REGULAR PAPER

Effects of leaf hair points of a desert moss on water retention and dew formation: implications for desiccation tolerance

Ye Tao · Yuan Ming Zhang

Abstract Leaf hair points (LHPs) are important morphological structures in many desiccation-tolerant mosses, but study of their functions has been limited. A desert moss, *Syntrichia caninervis*, was chosen for examination of the ecological effects of LHPs on water retention and dew formation at individual and population (patch) levels. Although LHPs were only 4.77% of shoot weight, they were able to increase absolute water content (AWC) by 24.87%. The AWC of samples with LHPs was always greater than for those without LHPs during dehydration. The accumulative evaporation ratio (AER) showed an opposite trend. AWC, evaporation ratio and AER of shoots with LHPs took 20 min longer to reach a completely dehydrated state than shoots without LHPs. At the population level, dew formation on moss crusts with LHPs was faster than on crusts without LHPs, and the former had higher daily and total dew amounts. LHPs were able to improve dew amounts on crusts by 10.26%. Following three simulated rainfall events (1, 3 and 6 mm), AERs from crusts with LHPs were always lower than from crusts without LHPs. LHPs can therefore significantly delay and reduce evaporation. We confirm that LHPs are important desiccation-tolerant features of *S. caninervis* at both individual and population levels. LHPs greatly aid moss crusts in adapting to arid conditions.

Keywords Biological soil crusts (BSCs) · Bryophytes · Evaporation · Gurbantunggut Desert · Hydration and dehydration · *Syntrichia caninervis*

Y. Tao · Y. M. Zhang (✉)
Key Laboratory of Biogeography and Bioresource in Arid Land, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, South Beijing Road 818, Urumqi 830011, China
e-mail: Zhangym@ms.xjb.ac.cn

Y. Tao
Graduate University of Chinese Academy of Sciences, Yuquan Road 19(A), Beijing 100049, China

Introduction

In arid areas where rainfall is rare and solar radiation is strong (Perry and Perry 1989), reducing water loss and enhancing water use efficiency are extremely important functions for plant survival (Jones 1983; Kramer and Boyer 1995). Generally, seed plants in deserts possess strong roots, and leaves that are succulent, waxy, leathery, tomentose, or even degenerative. Their stomata and conducting tissues are developed to give water retention ability (Phillips and Comus 2000; Li 2002a). Mosses belong to a plant group that have no true roots, stems, leaves, or water transport system compared with seed plants; they are typical poikilohydric plants and it is difficult for them to control the amount of water in their tissues, and thus water is easily lost, especially from desert mosses (Wu 1998; Grill et al. 2001; Watson 2004). However, they rarely die of water loss or lack of water, as they can absorb water immediately that it is available, and rapidly recover physiological activity (Oliver et al. 2000, 2005; Proctor 2000; Proctor and Nicholas 2000; Oliver and Payton 2007). Previous investigations have indicated that this efficient adaptive mechanism possessed by desert mosses is related to their exterior morphology, cell structure and physiology (Oliver et al. 2000, 2005; Proctor 2000; Proctor and Nicholas 2000; Tian et al. 2005; Pressel et al. 2006, 2008; Proctor et al. 2007; Wei and Zhang 2009; Zheng et al. 2009a, b; Layton et al. 2010).

Desiccation-tolerant mosses are important components of biological soil crusts (BSCs) in some desert ecosystems (Hoppert et al. 2004; Li et al. 2006; Thompson et al. 2006; Bamforth 2008; Neher et al. 2009; Cole et al. 2010). These mosses play important roles in soil surface stability, fertility, and ecological restoration (Belnap 2002, 2003, 2006; Belnap et al. 2004; Zhang et al. 2006; Jimenez et al. 2009). Crust-forming mosses have presumably developed special morphological and anatomical features to cope with harsh desert conditions (Vitt 1981; Danin et al. 1998; Wu 1998), but the nature of these remains largely unknown. Previous studies of morphology have found features such as convex or concave leaves, papillae, and thick marginal cell walls; providing evidence of long-term adaptation to the desert environment (Howard and Levis 1981; Danin et al. 1998; Tian et al. 2005; Wei and Zhang 2009; Zheng et al. 2009a, b). The leaf hair points (LHPs) are extended from leaf midribs, and their length varies between species (Howard and Levis 1981; Wu 1998; Gallego et al. 2002). LHPs are generally white and hyaline, in some species smooth and in some spinulose (Howard and Levis 1981; Hu 1987; Wu 1998). LHPs are, thus, important taxonomic characters (Gallego et al. 2002). It has been suggested that LHPs can reflect sunlight (Wu 1998; Zhang and Wang 2008), and reduce water loss in several cushion mosses (Sccot 1982). Consequently, LHPs appear to be important exterior structures in many mosses, especially those that are desiccation-tolerant.

Syntrichia caninervis Mitt. (Pottiaceae) (Kramer 1978; Gallego et al. 2002) is a dominant species forming BSCs in the Gurbantunggut Desert (Zhang et al. 2006). It is also found in other arid areas of central Asia (Li et al. 2002; Tian et al. 2005; Liu et al. 2006), and in the Mojave Desert of North America (Stark et al. 2005; Stark and McLetchie 2006). It is important in maintaining stability in the desert ecosystem (Zhang et al. 2006), and has gradually become a new model plant for studies of desiccation tolerance, dehydration, and recovery (Wood et al. 2000; Stark et al. 2005; Xu et al. 2007, 2008, 2009). *S. caninervis* is a typical moss with obvious LHPs, but these are easily broken or fall off as a result of erosive forces (wind mainly) in the desert. LHPs on lower parts of shoots are always lost, and sometimes LHPs on upper parts of shoots are lost also.

Precipitation is the main source of water in the desert (Wei et al. 2008). Rainfall in Gurbantunggut Desert is rare; only 70–150 mm per annum, and most rainfall events (89.8% in 1998–2007) are of <5 mm (Wang and Tang 2009). Even so, these events enable desert mosses to reach and to maintain hydration for a time. In addition, dew and fog (occult precipitation) provide small amounts of water; not enough to hydrate mosses, but with greater frequency than rainfall (Elias et al. 1995). Occult precipitation is thus an important water source, and has a crucial role in desert

ecosystems (Moffett 1985; Zangvil 1996; Feild and Dawson 1998; Kidron 2000; Kidron et al. 2002; Zhang et al. 2009; Zhou et al. 2010).

It has been confirmed that LHPs reflect solar radiation and reduce water loss in several mosses (Sccot 1982; Wu 1998; Zhang and Wang 2008), but whether LHPs of desert mosses have other ecological functions, such as water gain and retention, remains unclear. In view of the crucial role of desert mosses in the hydrology of arid areas, we hypothesized that LHPs would increase water holding capacity, reduce water loss, benefit dew formation, and be key structures in adaptation to arid conditions.

Materials and methods

Study area

The Gurbantunggut Desert (44°11′N–46°20′N and 84°31′E–90°00′E) is situated in the center of the Junggar Basin, Xinjiang Province, China. With an area of 4.88×10^4 km^2, it is the second largest desert in China. The mean annual pan evaporation is more than 2,500 mm, and the average annual temperature is 7.26°C. Wind speeds are greatest during late spring, with an annual average of 11.17 m s^{-1}, and are predominantly from the WSW, NW and N (Guo et al. 2010). The natural vegetation is dominated by *Haloxylon ammodendron* (C.A. Mey.) Bunge and *H. persicum* Bunge (Chenopodioideae), with vegetation cover of <30% (Zhang and Chen 2002). The area is covered by massive, dense, semi-fixed sand dunes with stable moisture content. Much of the sand surface is covered by BSCs, composed of cyanobacteria, lichens and mosses (Zhang et al. 2006, 2009).

Materials and preparation

To understand the function of LHPs, patches of *S. caninervis* with LHPs were investigated. Controls were individuals chosen from these patches, and also several patches (at population level); LHPs were manually removed from both.

Fifty similar *S. caninervis* patches with LHPs were collected using polyvinyl chloride (PVC) tubes (5.7 cm in diam., and 3.5 cm in height), from the *S. caninervis* area on the southern verge of the Gurbantunggut Desert, in September 2009. The bases of the PVC tubes were sealed using iron sheets. Mosses were not collected near shrub canopies to avoid any impacts that shrubs might have on microclimate. In the laboratory, LHPs were completely removed from all individuals in 25 patches using fine forceps under a stereomicroscope (XTZ-E, Shangguang Corp., Shanghai, China); leaf destruction was avoided. These treated

samples were returned to the wild and placed in the original sample points along with the other 25 samples for investigation.

In early March 2010, 10 replicated samples (patches) with and without LHPs were carried back to the laboratory. Shoots were selected from samples and controls, using fine forceps at the sand level. To remove surface impurities and sand, shoots were hydrated for 10 min in a glass beaker, stirred lightly using a glass rod for 3 min, fished out using a small plastic filter, then put into another beaker. The washing was repeated five times. The washed shoots were placed on filter paper in Petri dishes, in preparation for measurement of water content during dehydration, and investigation of weight and morphology of LHPs. The other 40 samples in PVC tubes in the wild were used for the study of dew formation and rainfall evaporation.

Morphological measurements

Several moss shoots with LHPs and with LHPs naturally lost, and leaves with LHPs, were placed on graph paper under an anatomical lens, and photographs were taken using a digital camera (PowerShot A650 IS, Canon Inc., Zhuhai, China) for measurement of shoot height and LHP length ($n = 50$). Shoots with LHPs and with LHPs naturally lost, and shoots with LHPs manually removed, were observed through a stereomicroscope and a digital camera described before under both dry and wet conditions. Some leaves with LHPs were placed flat on a microscope slide, and covered with a coverslip, and exterior morphological changes in LHPs were observed under both dry and wet conditions, using a light microscope (BX-51, Olympus Corp., Tokyo, Japan). Leaves with LHPs were dried in an oven at 75°C for 24 h; the fine outer structures of LHPs were investigated with a scanning electron microscope (LEO 1430VP, Carl Zeiss Inc., Oberkochen, Germany) operating at 20 kV.

Weight determination of leaf hair points

A dry Petri dish was selected, and weighed (W_A is the Petri dish weight). Fifty dehydrated shoots with LHPs were placed in the Petri dish, and then weighed (W_X) after drying in an oven for 15 min at 105°C, and at 75°C for 24 h. LHPs were then manually removed using fine forceps under an anatomical lens. Shoots without LHPs were also placed in the same Petri dish, and then weighed (W_Y) after drying in an oven for 15 min at 105°C, and at 75°C for 24 h. The electronic balance (FA1604N, Minqiao Co. Ltd., Shanghai, China) used for all weighing was accurate to 0.0001 g. The ratio of LHP weight to shoot weight was calculated as $(W_X - W_Y)/(W_X - W_A) \times 100\%$. The ratio was measured five times and then averaged.

Shoot water content measurements

One hundred and twenty-five shoots with LHPs and 125 shoots without LHPs were divided into five replications, and placed in 10 Petri dishes. Shoots were hydrated completely at least for 2 h. Small bubbles were wiped off using fine forceps. Hydrated samples were placed on filter paper, and redundant water on shoot surfaces was absorbed using another piece of filter paper. Shoots were then immediately placed in dry Petri dishes, and weighed every 5 min until completely dehydrated. Room temperature was 20°C, relative humidity was 27%. The saturated water content (%), absolute water content (AWC, %), evaporation ratio (ER, %) and accumulative evaporation ratio (AER, %) were assayed from these weights, to compare water content of shoots with and without LHPs.

Dew determination in the field

Dewfall and dew evaporation of moss crusts with and without LHPs were measured using microlysimeters ($d = 5.7$ cm, $h = 3.5$ cm) designed by Zhang et al. (2009). To avoid sand or soil water influencing dewfall on the microlysimeter, several additional, larger PVC tubes ($d = 7.5$ cm, $h = 5$ cm) were pushed into the ground, and their bases covered, then the microlysimeters were placed in the protection of these tubes, so that the edges of the microlysimeters were close to the ground surface. To reduce water influence in microlysimeters, these were in situ for 1 week before measurements began. These treatments were replicated eight times for samples with LHPs and ten times for those without LHPs. Daily dewfall was determined by calculating the difference between the weight at 0900 and at 1700 hours on 7 days between May 4 and May 11, 2010. To obtain a better insight into differences between patches with and without LHPs, intensive measurements were carried out during one 24 h period (from 1700 hours, May 6 to 1700 hours, May 7). Samples were weighed at 1 h intervals to obtain the time course of dew deposition and duration. Dew quantity (millimeters) was calculated from these weights. May 6–7 was clear with very few clouds and low wind speeds.

Determination of rainfall evaporation rates

Based on the frequency and contribution of natural rainfall amounts (Wang and Tang 2009), three simulated rainfall events were set up above the microlysimeters to allow analysis of differences in evaporation between mosses with and without LHPs. These rainfall events were 1, 3 and 6 mm (weighing 2.55, 7.66 and 15.31 g). The evaporation experiment was conducted between 1000 and 2100 hours, on May 12, 2010. Weighing intervals were 10 min, 20 min,

30 min and 1 h. The AERs (%) of different patches were calculated from these measurements.

Statistics

SPSS 13.0 statistical package (SPSS Inc., Chicago, IL, USA) was used for data analysis. The effects of LHPs on AWC, ER and AER of *S. caninervis* shoots, and the effects of LHPs on dew amounts and rainfall evaporation rates of *S. caninervis* patches were compared using an independent samples *t* test. Determination of whether shoots with and without LHPs had reached invariable states was made using a one-way ANOVA followed by a post hoc LSD test.

Results

Morphological characteristics of *S. caninervis*

The typical, above ground height of *S. caninervis* individuals with LHPs is 5.77 ± 0.92 mm [mean $\pm$ standard deviation (SD), $n = 50$]. LHPs average 1.21 ± 0.51 mm in length (mean $\pm$ SD, $n = 50$), with the longest measured at 2.1 mm. Leaves on the upper part of shoots have more and longer LHPs than those below. Shoots with LHPs are green or yellowish-green (Fig. 1a, b) when hydrated, while shoots without LHPs are brown or brownish-yellow (Fig. 1c, d). The latter shoots are not as long (1.67 ± 0.42 mm, mean $\pm$ SD, $n = 50$) as normal shoots. There were no evident differences in morphology between samples with LHPs and samples with LHPs removed artificially and placed in situ for several months (Fig. 1e, f).

When shoots dehydrate, LHPs curve towards their centers following the leaves, always arranging vertically and curling slightly (Fig. 1a). This helps to concentrate sunshine. When hydrated, LHPs spread out and extend with the leaves (Fig. 1b); this is beneficial in avoiding each other's shade. LHPs are bright and hard after dehydration, and easily ruptured if pressed. When hydrated they are comparatively pliable.

Surfaces of LHPs and midribs are spinulose (Figs. 1g, 2), and the bases of LHPs are wider and more spinulose (Fig. 2b) than the apices (Fig. 2c). Spinules (12.19 ± 3.17 μm, mean $\pm$ SD, $n = 25$) are arranged in groups, like short branches (Figs. 1g, 2b). Spinules consequently improve the surface area and volume of LHPs. The LHPs, costae, and spinules filled with water and expanded when hydrated (Fig. 1g). Spinules are arranged at a particular angle ($52.15° \pm 6.02°$, mean $\pm$ SD, $n = 20$) to the LHPs. When dehydrated, the surfaces of LHPs contract inward irregularly, spinules curve towards LHPs, and angles of spinules and LHPs reduce (Fig. 2b, c). Apices of LHPs are closed (Fig. 2c), thus forming a closed vessel system between the LHPs and leaves. The percentage of LHPs in the above ground biomass was only $4.77 \pm 0.19\%$.

Water content of shoots with and without leaf hair points during dehydration

During the first 70 min of dehydration, the AWCs of samples with LHPs were always greater than that of those without LHPs. However, there was no significant difference from 75 to 85 min (Fig. 3a). The AWC of samples without LHPs reached an invariable state after 50 min, while those with LHPs reached this state after 70 min. The
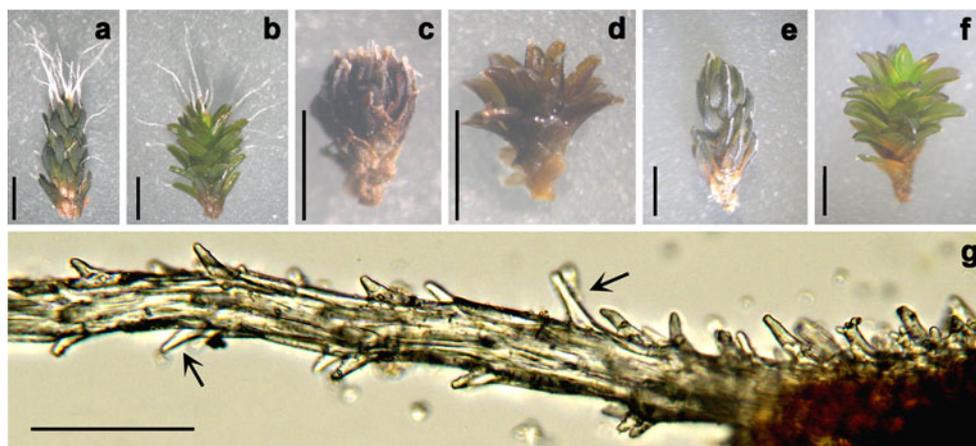
Fig. 1 Morphology of *S. caninervis* shoots and leaf hair points (LHPs) under dehydrated and hydrated conditions. **a** Natural shoots with LHPs under dehydration. **b** Natural shoots with LHPs under hydration. **c** Natural shoots without LHPs under dehydration. **d** Natural shoots without LHPs under hydration. **e** Shoots with LHPs manually removed under dehydration. **f** Shoots with LHPs manually removed under hydration. **g** The middle and base of one hydrated LHP. *Arrows* show spinules on the surfaces of the LHP and midrib. *Scale bars* 1 mm in **a–f**; 50 μm in **g**
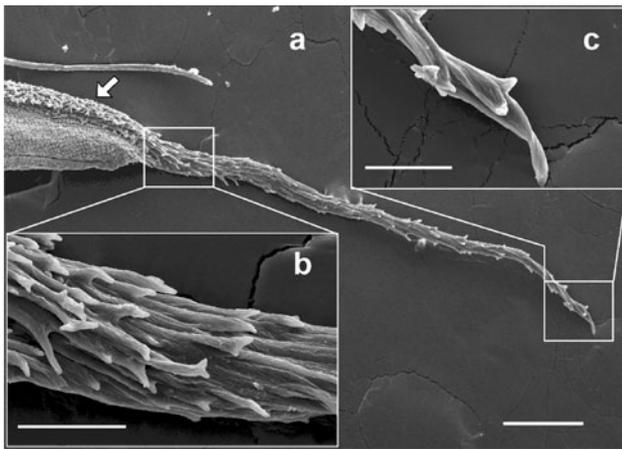
Fig. 2 Scanning electron micrographs of LHPs in *S. caninervis* under dehydrated condition. **a** The overall micrograph of LHP and the upper part of leaf. **b** The base of LHP. **c** The apex of LHP. **b–c** Many spinules on LHP; more at bases than apices. The *arrow* indicates the leaf midrib (costa). *Scale bars* 200 μm in **a**; 50 μm in **b**, **c**

invariable state of AWC (ER or AER) meant that differences between AWC (ER or AER) values of samples with LHPs (or without LHPs) were not significant ($P > 0.05$).

During the early period of dehydration, samples without LHPs showed much greater ER than those with LHPs (Fig. 3b); significant differences were found between 5 and 65 min, except at 30 min. At 30 min, the AER of samples without LHPs was 78.28%, while that of samples with LHPs was 59.14% (Fig. 3c). The ER of samples without LHPs was steady at 50 min, and the AWC was 15.55%, while that of samples with LHPs was 42.94%. The shoots with LHPs still contained large amounts of water at this time, not achieving a constant state (AWC 14.87%) until 70 min. The AER of samples without LHPs showed complete dehydration at 50 min, while those with LHPs did not show this until 70 min. Thus, in these experimental conditions, LHP presence appears to have delayed drying time for 20 min, when measured using any of the three water indices (AWC, ER and AER).

When shoots were completely hydrated, the saturated water content of those with LHPs was 24.87% higher than of those without LHPs; LHPs increased water content by 24.87%. When completely dehydrated, the mean AWC of samples without LHPs was 12.94% and of samples with LHPs was 12.25%. Based on the above, it appears that LHPs reliably slowed down evaporation amounts and rates in moss shoots.

Dew deposition of patches with and without leaf hair points

Dew accumulation was observed at 1700 hours, and was highest at 0900 hours in the morning (Fig. 4). The dew
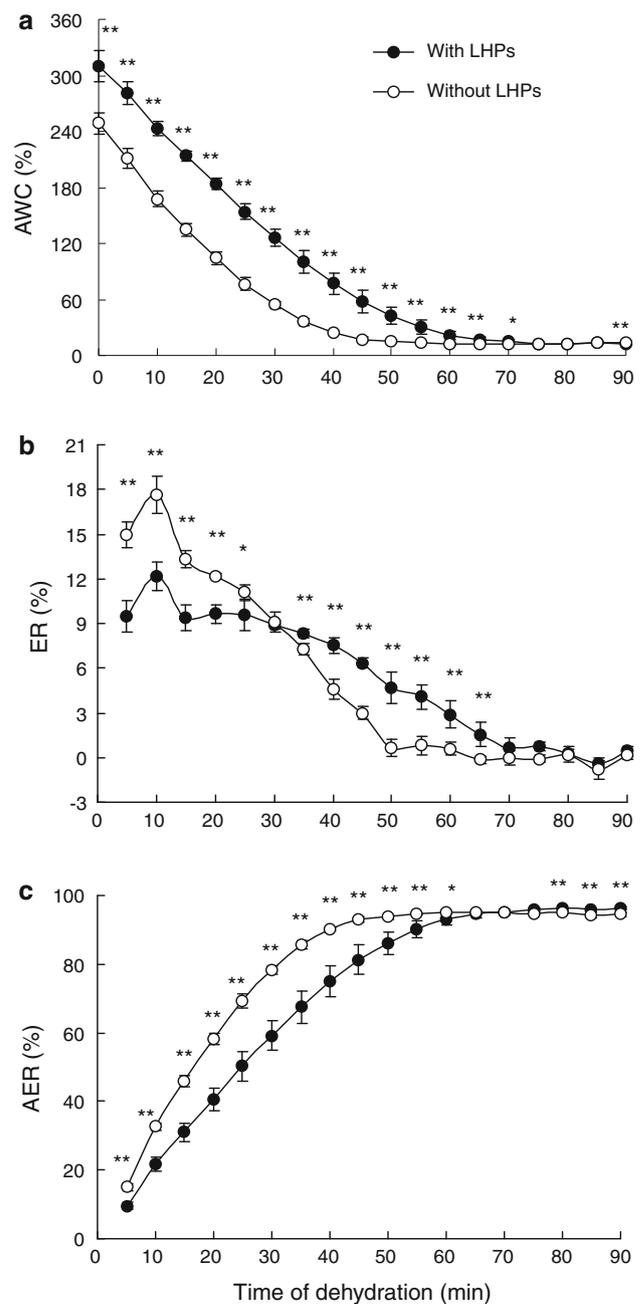
Fig. 3 Absolute water content (AWC), evaporation ratio (ER) and accumulative evaporation ratio (AER) of *S. caninervis* samples with and without LHPs. **a** AWC of samples with and without LHPs. **b** ER of samples with and without LHPs. **c** AER of samples with and without LHPs. *Bars* represent one standard deviation ($n = 5$). *Double asterisks* indicate a greatly significant difference between samples with and without LHPs ($P < 0.01$); *single asterisk* indicates a significant difference ($P < 0.05$)

deposition curve of crust patches with LHPs was similar to patches without LHPs; however dew amounts on the former were greater than on the latter from 1700 hours, May 6 to 1200 hours, May 7. In the process of dew accumulation (1800–0900 hours), the accumulation rate of patches with

Fig. 4 The time course of measured cumulative dew and the drying process on moss patches with and without LHPs. *Bars* represent one standard deviation ($n = 8$ and 10, respectively). *Double asterisks* indicate a greatly significant difference between samples with and without LHPs ($P < 0.01$); *single asterisk* indicates a significant difference ($P < 0.05$)
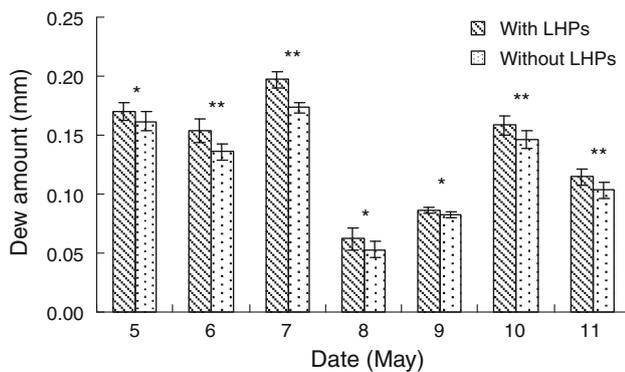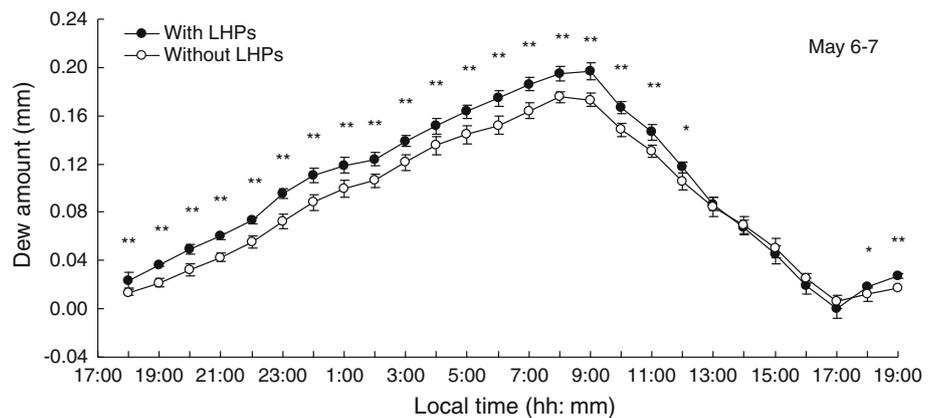
Fig. 5 Daily dew amounts of *S. caninervis* patches with and without LHPs. *Bars* represent one standard deviation ($n = 8$ and 10, respectively). *Double asterisks* indicate a greatly significant difference between samples with and without LHPs ($P < 0.01$); *single asterisk* indicates a significant difference ($P < 0.05$)

LHPs was greater than of patches without LHPs. The evaporation rate of the former was slightly higher than the latter during the evaporation period following sunrise (0900–1700 hours).

There were significant or greatly significant differences between the daily dew amounts of the two samples (Fig. 5). The minimum dew amount occurred on May 8, 2010, with values of 0.062 and 0.053 mm, for two samples, while maximum values occurred on May 7, with values of 0.197 and 0.173 mm. Dew amounts on patches with LHPs were always higher than on patches without LHPs. Total dew amounts over 7 days were 0.942 mm on patches with LHPs, and 0.854 mm on patches without LHPs. Total dew amount on patches with LHPs was 10.26% higher than on those without LHPs; LHPs thus appear able to increase dew amounts by 10.26%.

Evaporation in patches with and without leaf hair points following three simulated rainfall events

During evaporation following three simulated rainfall events, AER values of patches with LHPs were always lower than those of patches without LHPs (Fig. 6). Significant or greatly significant differences were found between AER values of samples with and without LHPs during the early stages of evaporation. The three periods which showed differences between samples were 10–170 min (Fig. 6a), 0.5–4.5 h (Fig. 6b) and 0.5–5.5 h (Fig. 6c), respectively, following 1, 3, and 6 mm of rainfall. LHPs can thus slow evaporation rates during particular periods; extending hydration time and photosynthetic period and helping to provide protection against desiccation.

Discussion

Effect of leaf hair points on water content of *S. caninervis* shoots and patches

Our study confirms that LHPs are able to reduce water loss and increase water retention time at both individual and population (patch) levels. LHPs are made up of long hollow cells, and their bases are connected with leaf midribs (Howard and Levis 1981; Wu 1998; Watson 2004). LHPs and midribs thus constitute a closed water storage system, similar to a capillary (Fig. 2a). Not only do the LHPs absorb water themselves, but capillarity can help LHPs to absorb more water, and encourage the absorbed water to concentrate in the upper part of the leaf (Hu 1987; Wei and Zhang 2009). Shoots without LHPs lose water absorbed by LHPs, but the missing LHPs also impair the capillarity formed by LHPs and leaves. This may be an important reason for the differences in water content and water loss rates of *S. caninervis* shoots with and without LHPs.

The water content of samples with and without LHPs were equal in a completely dehydrated state; showing that then there is no water in LHPs. LHPs play other key roles such as reflecting strong light, protecting leaves from sunburn (Zhang and Wang 2008; Zheng et al. 2009a, b), and absorbing moisture from the air. These functions are
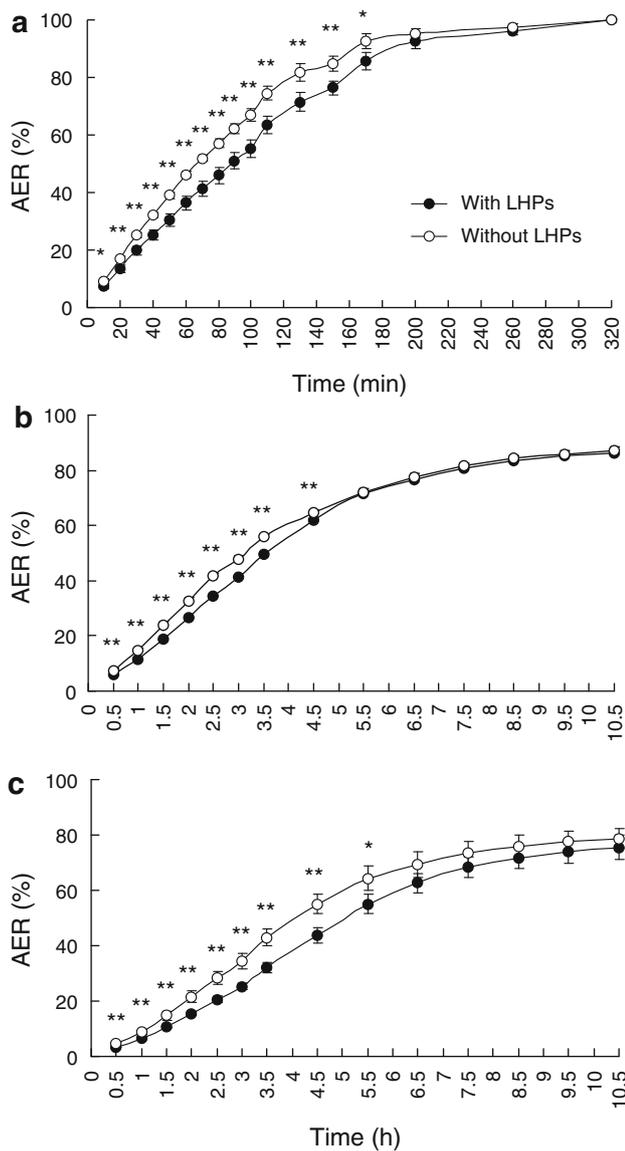
Fig. 6 Accumulative evaporation ratio (AER) of patches with and without LHPs, under 3 simulated rainfall events: **a** 1 mm, **b** 3 mm, **c** 6 mm. *Bars* represent one standard deviation ($n = 4$). *Double asterisks* indicate a greatly significant difference between samples with and without LHPs ($P < 0.01$); *single asterisk* indicates a significant difference ($P < 0.05$)

important in the water balances of individual mosses and moss crusts.

We suggest that LHPs are adaptations to arid conditions at the population (patch) level. Most rainfall events in this desert are small (<5 mm) (Wang and Tang 2009). Under these water deficit conditions, BSCs usually promote rainfall evaporation; the higher the degree of BSC development the more obvious the effects (Li et al. 2005; Liu et al. 2005; Xue et al. 2007). This is mainly because reflectivity declines and solar radiation increases with increasing developmental level of BSCs (e.g. sand → cyanobacterial crust → lichen crust → moss crust) (Li et al. 2005, 2006). Why, then, is evaporation in *S. caninervis* patches with LHPs manually removed greater than in those with LHPs present? There are several reasonable explanations. First, the LHPs themselves and the capillarity described above can help shoots absorb water. LHPs thus extend the evaporation pathway (Hu 1987; Zhang and Wang 2008), and enhance ability to absorb and retain water. Second, LHPs can improve the reflectivity of moss crusts, and reflect solar radiation (Zhang and Wang 2008), therefore reducing surface radiation and temperatures. Finally, when the plant hydrates, LHPs expand as the leaves unfold. LHPs and leaves of an individual and/or surrounding individuals together constitute a tridimensional overlapped mesh, that decreases gaps between individuals (see Electronic Supplementary Material Fig. 1a, b). This forms a barrier preventing and decreasing evaporation from the crust layer and the soil. Crusts without LHPs have lost these features (see *Tortula muralis* var. *aestiva* Brid. ex Hedw. for example, in Electronic Supplementary Material Fig. 1a). Sccot (1982) revealed that the evaporation rates of *Grimmia pulvinata* (Hedw.) Sm. cushions and *Tortula subulata* Hedw. cushions with LHPs were nearly 30% less than those without LHPs, under the same conditions. Accordingly, although LHPs are very small, they are able to decrease evaporation from moss crusts, and prolong hydration; this is of great importance for mosses in arid areas.

Generally, plant water content and speed of water loss influence physiological activity and cellular structure (Farrant 2000; Golovina and Hoekstra 2002; Li 2002a; Georgieva et al. 2007; Glime 2007; Charron and Quatrano 2009), but many plants (especially desiccation-tolerant plants) have several adaptive strategies against water stress (Kramer and Boyer 1995; Farrant 2000; Phillips and Comus 2000; Li 2002a). Under slow drying conditions, mosses are able to face desiccation stress through adjusting osmolyte levels, converting cytoplasm to a glassy state, folding cell walls, minimizing organelle surfaces, and synthesizing desiccation-related proteins (Oliver et al. 2000, 2005; Proctor 2000; Pressel et al. 2006, 2008; Proctor et al. 2007). In *Physcomitrella patens* (Hedw.) B.S.G., the average strength of hydrogen bonding in the cytoplasmic glassy matrix was found to increase upon slow drying, and there were relatively higher proportions of α-helical structures than in rapidly dried tissues (Oldenhof et al. 2006). Slow-dried, desiccation-tolerant tissues had stable membranes, retained their native protein secondary structure, and had densely packed, glassy, cytoplasmic matrices. Fast-dried tissues experienced some loss of phospholipids and an increase in free fatty acids, their proteins showed signs of denaturation and aggregation, and the glassy matrix reduced hydrogen bonding (Hoekstra et al. 2001). Tetteroo et al. (1998) demonstrated that

somatic embryos of carrot (*Daucus carota* L.) acquired complete desiccation tolerance when slowly dried, but failed to do so when rapidly dried. They explained that the plasma membranes of slowly dried somatic embryos retained permeability levels as low as for fresh embryos, whereas those of rapidly dried embryos became leaky. The dehydration process of *S. caninervis* individuals without LHPs was similar to rapid drying, thus there may have been insufficient water and time to induce desiccation-tolerant protection mechanisms during dehydration (Farrant et al. 1999). Accordingly, these mosses would die after several dry-wet cycles (Stark et al. 2007); this may be the main reason for very small shoots and brown leaves in *S. caninervis* individuals in which LHPs were broken naturally.

It is obvious that the speed of water loss can affect cell structure and activity in both seed plants and mosses; slow drying may always cause less damage to plants than rapid drying. LHPs can thus increase water content and delay water loss for *S. caninervis*, thus indicating that desiccation-tolerance, cell activity and function of mosses with LHPs will be better than in those without LHPs.

Effect of leaf hair points on dew formation on moss crusts

The total and daily dew amounts on crusts with LHPs were always greater than on crusts without LHPs. Dew deposition is affected by many factors, including meteorology (weather, near-surface temperature, soil temperature, air humidity, wind direction and speed), soil water content, season, location, slope aspect, and vegetation coverage (Zangvil 1996; Kidron 2000; Kidron et al. 2002; Li 2002b; Fang and Ding 2005; Liu et al. 2006; Zhang et al. 2009). Even when these conditions are consistent, mat quality (including dryness, texture, surface roughness, salt content and particle size) influences dew formation (Fang and Ding 2005; Guo and Liu 2005). Zhang et al. (2009) found a general increase in dew amounts corresponding to the developmental level of soil crusts; sand < cyanobacterial crust < lichen crust < moss crust. They explained that the surface temperatures of moss crusts decreased faster than sand surfaces at night, while the opposite trend was observed during daytime, resulting in much higher dew amounts at night and higher evaporation rates in the daytime from the moss crusts. However, the surface roughness may be the main factor affecting dew quantity in patches with and without LHPs.

Samples with and without LHPs originated from the same moss crusts in which features were otherwise consistent. Different dew-gaining abilities may have been caused by differences in surface roughness resultant from the presence or absence of LHPs. LHPs increase the plant–air interface; therefore patches with LHPs gained the most

dew. However, during daytime, dew evaporation rates from crusts with LHPs are slightly higher than from patches without LHPs, but crusts with LHPs kept some dew until 1700 hours. Our results are consistent with previous findings relating to different developmental levels of crusts (Zhang et al. 2009). In particular, the fast evaporation rate from crusts with LHPs did not show low dew utilization efficiency. On the contrary, the fast evaporation rate would effectively decrease the high surface temperatures of moss crusts during daytime; thus protecting *S. caninervis* crusts and individuals via the ability of LHPs to reflect sunshine.

In addition, LHPs also influence the freeze–thaw process during snowless winters. During the night, ice forms on surfaces of LHPs, but not on leaves (see Electronic Supplementary Material Fig. 2), melting after sunrise; this water enables individuals to hydrate. LHPs extend the mosses' ability to utilize different forms of water, and also indirectly protect leaf cells from freezing. These functions need further research.

Dew and other occult precipitation play important roles in the desert ecosystem; weakening respiration at night, decreasing evaporation during the day, and replenishing water; thus reducing water consumption by the plant and the soil (Elias et al. 1995; Zangvil 1996; Kidron 2000; Kidron et al. 2002; Zhang et al. 2009). Accordingly, normal *S. caninervis* crusts with LHPs will have survival advantages.

LHPs improve the mosses' abilities to absorb and retain dew and rain; differences in water utilization are a result of two aspects. More efficient dew use is mainly attributable to LHPs increasing the surface roughness of crusts. By reflecting light, forming internal capillaries, and reducing gaps between individuals, LHPs are able to reduce evaporation.

Implication for the desiccation tolerance of desert mosses

The presence of LHPs is favorable for *S. caninervis* crusts in their adaptation to arid conditions. Desert environments are extremely harsh, and thus challenging for crust survival (Belnap and Gillette 1997; Leys and Eldridge 1998; Zhang et al. 2006). Though we did not measure the physiological activities of samples with and without LHPs, the observed differences in sizes and colors of individuals could suggest that loss of LHPs leads to changes in morphology and physiology (Fig. 1c, d). Loss of LHPs may threaten the survival of *S. caninervis* individuals; from encroachments by wind and sandstorms, but also from decreases in water gain and retention capacities and surface reflectivity. LHPs account for a very small part of each shoot, but they obviously help *S. caninervis* individuals and populations to obtain more water (precipitation and occult precipitation),

reduce water loss and increase water retention time. In addition, they reflect sunlight. In conclusion, LHPs are crucial structures allowing *S. caninervis* to endure desiccation.

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