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The ecological role of dew in assisting seed germination of the annual desert plant species in a desert environment, northwestern China

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Abstract: It is important to understand the effects of dew events on non-mucilaginous seed germination of annual desert plant species during dry seasons, which is critical to maintaining long-term soil seed banks in a harsh desert environment. We hypothesize that dew deposition also assists in the non-mucilaginous seed germination of annual desert species. A common field dew treatment experiment was conducted in the Linze Inland River Basin Research Station to investigate the effects of dew deposition on the seed germination of four annual species, including *Agriophyllum squarrosum*, *Corispermum mongolicum*, *Bassia dasyphylla* and *Halogeton arachnoideus*. The results showed that the presence of dew significantly increased seed germination percentages and decreased the nonviable seed percentages of *B. dasyphylla* and *H. arachnoideus*, whereas there was no such trend for the seeds of *C. mongolicum* and *A. squarrosum*. The ecological effects of dew on the seed germination and viability of the annual desert plants were species specific. Although dew wetting is insufficient to cause seed germination, it may help in priming the seeds.

Keywords: dew deposition; seeds hydration and dehydration; seeds viability

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A steady supply of water is critical to seed germination, as well as to the growth and survival of plants, with conditions of water status being of particular importance in arid environments. Dew, as a supplementary water source, has an important ecological role in desert environments, where water resources are severely limited (Stone, 1957a, b; Breshears et al., 2008; He and Richards, 2015; Temina and Kidron, 2015). Dew provides a supplemental moisture source for plants, biological soil crusts, insects and small animals in arid environments (Jacobs et al., 1999; Kidron, 1999; Kidron et al., 2002; Zhuang and Ratcliffe, 2012, Kidron and Temina, 2013). Numerous studies in the last several decades have aimed at understanding the ecological significance of dew for the survival of plants, especially water-stressed plants in sandy areas (Stone, 1957a, b; Grammatikopoulus and Manetas, 1994; Boucher et al., 1995; Munné-Bosch et al., 1999; Hill et al., 2015). Coniferous species, rainforest trees, Presaharian plants and Mediterranean plants benefit from dew. Dew has been found to improve the survival rates of tree species (Stone, 1957a, b; Barradas and Glez-Medellín, 1999; Jacobs et al., 2000) and the water supplies of two evergreen shrubs (Munné-Bosch et al., 1999), as well as to reduce plant transpiration rates (Stewart, 1977)

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during the dry season. Dew also helps many trees (such as citrus, tropical deciduous trees and coniferous species) and food plants (such as watermelon, cucumber and beans) recover from water stress (Stone, 1957b; Duvdevani, 1964; Boucher et al., 1995; Clus et al., 2008). Therefore, the ecological significance of dew as an important additional water resource in the desert ecosystem cannot be ignored.

The role of dew in seed germination of psammophytes has been recognized. It has been suggested that the germination of desert annual plant species producing mucilaginous seeds is enhanced by frequent dew events (Gutterman and Shem-Tov, 1997). Desert dew assists seed cells by providing them with mucilage, which has a high capacity for absorbing and retaining water, thereby improving the seeds' ability to maintain DNA integrity (Yang et al., 2011) and giving them an advantage over plants with non-mucilaginous seeds. Yet, a less clearly appreciated characteristic of dew events is their importance to the non-mucilaginous seed germination of the annual desert plants. Knowing if and how the non-mucilaginous seed germination of the annual desert plants is influenced by dew events during the dry season is critical to maintaining a long-term soil seed bank in harsh desert environments.

A unique characteristic of the seed banks of the annual desert plants is their location at or very near the soil surface (Gutterman, 2002). The dew active layer is limited to the first 0–3 cm depth of the upper soil in the desert environment (Pan et al., 2010; Zhuang and Zhao, 2014), which enables it to moisturize this important surface layer. The frequent occurrence of dew events and the characteristics of the top soil layer lead us to question previous assumptions about the ecological significance of dew events to the seeds of the annual desert plants. As the first step in understanding the role of dew events in desert ecosystems, we investigated the influence of dew events on seeds of *Agriophyllum squarrosum* (Linn.) Moq, *Corispermum mongolicum* lljin, *Bassia dasyphylla* (Fisch. et Mey.) O. Kuntze and *Halogeton arachnoideus* Moq, the dominant annual grasses at the edge of Badain Jaran Desert of northwestern China. Our objective was to test the hypothesis that dew events are an important resource for the seed germination of the annual desert plants in arid lands and hence are ecologically significant to the survival and regeneration of these species in harsh desert environments.

1 Materials and methods

1.1 Study area

This study was conducted at a fixed sand dune near the Linze Inland River Basin Research Station (39°21′N, 100°07′E), Chinese Ecosystem Network Research at an elevation of 1,382 m asl, adjacent to the Badain Jaran Desert in Northwest China. The climate in this region is temperate continental, characterized mainly by aridity, high temperature and strong wind. The annual mean temperature is 7.6°C, with a maximum of 39.1°C in July and a minimum of –27°C in January. The mean annual precipitation is 117 mm, with 65% falling from July to September. The mean annual potential evaporation and total number of sunlight hours are 2,390 mm and 3,045 h, respectively. The soil is characterized by sandy, sandy loam and grayish brown desert soil. In the study region, dew occurs most frequently from June to the end of September, and makes a major contribution to the total growing season environment. Dew depositions occur in the early morning with low temperature and high relative humidity. Dew amounts in the sand include both dew formation and water absorption.

1.2 Plant species

A. squarrosum, *C. mongolicum*, *B. dasyphylla* and *H. arachnoideus*, the most important annual psammophytes, are widely distributed in the dunes of the temperate sandy deserts of Central Asia. In the study area, an arid region in northwestern China, these four species are also the dominant annual plants on active sand dunes. These species all have strong resistance to wind erosion and drought. Seeds of the four species usually germinate from late May to August, after the soil has been moistened by adequate precipitation, and fruits set in late September.

In October 2012, freshly matured seeds of four species were collected from dry unopened infructescences from natural populations near the Linze Inland River Basin Research Station, Chinese Ecosystem Network Research. In the laboratory, infructescences were manually shaken to detach the seeds and were stored in a closed bag at 5°C until being used in the experiments.

1.3 Dew exposure treatment in the desert

In a natural desert habitat, a dew observation experiment was conducted to clarify the trend of dew occurrences during the experiment (from 20:00 27 August to 20:00 31 August, 2013). One hundred milligrams of seeds were spread evenly on the surface of sand that had been collected from a nearby sand dune, rinsed with distilled water and dried in an oven. The sand samples were spread in Petri dishes to a depth of 10 mm. Petri dishes (4 species×4 nights×3 replicates) containing seeds were arranged on trays. At 20:00 27 August, 2013, the trays were brought to the sand dune, and three replicated Petri dishes of each species were sampled every 24 h at 20:00. The seeds absorbed water from the air when relative humidity (RH) was above 50% (Zhuang and Zhao, 2014); therefore, we defined the time period of RH above 50% as dew deposition time. Accumulative dew deposition time was recorded and considered as dew treatment time. Sampled seeds were immediately separated from sand by sieving and were enclosed in Eppendorf tubes until further analysis.

For monitoring the hydration and dehydration of seeds, we placed three replicates of 100 mg seeds on the trays and weighed every 1 h repeatedly using an analytical balance (BS221S, Sartorius, Germany) throughout the experiment. The dew treatment experiment was carried out for 96 consecutive hours and no rainfall occurred during the experimental period. Air temperature, relative humidity, wind speed and dew-point temperature at 2 m height above the soil surface were measured using an automated weather station (M520, Finland) in the field.

1.4 Germination and viability tests

For investigating the effects of dew on the germinability and viability of the seeds, we incubated seeds at 4 dew treatment times under germination conditions for 30 d, after which un-germinated seeds were tested for their viability. For each dew treatment time, three Petri dishes with 50 seeds of each species were used in the germination tests. Distilled water (2.5 mL) was added to each Petri dish (5-cm in diameter) with two layers of No. 1 Whatman filter paper, after which all Petri dishes were sealed with Parafilm to minimize water evaporation. These seeds were incubated in an incubator (BINDER, Germany) and germination was monitored every 24 h for 30 d. Seeds were considered germinated if radicles emerged. Germination percentages were then calculated. After the 30-d incubation, the viability of un-germinated seeds was tested by the TTC (2, 3, 5-triphenyl tetrazolium chloride) method (Baskin and Baskin, 1998). Embryos were placed in 0.5% TTC and incubated at 25°C for 24 h, and then embryos with more than 80% area stained were scored as viable; otherwise they were scored as nonviable.

1.5 Statistical analysis

The effects of dew deposition on seed germination and viability were analyzed using one-way ANOVA in the treatments. Least significant difference (LSD) tests were performed to determine significant differences ($P<0.05$) in dew treatment time on seed germination and viability in each species with Tukey's HSD test. Statistical analysis was performed with software R 3.2.0.

2 Results

2.1 Dew deposition in the desert

Temperature and RH are shown in Fig. 1. Throughout the dew observation experiment, dew deposition duration was different every night, ranging from 60 to 720 min per night. The longest and the shortest dew deposition times occurred on 27 August (720 min) and on 29 and 30 August (60 min), respectively. Dew deposition time was 660 min on 28 August. Therefore, accumulative dew time was 720, 1,380 (720+660), 1,440 (720+660+60) and 1,500 min (720+660+60+60)

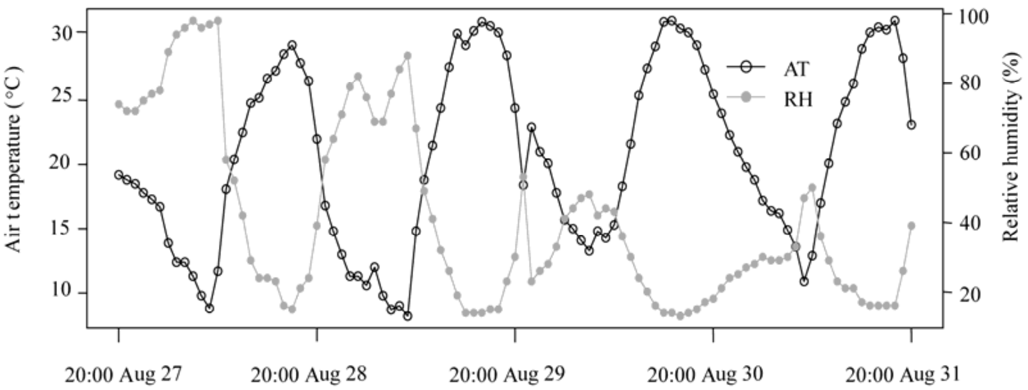

Fig. 1 Air temperature (AT) and relative humidity (RH) during the dew experiment

after 1, 2, 3 and 4 nights of dew treatment, respectively. From these data, it can be seen that dew formation, as a supplementary water source, is frequent and common in desert habitats. The previous study demonstrated the amount of dew per day at the study area was mostly below 0.1 mm. High temperatures would result in an increase of evaporation and a decrease of near surface relative humidity, with a consequent of reduction in dew formation.

2.2 Seed hydration and dehydration

The seed weights of *B. dasyphylla* were the highest after absorbing dew, over the entire observation period. The seed weights of *C. mongolicum* were the lowest compared to other species, whereas *H. arachnoideus* and *A. squarrosum* were intermediate. The average seed weights of *B. dasyphylla*, *H. arachnoideus*, *C. mongolicum* and *A. squarrosum* increased to 130.07%, 127.38%, 121.00% and 117.54% of their initial weights, respectively, at 7:00, over the whole observation period. At 7:00 on 28 August, the seeds of all four species reached their highest weights. The seed weights of *B. dasyphylla* and *H. arachnoideus* increased to 148.3% and 145.0% of their initial weights, respectively, at 7:00, while at the same time *C. mongolicum* and *A. squarrosum* increased to only 134.0% and 128.2%, respectively. In addition, after reaching to their highest weight at 7:00 on 28 August, *B. dasyphylla* and *H. arachnoideus* took 5 h to recover to their original weight, while *C. mongolicum* and *A. squarrosum* took only 3 h to do so (Fig. 2).

2.3 Seeds germination and viability

There was an accelerated trend in the germination percentages for *B. dasyphylla* and *H. arachnoideus*

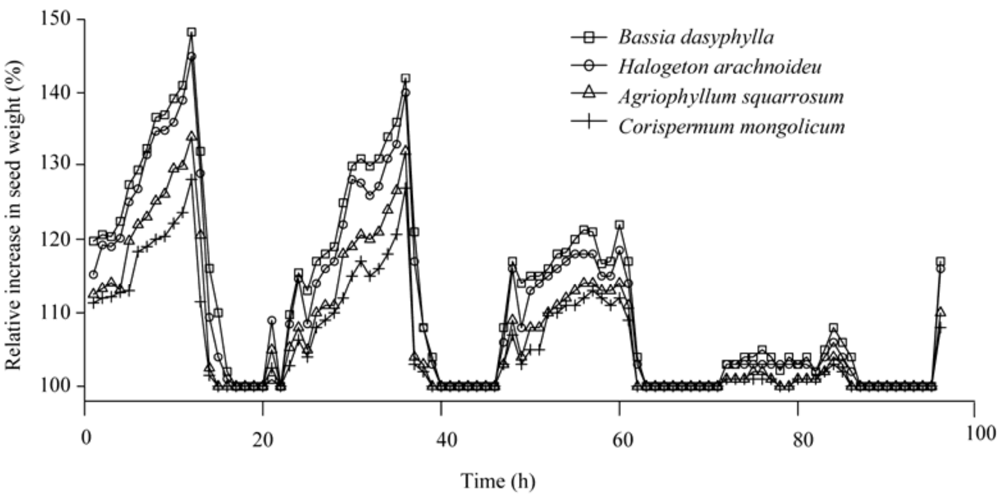

Fig. 2 Relative increases in seed weights of *A. squarrosum*, *B. dasyphylla*, *C. mongolicum* and *H. arachnoideus*

during the dew experiment (from 20:00 27 August to 20:00 31 August, 2013)
after dew treatment (Fig. 3). In addition, the germination percentages of the two species were significantly affected by dew treatments (*F*=83.6, *P*<0.001; *F*=108.2, *P*<0.001, respectively), whereas dew did not cause a significant difference for *C. mongolicum* and *A. squarrosum* (*F*=0.999, *P*=0.336; *F*=0.591, *P*=0.456, respectively). Moreover, the germination percentages for *B. dasyphylla* and *H. arachnoideus* increased to 17.5% and 19.1% after the first day of dew treatment, and the highest increases (28.3% and 30.0%, respectively) occurred at the fourth day for *B. dasyphylla* and *H. arachnoideus*. However, there was no increasing trend in the germination percentages for *C. mongolicum* or *A. squarrosum* after 4 nights of dew treatment.

The percentages of nonviable seeds for *B. dasyphylla* and *H. arachnoideus* were significantly decreased (*F*=97.43, *P*<0.001; *F*=128.8, *P*<0.001, respectively), whereas there was no significant decrease for *A. squarrosum* after the dew treatment (*F*=0.591, *P*=0.456; Fig. 4). Meanwhile, there

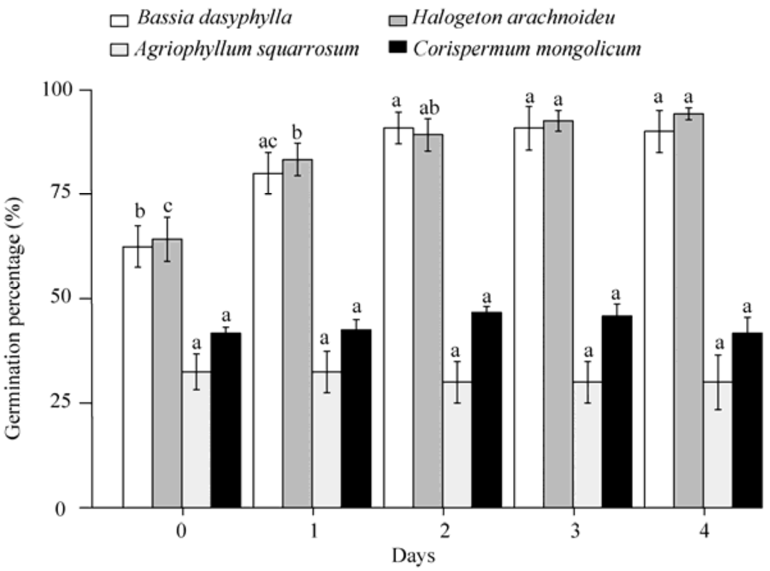

Fig. 3 Germination percentages of *A. squarrosum*, *B. dasyphylla*, *C. mongolicum* and *H. arachnoideus* after dew treatment. Different lowercase letters indicate significant differences among treatments. Mean±SE, *n*=3.

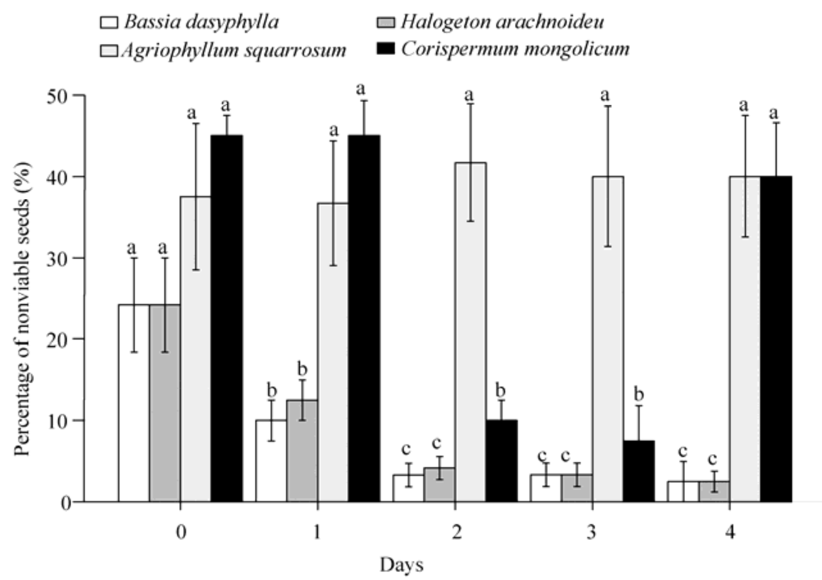

Fig. 4 Nonviable seed percentages of *A. squarrosum*, *B. dasyphylla*, *C. mongolicum* and *H. arachnoideus* after dew treatment. Different lowercase letters indicate significant differences among treatments. Mean±SE, *n*=3.

was a nearly 20% decrease in nonviable seeds for *B. dasyphylla* and *H. arachnoideus* after the first day of dew treatment. In addition, the percentage of nonviable seeds of *C. mongolicum* also significantly decreased to 7.5%, after 2 days of dew treatment, but it subsequently increased again at the fourth day of dew exposure.

3 Discussion

Previous studies have indicated that dew is an important usable water resource in desert environments. Dew-water utilization by desert plants is ecologically significant and thus may be more common than previously thought (Hill et al., 2015). Dew has been shown to decrease water consumption through soil evaporation (Malek et al., 1999), to moisten desert plant species (Jacobs et al., 1999; Rao et al., 2009), and to improve the rate of mucilaginous seed germination (Gutterman and ShemTov, 1997). In Negev Desert, the shallow-rooted annual species (such as *Salsola inermis*) absorbed more dew when dew was available and might depend on dew for its survival. However, the perennial deep-rooted plants (such as *Artemisia sieberi* and *Haloxylon scoparium*) depend less on dew water, but rather use soil water, a deeper water source (Hill et al., 2015). We found out that dew deposition occurred frequently and abundant in our study area (Zhuang and Zhao, 2014). Importantly, our data showed that the effects of dew on seed germination and the viability of the annual desert plants were species specific. These results support the hypothesis that daily dew deposition has a supplementary role only for some annual desert species rather than for all the annual desert species in the harsh desert environment. These results can be attributed to the difference in water-absorbing and water-holding capacities of the different seeds.

In our study, the seed weights of *B. dasyphylla* and *H. arachnoideus* were higher than those of *C. mongolicum* and *A. squarrosum* after absorbing the early morning dew for four consecutive days (Fig. 2), suggesting that *B. dasyphylla* and *H. arachnoideus* might have higher water-carrying capacity, enabling them to absorb more water during dew formation. Furthermore, due to the evaporation, the dew that condensed on the seeds' surface depleted quickly following sunrise (Fig. 2). As for the weight losses, it took longer for *B. dasyphylla* and *H. arachnoideus* seeds than the other two species. This result also implied that the seeds of *B. dasyphylla* and *H. arachnoideus* were likely to have higher water-retention capacity, which ultimately led to a longer hydration time. The present findings were similar to those previously reported in Mu Us Sand Land for the *Artemisia sphaerocephala* achenes with mucilage, which also absorbed more water and retained it for a longer hydration time than did demucilaged achenes (Yang et al., 2011).

The responses of seed germination to environmental conditions are crucial for recruitment, especially for annual plants, which produce seeds only once a year (Tobe et al., 2005). In our study, the presence of dew had a significant positive effect on the seed germination of *B. dasyphylla* and *H. arachnoideus*, enhancing the germination percentages of these two species, whereas dew did not cause a significant increase in the seed germination of either *C. mongolicum* or *A. squarrosum* (Fig. 3). This result, together with preliminary results of seed hydration and dehydration, implied that during dew formation, the excellent water-absorbing and water-carrying capacity of *B. dasyphylla* and *H. arachnoideus* increased water availability and retention in their seed cells. Another potential explanation for the increases of the germination percentage of these two species is that the more hydrated state allows the seeds, which suffered high temperatures and strong radiation in the daytime, to recover by repairing their damaged DNA, proteins or membranes during the early morning hours (Yang et al., 2011).

It has been proved that rehydration is able to activate the repair processes of living seed cells, so that hydration-rehydration cycles can improve seed vigor and germination (Rajjou et al., 2008; Kranner et al., 2010). Our results also showed the evidence of a decrease in the number of nonviable seeds for *B. dasyphylla* and *H. arachnoideus* with continuous dew deposition during the four early mornings, whereas there was no decrease in the number of nonviable seeds for *A. squarrosum* after dew treatment (Fig. 4), and for *C. mongolicum* there was no synchronic correlation between dew treatment and seed germination or viability. This result was also in agreement with reports from other dry environments (Yang et al., 2011). However, dense dew during three consecutive mornings may help *C. mongolicum* seeds restore viability, but the effect of dew would be inadequate for this plant species in the very dry desert environment.

4 Conclusions

In this paper, we investigated the effects of dew deposition on the germination of four species seeds. We hypothesize that dew availability in harsh desert environments has positive ecological effects on the annual desert plant species. Based on the foregoing results and discussions, we may conclude that the effects of dew on the annual desert plants vary depending on the plant species, and although dew wetting is insufficient to cause seed germination, it may help in priming the seed. In our study, dew played an important role for *B. dasyphylla* and *H. arachnoideus* but not for *C. mongolicum* or *A. squarrosum*, demonstrating a greater water-absorbing and water-holding capacity for *B. dasyphylla* and *H. arachnoideus* than for *C. mongolicum* and *A. squarrosum*. This greater capacity resulted in better retention of seed viability, which would increase the seed germination percentages for these two species.

However, the present study did not examine the amount of dew actually absorbed by the seed cells for these four species. Furthermore, since the ecological effects of dew on the annual desert plant species obviously vary depending on the species, it is still unclear how the size, mass and structure of particular seeds would affect those seeds' water-absorbing and water-holding capacities. Hence, future study would be valuable to determine how much water is absorbed by the seed cells, and how the anatomical structure of various seeds changes after absorbing dew. Nevertheless, the present study on the possible ecological role of dew in assisting the seed germination of the annual desert plants has important implications for facilitating survival and regeneration of these plant species, as well as for maintaining a viable soil seed bank in harsh desert environments.

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References

Barradas V L, Glez-Medellín M G. 1999. Dew and its effect on two heliophile understorey species of a tropical dry deciduous forest in Mexico. International Journal of Biometeorology, 43(1): 1–7.

Baskin C C, Baskin J M. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. San Diego: Academic Press.

Boucher J F, Munson A D, Bernier P Y. 1995. Foliar absorption of dew influences shoot water potential and root growth in *Pinus strobus* seedlings. Tree Physiology, 15(12): 819–823.

Breshears D D, McDowell N G, Goddard K L, et al. 2008. Foliar absorption of intercepted rainfall improves woody plant water status most during drought. Ecology, 89(1): 41–47.

Clus O, Ortega P, Muselli M, et al. 2008. Study of dew water collection in humid tropical islands. Journal of Hydrology, 361(1–2): 159–171.

Duvdevani S. 1964. Dew in Israel and its effect on plants. Soil Science, 2: 14–21.

Grammatikopoulus G, Manetas Y. 1994. Direct absorption of water by hairy leaves of *Phlomis fruticosa* and its contribution to drought avoidance. Canadian Journal of Botany, 72(12): 1805–1811.

Gutterman Y, Shem-Tov S. 1997. Mucilaginous seed coat structure of *Carrichtera annua* and *Anastatica hierochuntica* from the Negev Desert highlands of Israel, and its adhesion to the soil crust. Journal of Arid Environments, 35(4): 695–705.

Gutterman Y. 2002. Survival Strategies of Annual Desert Plants: Adaptations of Desert Organisms. Berlin Heidelberg: Springer-Verlag.

He S Y, Richards K. 2015. The role of dew in the monsoon season assessed via stable isotopes in an alpine meadow in Northern Tibet. Atmospheric Research, 151: 101–109.

Hill A J, Dawson T E, Shelef O, et al. 2015. The role of dew in Negev Desert plants. Oecologia, 178(2): 317–327.

Jacobs A F G, Heusinkveld B G, Berkowicz S M. 1999. Dew deposition and drying in a desert system: a simple simulation model. Journal of Arid Environments, 42(3): 211–222.

Jacobs A F G, Heusinkveld B G, Berkowicz S M. 2000. Dew measurements along a longitudinal sand dune transect, Negev Desert, Israel. International Journal of Biometeorology, 43(4): 184–190.

Kidron G J. 1999. Differential water distribution over dune slopes as affected by slope position and microbiotic crust, Negev Desert, Israel. Hydrological Processes, 13(11): 1665–1682.

Kidron G J, Herrnstadt I, Barzilay E. 2002. The role of dew as a moisture source for sand microbiotic crusts in the Negev Desert, Israel. Journal of Arid Environments, 52(4): 517–533.

Kidron G J, Temina M. 2013. The effect of dew and fog on lithic lichens along an altitudinal gradient in the Negev Desert. Geomicrobiology Journal, 30(4): 281–290.

Kranner I, Minibayeva F V, Beckett R P, et al. 2010. What is stress? Concepts, definitions and applications in seed science. New Phytologist, 188(3): 655–673.

Malek E, McCurdy G, Giles B. 1999. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments, 42(2): 71–80.

Munné-Bosch S, Nogués S, Alegre L. 1999. Diurnal variations of photosynthesis and dew absorption by leaves in two evergreen shrubs growing in Mediterranean field conditions. New Phytologist, 144(1): 109–119.

Pan Y X, Wang X P, Zhang Y F. 2010. Dew formation characteristics in a revegetation-stabilized desert ecosystem in Shapotou area, Northern China. Journal of Hydrology, 387(3–4): 265–272.

Rajjou L, Lovigny Y, Groot S P C, et al. 2008. Proteome-wide characterization of seed aging in Arabidopsis: a comparison between artificial and natural aging protocols. Plant Physiology, 148(1): 620–641.

Rao B Q, Liu Y D, Wang W B, et al. 2009. Influence of dew on biomass and photosystem II activity of cyanobacterial crusts in the Hopq Desert, northwest China. Soil Biology and Biochemistry, 41(12): 2387–2393.

Stewart J B. 1977. Evaporation from the wet canopy of a pine forest. Water Resource Research, 13(6): 915–921.

Stone E C. 1957a. Dew as an ecological factor: I. A review of the literature. Ecology, 38(3): 407–413.

Stone E C. 1957b. Dew as an ecological factor: II. The effect of artificial dew on the survival of *Pinus ponderosa* and associated species. Ecology, 38(3): 414–422.

Temina M, Kidron G J. 2015. The effect of dew on flint and limestone lichen communities in the Negev Desert. Flora-Morphology, Distribution, Functional Ecology of Plants, 213: 77–84, doi: 10.1016/j.flora.2015.04.005.

Tobe K Z, Zhang L P, Omasa K. 2005. Seed germination and seedling emergence of three annuals growing on desert sand dunes in China. Annals of Botany, 95(4): 649–659.

Yang X J, Zhang W H, Dong M, et al. 2011. The achene mucilage hydrated in desert dew assists seed cells in maintaining DNA integrity: adaptive strategy of desert plant *Artemisia sphaerocephala*. PLoS One, 6(9): e24346.

Zhuang Y L, Ratcliffe S. 2012. Relationship between dew presence and *Bassia dasyphylla* plant growth. Journal of Arid Land, 4(1): 11–18.

Zhuang Y L, Zhao W Z. 2014. Dew variability in three habitats of a sand dune transect in a desert oasis ecotone, Northwestern China. Hydrological Processes, 28(3): 1399–1408.