant's ability to use other water sources, such as dew, would be highly advantageous. In fact, in some exceptional cases, dew is probably the sole water source for plants, such as in the case of *Prosopis tamarugo* in the rainless Atacama Desert of northern Chile (Mooney 1978). Went (1975) calculated that cooling of the *Prosopis* spp. during the moist summer nights should produce sufficient condensation to provide a full water supply for the plant. Moreover, the capacity to utilize dew water may also extend the growth and reproductive periods for certain species.

There are also important ecophysiological implications of the data here that suggest further investigation. First, it appears that certain desert plants, especially shallow-rooted annual species, may depend on dew for survival. The isotopic signatures of dew water and stem water are correlated, suggesting use of dew water rather than soil water, as we could distinguish between these water sources. Second, the perennial deep-rooted plants have less dependence on dew water, but rather use soil water, a deeper water source. This may explain their survival in summer and drought seasons, based on dew usage for certain desert plants. In addition, plant relative water content was correlated with the amount of dew that accumulated on the plants and corroborated the isotope data. For example, we can see that the annual species absorbed more dew when there was more dew available.

The Intergovernmental Panel on Climate Change has evaluated the historical records from many weather stations worldwide. These data show a trend towards increasing durations of severe droughts, a trend toward increased surface temperatures, and a trend towards decreasing rainfall (Solomon et al. 2007). These major components of climatic change constitute the key elements of the desertification processes that countries within and bordering semi-arid regions, and even within some temperate zones, are experiencing, and that have increased in recent decades (García-Ruiz et al. 2011). In this context, current model predictions for arid and semi-arid regions clearly show that future precipitation patterns for the entire Middle East, including Israel and the Negev Desert, are characterized by a trend towards diminished precipitation and further enhancement of desertification (García-Ruiz et al. 2011). However, other models predict dramatic shifts in rainfall patterns worldwide (Arnell 2004), with more precipitation in the rainy season coupled with longer and more acute dry seasons (Trigo et al. 2004). In Mediterranean climate zones in general, most models still predict a decrease in precipitation, as well as an overall temperature increase (Abdulla et al. 2009). If drought were to increase in magnitude and duration in the future, the capacity of plants to utilize dew water will become even more important than it currently is. But how dewfall may also change, if in fact it does, is not yet known nor represented in any climate change models or predictions.

Author contribution statement A. J. H. designed and carried out the experiment, analyzed the data and wrote the manuscript. T. E. D. analyzed the isotope samples and helped analyze/interpret the data and write the manuscript. O. S. helped set up the experiment, perform measurements and write the manuscript. S. R. helped design the experiment, analyze results and write the manuscript. All authors helped with revisions.

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