

Dew formation characteristics of meadow plants canopy at different heights in Hulunbuir grassland, China

Jingjie Xie, Derong Su, Shihai Lyu, He Bu and Qiang Wo

ABSTRACT

A plant's foliar uptake of dew can mitigate the adverse effects caused by drought stress. However, in grassland ecosystems, it is inconclusive whether the dew condensation characteristics of plants at different heights are consistent. In this study, we wanted to know whether plant height had a significant effect on the formation of dew. In addition, we wanted to understand the difference of dew formation between C₃ plant *Leymus chinensis* (LC) and C₄ plant *Cleistogenes squarrosa* (CS) which have different heights and can succeed each other in the community. In nine dew nights, we measured the amount of dew formed on simulated condensation surface (different heights) and two plants at the same time. The results showed that in the height range of 5–80 cm, the dew amount increases with the canopy height, but its increase rate gradually slows down and approaches zero. The shorter CS (5–15 cm) has a similar dew amount (0.095 mm) as LC (40–70 cm) due to its compact structure of the leaves with pubescence and the more stable micro-meteorological conditions. The CS can obtain more potential dew per unit organic matter, and this may be one of the potential mechanisms for the succession from LC communities to CS communities under drought stress.

Key words | *Cleistogenes squarrosa*, dew formation, Hulunbuier grassland, *Leymus chinensis*, plant heights, simulated condensation surface

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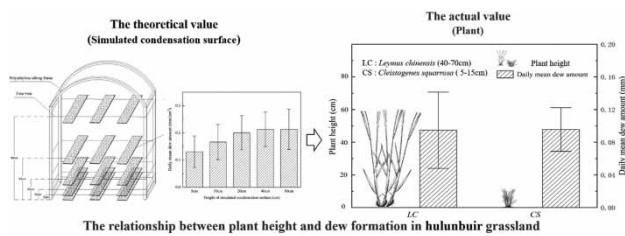
HIGHLIGHTS

- The dew formation on leaves theoretically changes exponentially with steppe plant height: $y = a(1 - e^{-bx})$.
- Both plant height and morphological characteristics affect dew formation.
- One of the potential mechanisms of succession from *Leymus chinensis* (LC) community to *Cleistogenes squarrosa* (CS) community under drought stress was proposed.

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GRAPHICAL ABSTRACT



INTRODUCTION

Plants have two methods of dew utilization. One is to utilize the dew formed on the soil surface and the dew flowing down the stem into the soil; the other one is foliar uptake. The foliar uptake of dew through the pores, cracks, drainage organs or other tissues on the leaf surface can alleviate water deficit in the body and reduce the transpiration loss of plants (Jacobs *et al.* 2000; Kidron 2000; Agam & Berliner 2006). As early as 1957, the foliar uptake of dew and rainwater had been found on *Ponderosa* (Stone 1957). Many studies have also found that dew can improve the physiological indices of plants, such as leaf area, fresh weight, photosynthetic rate, and have a positive effect on root growth (Boucher *et al.* 1995; MunnéBosch & Alegre 1999; Zhuang & Zhao 2010; Cen & Liu 2017). A study using hydrogen and oxygen stable isotope techniques on grasslands in the United States indicates that dew accounts for 30% of the annual water input to the entire ecosystem, and 20% to 60% of the dew can be utilized by plants (Corbin *et al.* 2005). More researches have shown that dew is an important source of water for plants in arid regions, semi-arid regions and humid regions, and it plays an important ecological role (Gutterman & Shem-Tov 1997; Kidron *et al.* 2002; Agam & Berliner 2006; Jacobs *et al.* 2006; Meissner *et al.* 2007; Xiao *et al.* 2009; Fessehaye *et al.* 2014; Groh *et al.* 2018, 2019). Therefore, as an additional water source other than rainfall, dew formation plays a key role in the growth and development of plants in different ecosystems.

In communities of different ecosystems, investigations have shown that canopy height often affects the formation of dew on leaf surfaces. For example, a study in a farmland ecosystem that used Leick discs and absorbent paper to

actually measure the dew amount found that the dew amount of maize increased with its canopy height (Jacobs *et al.* 1994). A study on the tropical rainforest in Xishuangbanna, China, found that the dew first formed in the upper canopy, and the formation of dew under the forest was 3–4 hours later due to its slower rate of temperature drop (Liu *et al.* 2001). For marshes, a study has also found that the dew amount on the ground is lower than that of the top of the canopy (Bai *et al.* 2004). A similar feature was also shown in a related study in the desert (Guo *et al.* 2016). The differences in dew formation exhibited by canopies of different heights are affected by many factors. Many studies have found that the formation of dew on the leaf surface of plants is greatly affected by meteorological factors such as temperature, relative humidity (RH), wind speed and cloud amount which were influenced by each other (Zangvil 1994; Luo & Goudriaan 2000; Muselli *et al.* 2009; Xu *et al.* 2009, 2012). Investigations have shown that, compared with the leaves deeper in the canopy, the dew formed at the top of the canopy is more susceptible to evaporation due to the changes in meteorological factors (Jacobs *et al.* 2005; Groh *et al.* 2019). The temperature decrease rate of leaves at different heights is also an important factor affecting the formation of dew (Andrade 2003). The most suitable meteorological conditions for dew formation were considered as no clouds, no wind and 100% RH (Xiao *et al.* 2013). In addition, leaf surface properties are also an important factor for the formation of dew droplets (nucleation and droplet growth). The properties of the plant/leaf surface are the key factors affecting the condensation of

dew. Some investigations have found that the surface properties of different cactus largely differed in their hydrophilic or hydrophobic features (Malik *et al.* 2015), and plants with pubescence have a greater condensation advantage (Zhuang & Zhao 2010). The study of the formation characteristics of dew in communities is of great significance to the northern grasslands of China's semi-arid regions, but the related research is still lacking.

The ecological significance of dew in the grassland is more reflected in its ability to provide non-rainfall water to plants under water stress in drought years. However, there is still no conclusion about whether the plants with more dew formation on their leaf surface can also obtain more beneficial effects under water stress. One of the common phenomenon in the grasslands of Inner Mongolia, China, is that the community of C₃ plant *Leymus chinensis* (LC) will degenerate to the community of C₄ plant *Cleistogenes squarrosa* (CS) under longer periods of water stress (Pan *et al.* 2016). Globally, the expansion of C₄ plants driven by prolonged drought are also common (Auerswald *et al.* 2012; Shen *et al.* 2018). However, the height of LC and CS is 40–70 cm and 10–30 cm, respectively. The shorter CS will be more resistant to water stress due to the more efficient photosynthetic pathways and higher water use efficiency of C₄ plants (Ghannoum 2009). CS can seal more stomata under water stress, help leaves retain water and increase leaf water potential (Zhang & Kirkham 1995). Therefore, it is not appropriate to just use the dew amount (mm) as the criterion for determining the effectiveness of dew on LC and CS under water stress. Compared with LC, CS has a lower specific leaf weight (SLW) due to the adaptation strategies of C₄ plants, which are thinner leaves with an increased light receiving area (Mahendra *et al.* 1974; Oguro *et al.* 1985; Auerswald *et al.* 2012; Levey *et al.* 2019). Studies have shown that, for different species (Liu & Stützel 2003) or the same species (Songsri *et al.* 2009), the SLW of plants has a high correlation with their water use efficiency. The lower SLW of CS is also one of its manifestations of higher water use efficiency (Yang *et al.* 2011; Zheng 2018). Therefore, compared with the LC community, the CS community may be more efficient in the use of dew. It is more appropriate to use the ratio of dew amount to SLW to compare LC and CS from the perspective of dew use efficiency,

and it can express the potential dew that can be used to per unit organic matter.

There are many methods for observing dew. Researchers often use artificial condensation surface (Jacobs & Nieveen 1995; Xu *et al.* 2012), weighable lysimeters (Wang & Zhang 2011; Groh *et al.* 2018), micro-lysimeters (Ninari & Berliner 2002), humidity sensors (Sentelhas *et al.* 2008), energy conversion (Malek *et al.* 1999; Madeira *et al.* 2002) and other methods to observe the duration and the amount of dew on soil or plants. Although these methods can better reflect the dew production characteristics from the time and space scales, they are not able to accurately calculate the amount of dew generated from the level of individual plants. In the natural grassland, a more accurate dew amount of individual plant can be obtained by manual measurement, but related research is still lacking.

In order to understand the effect of plant height on dew formation in grassland ecosystems, it is necessary not only to observe the dew formation characteristics of the same texture material, but also to measure the dew amount of plants of different morphology and different leaf surface structures. The main purpose of this study is divided into three parts: (1) By setting simulated condensation surfaces at different heights in natural grassland, we explored the variation of the dew amount with different heights. (2) We used LC (40–70 cm) and CS (5–15 cm), which are dominant plants of different heights, as experimental materials to explore their dew formation characteristics in the dew night; in addition, the ratio of dew amount to SLW is used to compare the potential effectiveness of LC and CS for dew utilization. (3) To provide the support of meteorological data for the characteristics of dew formation and compare the meteorological difference between dew night and non-dew night.

MATERIALS AND METHODS

Experimental site

The study area is in the Huihe National Nature Reserve in Hulunbuir grassland. The geographical coordinates are 48°10'50"–48°57'00"N, 118°48'–119°45'E and 800–1,000 m above sea level. The climate belongs to the mid-temperate continental monsoon climate. The winter is

long and cold, the summer is warm and short, the annual average temperature is -2.4 – 2.2 °C, and the average annual precipitation is 300–350 mm. Seventy per cent of the precipitation falls during June–August, and the frost-free period is 100–120 d. The long cold period might indicate that hoar frost is also a relevant source of non-rainfall water at this site (Galek et al. 2015; Groh et al. 2018). The experimental site is a typical meadow grassland, in an enclosed state. Plant species include *Leymus chinensis*, *Agropyron cristatum*, *Stipa grandis*, *Cleistogenes squarrosa*, *Artemisia frigida*, *Artemisia capillaris*, *Potentilla acaulis*, *Serratula centauroides*, *Potentilla bifurca*, etc. Among them, *L. chinensis*, *C. squarrosa*, *A. cristatum* and *S. grandis* are typical dominant species.

Materials

The 0.8 mm thick qualitative filter papers with medium speed was used as the simulated condensation surface. Qualitative filter paper is a botanical material that has a similar specific heat capacity to plants and has a similar ability to coagulate. Moreover, its uniform specifications and uniform texture can reduce errors in the weighing process. The same materials have been used in many previous studies to calculate changes in dew at night (Jacobs et al. 1995; Luo & Goudriaan 2000; Richards & Oke 2002).

Two kinds of grasses with different average heights, C₃ plant *Leymus chinensis* (LC) and C₄ plant *Cleistogenes squarrosa* (CS), were selected as materials. The LC is one of the dominant species of the Hulunbuir grassland, and its morphological characteristics can be seen in Table 1. LC has the ability of foliar uptake of dew, which has a positive effect on its photosynthesis, water physiology and growth, and improves its drought resistance (Cen & Liu 2017). CS is an important companion species which can become a dominant species by overgrazing or in water stress years, and its morphological characteristics can be seen in Table 1. The pubescence of CS, which makes leaf surface irregular, can improve its dew holding capacity, provides more space for condensation during the formation of dew, and has more possibility of using dew for plants (Rundel 1982; Zhuang & Zhao 2010). In addition, many other studies have also found that plants with pubescence have the ability to utilize dew (Zheng & Feng 2006; Zhuang & Zhao 2010).

LC and CS are *gramineae*s of different heights with erect growth, with slender leaves and are closely related in spatial dimension and time dimension. During water stress, the dominant species of the community are easily replaced from LC to CS (Pan et al. 2016). Their different heights and close connection in the community are the reasons for choosing them as experimental materials in this study.

METHODS

Dew amount at different heights



This study was conducted from August 11 to September 5, 2015. The plants during this period are already in the mature stage, and the impact on the results due to plant growth around the experiment device can be ignored. As shown in Figure 1, a layered frame made of polyethylene tubing was placed in the experimental pasture where LC and CS grow together, which is divided into five layers by double-strand fine wires. The height of each layer from the ground is 5, 10, 20, 40 and 80 cm, respectively. In addition, we folded the qualitative filter paper into four strips of 30 cm long and 5 cm wide (Figure 1). The thicker filter paper ensures that the dew formed on the paper surface at night will not drip after absorption saturation. Thereafter, the long strip of filter paper on each layer was fixed by both ends to make the surface of the filter paper contact the air as much as possible to avoid errors due to the reduction of the condensation surface. The qualitative filter paper was set three times at each height. On the test day, the filter paper of each layer was weighed and fixed from 8:00 pm, and filter paper of each layer was weighed every 2 hours until 6 o'clock the next morning (6 times in total, duration is 10 h, weighing accuracy is 0.01 g).

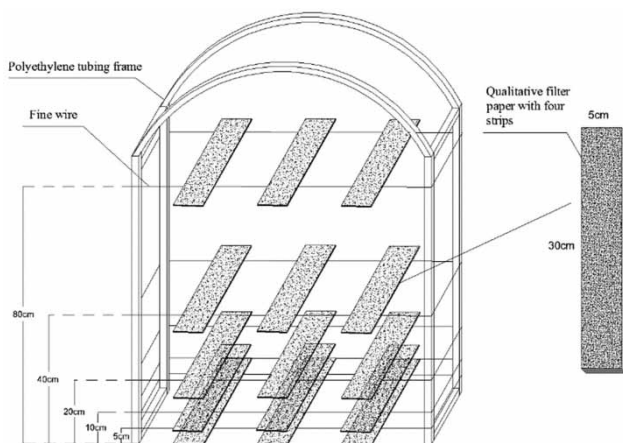
We used the height of dew accumulation per unit area (H) as the dew amount to judge the characteristics of dew formation with height. The specific calculation process is as follows:

$$D_{area} = \frac{M_{dew}}{S} \quad (1)$$

$$V_{dew} = \frac{M_{dew}}{\rho} = S \cdot H \quad (2)$$

Table 1 | A summary of the morphological characteristics of LC and CS

Name	<i>Leymus chinensis</i> (LC)	<i>Cleistogenes squarrosa</i> (CS)
Appearance		
Family	Gramineae	Gramineae
Genus	<i>Leymus</i>	<i>Cleistogenes</i> Keng
Plant type	C ₃ plant	C ₄ plant
Feature and height	Scattered and erect; 40–70 cm	Tufted and erect; 10–20 cm
Leaf type	Slender; 7–18 cm	Slender; 3–6 cm
Leaf surface characteristic	The top surface is rough; the bottom is smooth	Surface rough with short pubescence
Root characteristic	Rhizome type	Fibrous root type
Main status in community	Dominant species	Accompanying species

**Figure 1** | Dew collection device using simulated condensation surface.

D_{area} is the weight of dew per unit area (g/cm^2), M_{dew} is the weight of dew (g), S is the area (cm^2), V_{dew} is the volume of dew (cm^3), H is the height of dew accumulation per unit area (mm), ρ is the density of water (g/cm^3).

Equations (1) and (2) were combined to get the equation:

$$H = \frac{M_{dew}}{\rho \cdot S} = \frac{D_{area}}{\rho} \quad (3)$$

Then, we subtracted the weighing result from the i th hour with the weighing result of the $i - 2$ th hour, and

obtained the dew amount on the filter paper of specific height in 2 hours. The specific calculation process is as follows:

$$DA_{2h}(t_i) = H(t_i) - H(t_{i-2}) \quad i = 2, 4, 6, 8, 10 \quad (4)$$

t_i is the i th hour of the test night, $DA_{2h}(t_i)$ is the dew amount (mm) that increases between the 2 hours from $i-2$ to i , $H(t_i)$ is the height of dew accumulation per unit area (mm) from the start of the experiment to the i th hour.

The total dew amount on the simulated condensation surface in specific height in the dew night can be obtained by adding the dew amount in every 2 hours ($DA_{2h}(t_i)$). The specific calculation process is as follows:

$$A(t_j) = \sum_{i=2}^{10} DA_{2h}(t_i) \quad i = 2, 4, 6, 8, 10 \quad (5)$$

$A(t_j)$ is the total dew amount in the j th day.

The model of dew amount change with height was fitted using the curve fitting tool of Matlab R2017a (MathWorks, USA).

Dew formation of LC and CS

We used the mowed plants as experimental materials to measure their dew amount. The high vapour pressure in the air can inhibit the water loss inside the plant after mowing, which makes it possible to use the mowed plant as a condensation surface. In addition, the mowed plants will not absorb the water through the roots, which avoids guttation from the tip of leaves at night, thereby avoiding weighing errors.

This study was conducted from August 11 to September 5, 2015. In the dew night, three mature and healthy plants (LC and CS) were selected for mowing (cut along the land surface) after the dew began to condense on the surface of the plant. As Figure 2 shows, they were then loosely tied from the lower end with a thin cotton rope to keep the upper part in a natural loose state, and another rope was used to loosely surround the canopy to prevent the plant

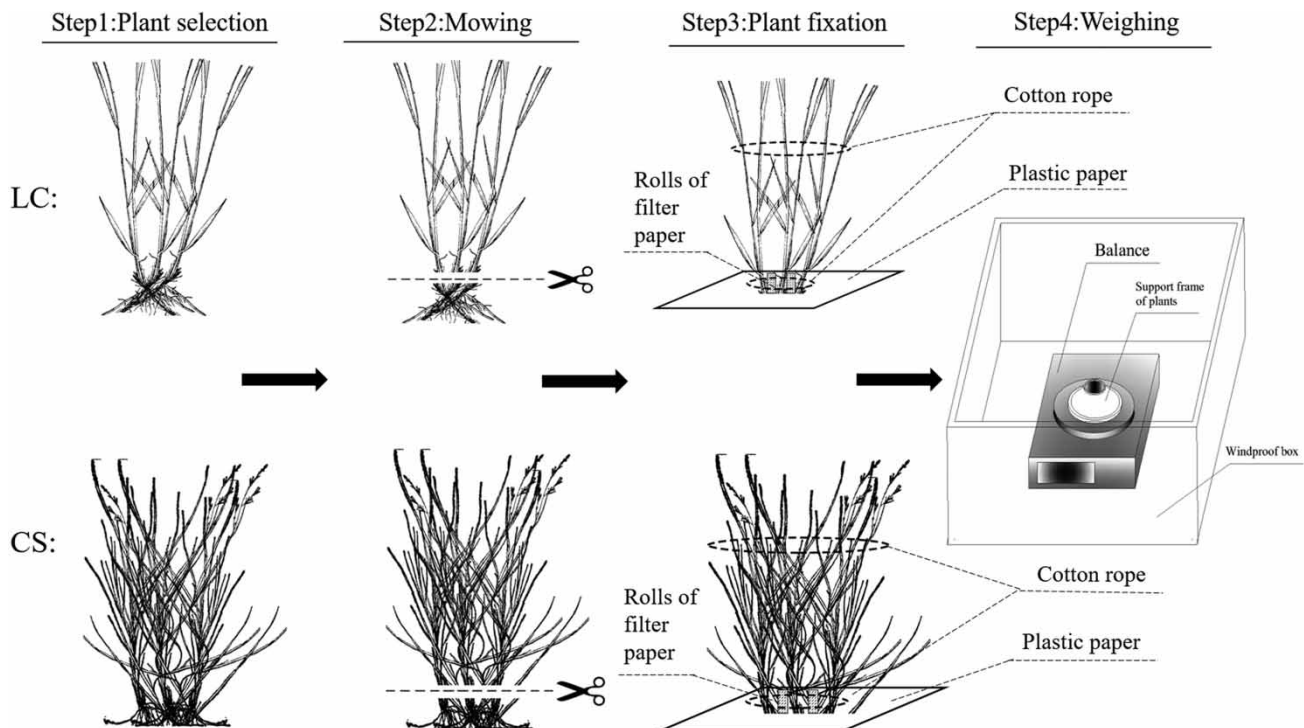


Figure 2 | Dew collection process of *Leymus chinensis* (LC) and *Cleistogenes squarrosa* (CS).

from excessive tilt. To prevent dew flowing down from the stem to the soil, two rolls of filter papers were inserted into the base of each plant bunch to absorb the dew that flows down the plant leaves or stem. At the same time, a piece of plastic paper was placed under each plant bunch to prevent the filter paper roll from absorbing water from the soil. In addition, a support frame was set up at the bottom of the LC to ensure that the plant bunch stayed upright (the CS can be placed upright in the community without special fixation because of its lower height). We mowed new plants each experimental day and fixed them in their origin community to collect dew, and three replicates for each plant with spacing of 50 cm. There were three mowing times for each experimental day: 19:30–20:00, 21:30–22:00 and 23:30–0:00 (depending on the dew formation time). The sample plants were weighed by electronic balance every 2 hours from start time (20:00, 22:00, 0:00) to 6:00 am the next day (4–6 times, the weighing accuracy is 0.01 g). The electronic balance was placed in a windproof box to prevent wind interference during the weighing of plants. Due to the upward leaf state of both LC and CS, the dew excessively condensed on the leaf surface will only flow down from the stem and not drip to the soil from the leaf tip. The filter paper roll in the bottom of the plant bunch will retain the dew flowing down from the stem to avoid the loss of dew from the stem during plant movement. During the weighing process, we slowly move the plants to the shelf of the balance and keep the plants upright. The filter paper roll in the bottom of each plant bunch will retain the dew flowing down from the stem to avoid the loss of dew during plant movement. After all the plant materials were weighed in the experimental day, they were placed in an oven at 120 °C for 1 h and then at 90 °C for 24 h to obtain the aboveground biomass. After cooling, the dry weight was measured to obtain biomass. The plant leaf area was measured (accuracy is 1 cm²) by the grid method (Pandey & Singh 2011). The specific calculation process of SLW is as follows.

$$SLW = \frac{m_{leaf}}{a_{leaf}} \quad (6)$$

SLW is specific leaf weight (g/cm²), *m_{leaf}* is the dry weight of leaf (g), *a_{leaf}* is leaf area (cm²).

The calculation process of dew amount (*H*) is the same as the experimental part of the simulated condensation surface (Equations (1)–(5)). The measurement data of the two plants (LC and CS) on each experimental day are shown in Table 2.

Meteorological data

The meteorological data were continuously monitored for 24 h during the test using a WeatherHawk's portable weather station. The altitude of the weather station is 1.5 m from the ground and 3 m from the experimental site. Data collection was performed every 5 min, and the collected data included temperature (*T*, accuracy is 0.1 °C), relative humidity (*RH*, accuracy is 1%) and wind speed (*WS*, accuracy is 0.1 m/s).

RESULTS

Dew formation with height

The dew amount with different ground heights had a similar dynamic trend in the dew night and the whole period of the experiment (Figure 3(a) and 3(b)). During the experiment, the mean dew amount in the height range of 5–80 cm was 0.13–0.21 mm (Figure 4). For different time periods in the night, as Figure 3(a) showed, the minimum value of dew amount for all heights appeared in the period from 4:00 to 6:00 with the variable range from 0.023 to 0.036 mm. The highest peak appeared from 24:00 to 2:00 for the 80 cm height and from 20:00 to 22:00 for the other heights. During the periods from 24:00 to 2:00 and 2:00 to 4:00, the dew amount increased with the height with the variable range from 0.03 to 0.059 mm and 0.023 to 0.044 mm, respectively. In the other three time periods, the dew amount of the three heights of 20 cm, 40 cm, and 80 cm did not vary significantly with height. For all experimental days (Figure 3(b)), the highest daily dew amount appeared at 80 cm, Aug 16, which was 0.348 mm, and the lowest appeared at 5 cm, Sep 5, which was 0.053 mm. For the heights of 5, 10 and 20 cm, their dew amount increases with height. However, as the height continues to rise, at the height gradients of 20, 40 and 80 cm, their dew amount began to stagger (Figure 3(a) and 3(b)).

Table 2 | Summary of measurement data for LC and CS

Date of dew	Aug 11	Aug 16	Aug 17	Aug 22	Aug 23	Aug 26	Aug 31	Sep 3	Sep 5
LC Aboveground biomass (g)	5.93 ± 0.3	5.66 ± 0.5	7.29 ± 0.74	6.38 ± 0.44	5 ± 0.64	6.14 ± 0.71	5.77 ± 0.43	7.31 ± 0.76	6.16 ± 1.83
Stem biomass (g)	2.08 ± 0.04	1.93 ± 0.29	2.8 ± 0.22	2.33 ± 0.24	2.13 ± 0.31	2.27 ± 0.25	2.4 ± 0.2	3.08 ± 0.24	2.61 ± 0.75
Leaf biomass (g)	3.85 ± 0.27	3.73 ± 0.21	4.49 ± 0.53	4.05 ± 0.21	2.87 ± 0.34	3.87 ± 0.47	3.36 ± 0.24	4.23 ± 0.52	3.55 ± 1.09
Leaf area (cm ²)	187.33 ± 20.24	173.67 ± 20.68	232.33 ± 45.32	197.33 ± 14.7	125 ± 19.13	190.33 ± 35.72	159 ± 15.64	210.33 ± 38.23	187.67 ± 58.78
Specific leaf weight (g/cm ²)	0.0207 ± 0.0013	0.0217 ± 0.0017	0.0197 ± 0.0017	0.0207 ± 0.0021	0.023 ± 0.0008	0.0207 ± 0.0024	0.0213 ± 0.0017	0.0203 ± 0.0013	0.019 ± 0.0008
CS Aboveground biomass (g)		1.63 ± 0.2	1.51 ± 0.26	1.56 ± 0.28	1.68 ± 0.26	1.73 ± 0.37	0.95 ± 0.07	1.71 ± 0.12	1.93 ± 0.17
Stem biomass (g)		0.75 ± 0.09	0.71 ± 0.12	0.75 ± 0.16	0.72 ± 0.11	0.73 ± 0.11	0.4 ± 0.02	0.75 ± 0.02	0.83 ± 0.08
Leaf biomass (g)		0.89 ± 0.11	0.8 ± 0.14	0.82 ± 0.12	0.96 ± 0.15	1 ± 0.26	0.55 ± 0.05	0.96 ± 0.11	1.09 ± 0.14
Leaf area (cm ²)		63.67 ± 5.79	56 ± 11.43	59.33 ± 7.59	61.33 ± 15.69	72 ± 19.3	38 ± 3.27	66 ± 7.87	78 ± 8.52
Specific leaf weight (g/cm ²)		0.0139 ± 0.0009	0.0145 ± 0.0012	0.0138 ± 0.0011	0.016 ± 0.0016	0.0139 ± 0.0007	0.0144 ± 0.0012	0.0146 ± 0.0009	0.014 ± 0.0008

Measurement indicators include Aboveground biomass (g), Stem biomass (g), Leaf biomass (g), Leaf area (cm²), Specific leaf weight (g/cm²).

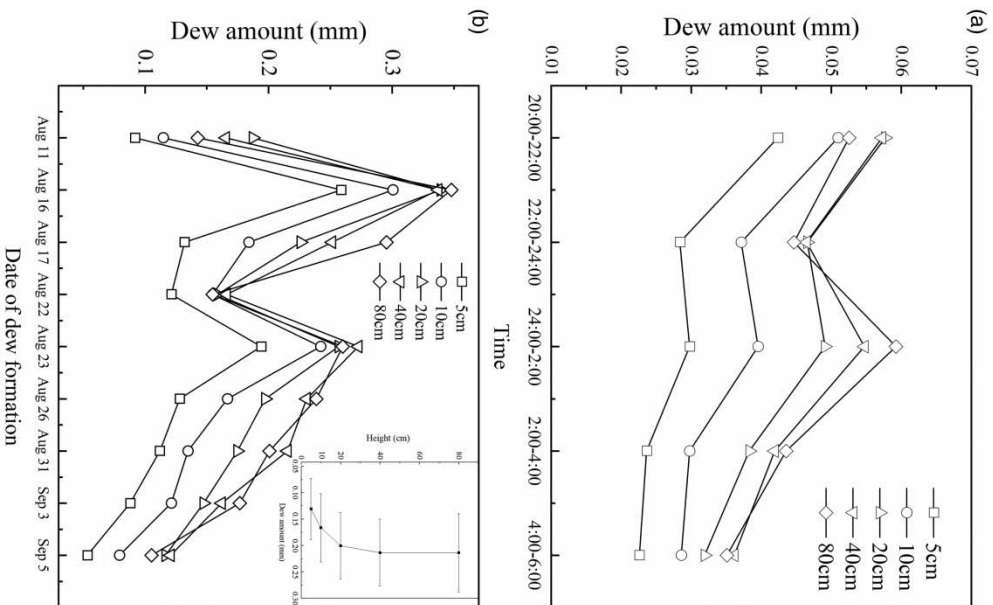


Figure 3 | (a) Changes of mean dew amount on different height-simulated condensation surfaces during dew night. (b) Dew amount of different height-simulated condensation surfaces on each experimental day (attached with a figure of average daily dew amount in each layer).

As shown in **Figure 4**, in the height range of 5–80 cm, the dew amount increased with the height, but the growth rate decreased and gradually approached zero after reaching 40 cm. The change process was in the form of the equation $y = a(1 - e^{-bx})$.

Dew formation of LC and CS

As shown in **Figure 5(a)**, the higher dew amount for LC and CS during dew nights appeared at 24:00–2:00 (LC: 0.038 mm, CS: 0.027 mm) and 2:00–4:00 (LC: 0.038 mm, CS: 0.024 mm), and the dew amount of LC in these two

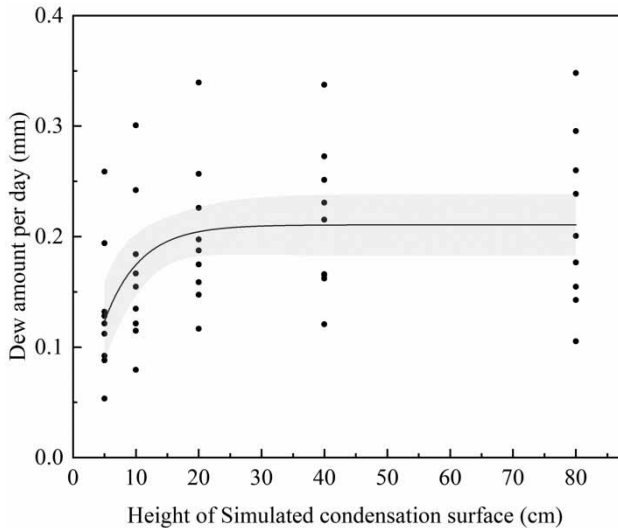


Figure 4 | Effects of change in height on dew amount per day at 5 height-simulated condensation surfaces. The structure of the equation is $y = a(1 - e^{-bx})$ (The fitted curve shown uses the daily mean value of each height as the independent variable. $a = 0.2106$, $b = 0.1761$, $R^2 = 0.99$.) The grey region indicates the 95% confidence interval around the regression ($P < 0.05$).

time periods was higher than CS. For the other three time periods (20:00–22:00, 22:00–24:00, 4:00–6:00), the dew amount of LC was lower than CS, and the dew on the LC leaves decreased due to evaporation in these three periods (the daily dew change can be seen in the Supplementary material, Figure S1). As shown in Figure 5(b), LC had the highest level of dew formation during the 3 days of the experiment (Aug 17, Aug 23 and Aug 26; 0.164 mm, 0.162 mm, 0.140 mm, respectively). The dew amount of LC at other days was mostly lower than CS (only slightly higher than CS on Sep 5), and the minimum dew amount during the experiment was formed by LC at Aug 22 (0.022 mm). The average daily dew amount of LC and CS was 0.095 mm and 0.096 mm, with standard deviation of 0.047 mm and 0.027 mm, respectively (Figure 5(c)).

As shown in Figure 6, the ratios of the dew amount to SLW of LC and CS on all experimental days were 1.09 (Aug 22)–8.50 (Aug 17) and 3.89 (Sep 5)–9.31 (Aug 16). The ratios of the dew amount to SLW of CS were higher than LC on all experimental days with the exception of Aug 11 (dew amount of CS was not measured) and Aug 26. The average ratio of the dew amount to SLW of LC and CS was 4.61 and 6.69 and the standard deviation was 2.27 and 1.79, respectively.

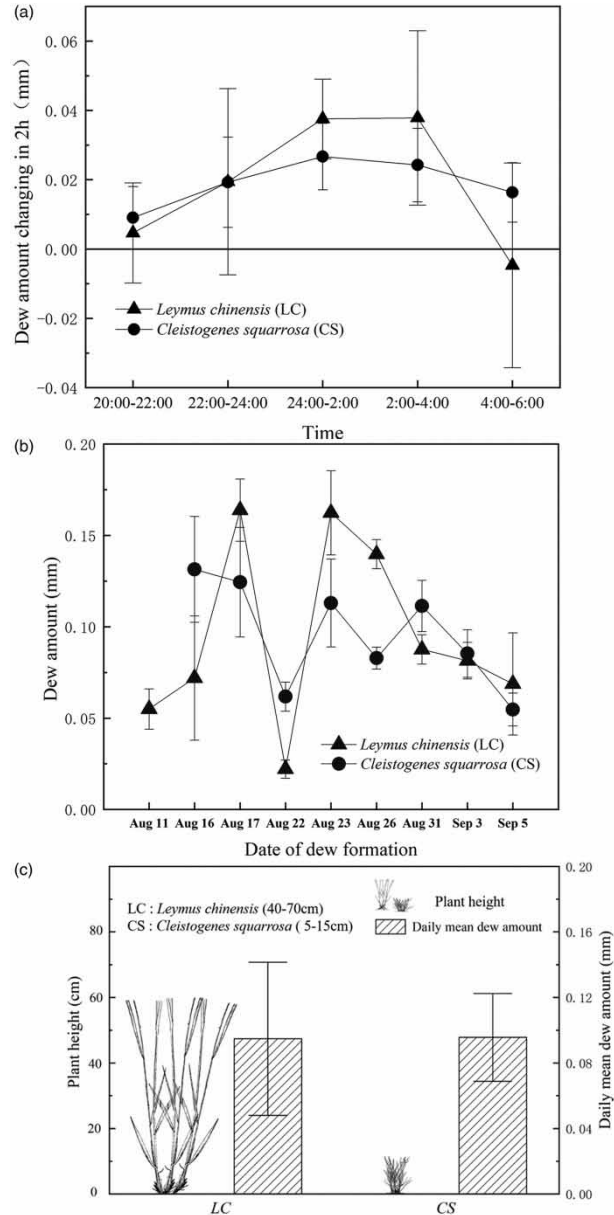


Figure 5 | (a) Changes of mean dew amount on LC and CS surface during dew night. Strong evaporation of dew during dew night usually leads to dew reduction of plant surface (< 0 on x axis). (b) Dew amount of LC and CS on each experimental day. Dew measurement of CS was not performed on Aug 11. (c) The mean daily dew amount comparison of LC and CS. The error bar is standard deviation. The dew amount changes of LC and CS at different time periods of each experimental night are shown in the Supplementary material, Figure S1.

Meteorological impact

It can be seen from Figure 7 that before 05:00 am RH continuously increased and was accompanied by continuous decrease of T. RH and T reached extreme values at 5:00,

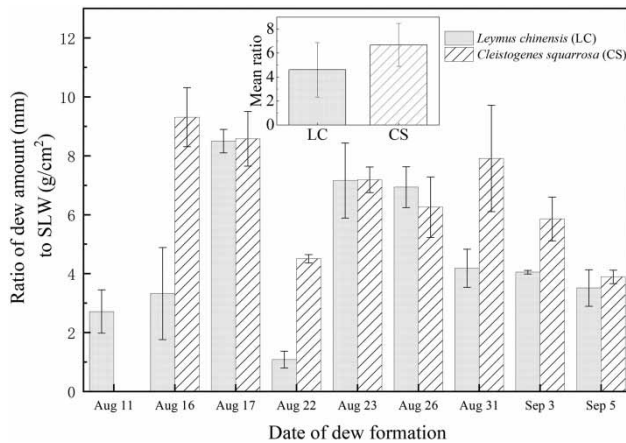


Figure 6 | Ratio of dew amount (mm) to SLW (g/cm^2) of LC and CS in each dew night. The additional figure shows the mean daily ratio of dew amount to SLW comparison of LC and CS. SLW is the specific leaf weight. The error bar is standard deviation. Dew measurement of CS was not performed on Aug 11.

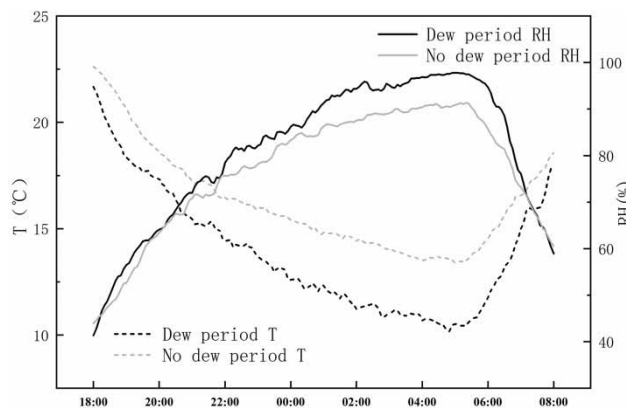


Figure 7 | Comparison of average temperature (T) and average relative humidity (RH) changes at dew and non-dew nights. Data of non-dew nights: Aug 8, Aug 9, Aug 10, Aug 12, Aug 13 Aug 14, Aug 15, Aug 18, Aug 19, Aug 20, Aug 21, Aug 24, Aug 25, Aug 27, Aug 28, Aug 30. Data of dew nights: Aug 11, Aug 16, Aug 17, Aug 22, Aug 23, Aug 26, Aug 31, Sep 3, Sep 5.

after which RH decreased rapidly and T rose rapidly. Compared with non-dew night, the T and RH range was larger during the dew night. From the extreme values at night, the maximum relative humidity at dew night was about 10% higher than that at non-dew night, and the lowest temperature was about 3 °C lower than the non-dew night. The specific atmospheric data at different periods of the night are shown in the Supplementary material, Table S1.

DISCUSSION

In the Hulunbuir grassland (semi-arid region), the dew in the height range of 5–80 cm was 0.13–0.21 mm. This is higher

than 0.07 mm on the island of Corsica (Beysens et al. 2005) and 0.06 mm in Israel's Negev Desert (Zangvil 1994). However, it is lower than 0.41–0.6 mm of the Croatian coast (Muselli et al. 2009). This study proves that the dew amount on natural grassland will increase with height, which is consistent with some research results in forests, marshes and desert ecosystems (Liu et al. 2001; Bai et al. 2004; Li et al. 2010). However, this feature is mainly reflected in the range of height below 40 cm, and its increase rate gradually decreases with height and tends to 0 (Figure 4). This is mainly due to the fact that, in the height range of 5–40 cm, the drop rate of temperature on the higher surface in the dew night is, in general, larger than that on the soil surface, which means that it will be much easier for the higher surface to reach the dew point temperature (Zangvil 1994), thereby forming more dew. When the height from the ground rises further (40–80 cm), the airflow, due to the instability of the air, will mix the air in the upper layer which will cause its temperature and relative humidity to converge and make the air in the height of 40–80 cm have the same dew point (Muselli et al. 2012). This may cause the air within 40–80 cm to have similar condensation ability. At the same time, the instability of the air gradually increases with height in a certain range, which also makes it easier to generate wind from a higher place, thereby suppressing the formation of dew (Beysens et al. 2005; Muselli et al. 2012). In plants, the lower leaves often suffer from the effects of shading preventing them from performing sufficient photosynthesis, leading to an increase in the specific leaf area, which causes the specific leaf area of the plant to rise as the height increases. The result that the top layer canopy of grassland plants can form more dew can be an effective way to supplement water for the top leaves of plants that can use dew through foliar uptake, enabling them to perform more effective photosynthesis. This may also be one of the driving forces for reducing the specific leaf area of the upper leaves of plants.

The water absorption ability of the filter paper of the artificial condensation can shorten the nucleation stage of the dew, and the initial condensation rate of filter paper can be accelerated by the moisture adsorption force caused by the internal moisture movement. These all increase the dew formation on the simulated condensation surface at the beginning of the dew night which means that the actual

dew amount between 20:00 and 22:00 should be lower than its measured value. Therefore, the period of 24:00–2:00 may be the most suitable time for the formation of dew. However, in the period of 24:00–2:00, it can be seen from Figure 7 that the RH and T do not reach their highest value and lowest value, respectively. This is because the weather station is located 1.5 m above the ground, which does not represent the meteorological conditions of the air at 0–80 cm. Although the temperature drop rate of air at the height of 0–80 cm may be slower than the air of 1.5 m (Scherm & Van Bruggen 1993), the evaporation of water from the soil into the air will maintain a relatively high RH growth rate in the air of 0–80 cm (Zangvil 1994). This will allow it to reach the dew point temperature faster and obtain the most suitable meteorological conditions for dew formation between 24:00 and 2:00. This shows that the relatively high and stable RH during nights (Aug 16, Aug 17, Aug 23 and Aug 26, Supplementary material, Table S1) can make the plant surface reach the dew point temperature faster and stay longer, which is helpful to the formation of dew. This is consistent with the results of previous studies (Beysens *et al.* 2005; Galek *et al.* 2015). For the day with the least dew formation, Aug 22, although its average RH also reached 89%, its average wind speed at night reached 0.7 m/s, which may hinder the formation of dew. Many studies have also found that higher wind speeds are not conducive to dew formation at night (Beysens *et al.* 2005; Muselli *et al.* 2012).

The dew amount per night of LC and CS are relatively consistent, being 0.095 mm and 0.096 mm, respectively (Figure 5(c)). These are much lower than the dew amount on maize canopy (about 4 mm) (Atzema *et al.* 1990; Jacobs *et al.* 1994) and the upper layer of lily (about 0.3 mm), but only slightly less than the dew amount in the lower layer of lily (0.15 mm) (Jacobs *et al.* 2005). For different plants, height can indeed affect dew formation, but it is not the decisive influencing factor. In a more suitable environment for condensation (24:00–2:00 and 2:00–4:00), the higher LC has greater dew formation advantages, which is similar to the results of other ecosystem studies (Zangvil 1994; Jacobs *et al.* 2005). However, in a relatively poor condensing environment (20:00–22:00; 22:00–24:00 and 4:00–6:00), the dew amount of LC is less than or equal to the dew amount of CS. In the dew night, the dew on the LC often decreases due to evaporation, but the dew on the CS

keeps increasing throughout the experimental period (Figure 5(a); Supplementary material, Figure S1). Recent studies also showed that night-time evapotranspiration occurs frequently at different grassland sites, and the dew formed on the soil or plant surface can quickly be re-evaporated (Groh *et al.* 2019; Padrón *et al.* 2019). This may be due to the fact that in an environment with unstable meteorological conditions, the upper space of the grassland community is more likely to form wind due to the mixing of air layers of different temperatures (Zhang *et al.* 2010), thereby causing the dew that has condensed on the surface of the upper plant leaves to evaporate. For CS in the lower structure of the community, staggered near-ground plants may hinder the flow of air to some extent, so that its dew formation is less affected by micrometeorological fluctuations, thus protecting the dew on its leaves from evaporation. In addition, the tighter arrangement of the slender leaves (Table 1) and the pubescence on the CS also help the formation and maintenance of dew (Rundel 1982; Jacobs & Nieveen 1995; Zhuang & Zhao 2010; Cen & Liu 2017). These are also the reasons why shorter CS has the same average daily dew amount as LC and has more stable dew capabilities.

As one of the indicators for measuring photosynthetic performance, SLW has a high correlation with the water use efficiency of plants (Liu & Stützel 2003; Songsri *et al.* 2009; Auerswald *et al.* 2012; Levey *et al.* 2019). It is more beneficial to use the ratio of dew amount to SLW to compare LC and CS from the perspective of dew use efficiency (leaf level), and it can explain the ratio of potential dew that can be used to organic matter per unit leaf area. As a C₄ plant, CS has lower SLW (Table 2) and higher photosynthetic efficiency (Yang *et al.* 2011; Auerswald *et al.* 2012; Zheng 2018; Levey *et al.* 2019) than C₃ plant LC. The higher ratio of dew amount to SLW of CS indicates that the shorter CS has more potential dew to provide to its organic matter, and this can help it obtain relatively more effective non-rainfall resources to sustain life in drought stress. This may be one of the potential mechanisms for the degradation of the LC community to become a CS community in dry years (Pan *et al.* 2016), but more investigations are still needed to discuss this.

The larger $T_{\text{difference}}$ (temperature difference) between day and night is one of the key favorable factors for the formation of dew (Scherm & Van Bruggen 1993; Luo &

Goudriaan 2000; Agam & Berliner 2006; Beysens 2015). The higher air temperatures can keep the surface of the plant at a higher temperature than the dew point and make it difficult for the formation of dew (Sentelhas *et al.* 2008). It can be seen from Figure 7 that T (temperature) during the dew night is always lower than that of the non-dew night, but the difference in RH (relative humidity) between the dew night and non-dew night is usually shown after the condensate has been produced for a while. RH of 100% is not a necessary factor for the formation of dew, which is also the same as the results of previous studies (Beysens 2015; Agam & Berliner 2006; Sentelhas *et al.* 2008). At the end of the dew night, the T and RH changed rapidly after reaching the extreme value. The RH rapidly decreased and the T rose rapidly, which makes the meteorological conditions suitable for dew formation disappear quickly, so the cessation of dew formation is also rapid (Jacobs *et al.* 1994).

CONCLUSION

In the height range from 5 to 80 cm, the dew amount in the Hulunbuir grassland generally increased with the height of the leaves, but the growth rate gradually decreased and approached zero. Its growth pattern is expressed in the form of an exponential function ($y = a(1 - e^{-bx})$). For grassland plants, the height of the canopy has an important influence on the formation of dew, but it is not a decisive factor. The shorter CS (5–15 cm) has the same dew amount (0.095 mm) as the LC (40–70 cm). For the CS, its tighter arrangement of the slender leaves (with the pubescence) and more stable micro-meteorological conditions where it is located can help the formation and maintenance of dew. The morphological feature of CS that contributes to dew formation may be one of its plant strategies to increase drought resistance. The lower ratio of dew amount to SLW of CS than LC indicated that CS could obtain more potential dew per unit organic matter during dew night. This may be one of the potential mechanisms for the succession from LC communities to CS communities under drought stress. The time period of 24:00–4:00 is more suitable for dew formation, and higher RH and breeze or windless environment helps the formation of dew.

DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

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