Trees
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ORIGINAL ARTICLE

Transpiration of *Pinus sylvestris* var. *mongolica* trees at different positions of sand dunes in a semiarid sandy region of Northeast China

Lining Song[1,2,3] · Jiaojun Zhu[1,2,3] · Xinjunyan Li[1,2,3] · Kai Wang[4] · Guochen Wang[5] · Haihong Sun[5]

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Abstract

Key message **Mongolian pine transpiration was driven by soil water at the top and vapor pressure deficit at the bottom of sand dunes; this was modulated by interannual variability in water availability.**

Abstract Mongolian pine (*Pinus sylvestris* var. *mongolica*) plantations have been suffering frequent diebacks in years of extreme drought due to water deficit in semiarid sandy regions of Northeast China. However, the transpiration dynamics of Mongolian pine trees at different positions of sand dunes and their responses to environmental variables remain unknown. Here, canopy transpiration and conductance of 38-year-old Mongolian pine trees at top (TS) and bottom (BS) of sand dunes were quantified using sap flow method from 2018 to 2019. Canopy transpiration per unit leaf area (E_L) was, respectively, 0.45 ± 0.13 and 0.53 ± 0.17 mm d^{-1} at TS and BS in 2018, with relatively low soil moisture, and it was, respectively, 0.51 ± 0.15 and 0.59 ± 0.19 mm d^{-1} in 2019, with relatively high soil moisture. Moreover, E_L variability explained by climate variables was greater at BS than at TS during 2018, but the trend was reversed during 2019. In addition, canopy conductance at BS was 11.5% higher than that at TS, but magnitude of increase from 2018 to 2019 was higher at TS. Stomatal sensitivity to vapor pressure deficit was higher at BS than at TS in 2018, but comparable in 2019. Consistently, stomatal sensitivity to soil moisture was higher at TS than at BS in 2018, but the trend was reversed in 2019. Taken together, these findings indicate that Mongolian pine trees at TS exhibit lower transpiration, which is primarily driven by soil moisture, than those at BS, presenting greater susceptibility to dieback under extreme drought.

Keywords Plantations · Water deficit · Sap flow · Soil moisture · Stomatal sensitivity

Introduction

Tree transpiration—the process of evaporation of water absorbed by trees from the soil into the atmosphere—is an important part of the forest water balance, and data on transpiration dynamics are fundamental to understand the ecophysiology of plantation forests in arid and semiarid regions (Ungar et al. 2013; Jiao et al. 2019). Tree transpiration is regulated via stomatal responses to environmental factors, such as air vapor pressure deficit (VPD), solar radiation, soil water availability, and precipitation (Ghimire et al. 2018; Oogathoo et al. 2020). As the air VPD increases, tree transpiration gradually increases up to a point when the stomata begin to close; thus, transpiration must be stabilized or lowered to prevent irreversible damage to the hydraulic system of trees (Running 1976; Franks et al. 1997; Wu et al. 2018a). In addition, reduced soil water availability triggers the gradual closure of stomata and reduces the transpiration rate, thereby avoiding embolism and conductive tissue

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✉ Jiaojun Zhu
jiaojunzhu@iae.ac.cn

1 CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang 110016, China

2 Qingyuan Forest CERN, National Observation and Research Station, Liaoning Province, Shenyang 110016, China

3 Key Laboratory for Management of Non-Commercial Forests, Liaoning Province, Shenyang 110016, China

4 College of Environmental Sciences and Engineering, Liaoning Technical University, Fuxin 123000, China

5 Liaoning Institute of Sandy Land Control and Utilization, Fuxin 123000, China

damage (Hayat et al. 2020; Liu and Biondi 2020). However, reduced stomatal conductance prevents excessive transpiration loss at the expense of carbon dioxide uptake for photosynthesis (Ghimire et al. 2018). Therefore, the stomatal control of transpiration drives the balance between carbon uptake and water loss, further affecting tree survival and growth (Ghimire et al. 2018).

Moreover, topography affects tree transpiration through the regulation of microenvironmental factors, such as soil moisture (Dai et al. 2015; Helman et al. 2017; Metzen et al. 2019), particularly in semiarid and arid sandy regions, which are characterized by undulating sand dune landscapes. Trees at the top of sand dunes (TS) exhibit more stringent stomatal regulation of transpiration than trees at the bottom of sand dunes (BS), due perhaps to the lower availability of water for trees at TS (Dai et al. 2015; Song et al. 2019). Although numerous studies have explored the impact of topographic position on tree transpiration (Kumagai et al. 2008; Kume et al. 2015; Méndez-Toribio et al. 2017; Hawthorne and Miniat 2018; Pei et al. 2019), simultaneous effects of environmental variables and topography-driven soil conditions on tree transpiration are not fully understood as yet (Hawthorne and Miniat 2018). Moreover, few studies have investigated these aspects in semiarid and arid sandy regions.

Mongolian pine (*Pinus sylvestris* var. *mongolica*) is a geographical variety of Scots pine (*Pinus sylvestris*), which is naturally distributed in the Daxinganling Mountains of China (50°10′ to 53°33′N, 121°11′ to 127°10′E), on sandy plains of Honghuaerji in Hulunbeier, China (47°35′ to 48°36′N, 118°58′ to 120°32′E), and in parts of Russia and Mongolia (46°30′ to 53°59′N, 118°00′ to 130°08′E). Owing to its high drought, cold, and barren tolerance, Mongolian pine has become one of the most important tree species for reforestation for windbreak and sand fixation in sandy regions of northern China (Zhu et al. 2008; Zheng et al. 2012; Song et al. 2020). However, Mongolian pine plantations aged approximately 35–40 years have been frequently suffering diebacks and mortality during the years of extreme drought. Moreover, Mongolian pine trees at TS exhibited a higher rate of dieback and mortality than those at BS (Zhu et al. 2005). Previous studies have indicated water deficit as the primary cause of this dieback and mortality (Jiao 2001; Jiang et al. 2006; Zhu et al. 2008; Zheng et al. 2012; Song et al. 2020). In addition, precipitation exhibits strong interannual variations in the Kereqin Sandy Land, and warming trends are expected to continue (Song et al. 2020). Therefore, the dynamics of transpiration water loss of Mongolian pine trees at different positions on sand dunes (e.g., TS and BS) and their response to environmental variables must be urgently assessed, which would contribute to the understanding of mechanisms underlying dieback and mortality and enable proper management of these plantations in semiarid sandy regions. Considering the differences in physical and hydraulic properties between TS and BS (Jiao 1989; Song et al. 2019), such as higher soil moisture at BS than at TS, we hypothesized that (1) Mongolian pine trees at TS exhibit lower transpiration rates and canopy conductance than those at BS. In addition, several studies have indicated that trees at higher topographic positions are shorter than those at lower topographic positions (Grigg et al. 2008; Kumagai et al. 2008). According to Oren et al. (1999) and Schäfer et al. (2000), stomatal sensitivity to VPD decreases with tree height through its effect on canopy coupling to the atmosphere. Nevertheless, other studies have demonstrated decreasing sensitivity of stomatal conductance to VPD under dry soil conditions, because stomatal conductance should remain low and be less sensitive to VPD to maintain leaf water potential and prevent catastrophic xylem functional loss (Kumagai et al. 2004; Gu et al. 2017; Ghimire et al. 2018). Moreover, the effects of reduced soil moisture on the stomatal sensitivity could offset or override the expected tree height (McDowell et al. 2005; Ambrose et al. 2010). Therefore, we hypothesized that (2) Mongolian pine trees at TS exhibit weaker stomatal regulation of transpiration than those at BS.

To this end, the objectives of the present study were to (1) evaluate the differences in transpiration and canopy conductance of Mongolian pine trees and (2) explore the variations in environmental and stomatal control of tree transpiration between TS and BS related to tree height. To test the above hypotheses and achieve the study objectives, we measured the canopy transpiration and conductance of 38-year-old Mongolian pine trees at TS and BS using the sap flow method during two consecutive growing seasons of 2018 and 2019 and simultaneously monitored specific environmental variables (ambient temperature, relative humidity, photosynthetically active radiation, soil moisture at different depths, wind speed, and precipitation).

Materials and methods

Study site

This experiment was conducted in the Zhanggutai region (42°43 N, 122°22 E, 226 m a.s.l.), Liaoning Province, China, located in the southeastern part of the Keerqin Sandy Land. This region is part of a semiarid climatic zone. The mean annual temperature is 6.7 °C (mean from 1965 to 2019). The mean annual precipitation is 479 mm (mean from 1954 to 2019), and the mean annual pan evaporation is approximately 1580 mm (Song et al. 2020). The frost-free period is approximately 154 days, and the snow cover lasts approximately 33 days (Zhu et al. 2005). The major soil types are Arenosols, which are developed from sandy parent material through wind action (Zhu et al. 2008). Based on the landforms, vegetation cover types, and soil characteristics, the study region was classified into active, semi-active, and fixed sand dunes; flat sandy land; and low-lying land (Zhu et al. 2005; Song et al. 2019). The soil physical properties differed according to the position of the sand dunes. For instance, soil particle size distribution was 32.4% coarse (1–0.250 mm), 48.8% fine (0.250–0.06 mm), and 18.8% silt (< 0.06 mm) at TS and 12.3% coarse, 58.5% fine, and 29.2% silt at BS (Jiao 1989; Song et al. 2019). The groundwater level was approximately 5.0 m in the flat sandy land (Song et al. 2020) and deeper than 5.0 m at TS. The dominant tree species included *Pinus sylvestris* var. *mongolica* Litv., *Pinus tabuliformis* Carriere, *Populus × xiaozhuanica* W. Y. Hsu et al. Liang, and *Ulmus pumila* L. The understory vegetation was dominated by annual grasses and herbs, including *Potentilla anserine* L., *Cleistogenes chinensis* (Maxim.) Keng, *Artemisia frigida* Willd., and *Setaria viridis* (L.) Beauv.

A Mongolian pine plantation characterized by undulating stabilized sand dunes was selected for the present study. The plantation was 38-year-old in 2018. A typical stabilized sand dune (horizontal length, ~ 60 m, slope angle, 40°, and vertical dimension, ~ 7.0 m) was selected in April 2018 (Fig. 1). The tree density at TS and BS was approximately 867 and 533 trees ha^{-1}, respectively, and the leaf area index was 0.8 and 1.1 m^2 m^{-2}, respectively (Table 1). The initial planting density at BS was the same as that at the TS. However, the trees at BS were thinned in 2000, whereas no management regime was conducted at TS. Therefore, tree density at TS was higher than that at BS. Although differences in tree density were expected to affect the water availability for and/or boundary layer conditions of trees between TS and BS, this effect was relatively small compared with that of topography (Kumagai et al. 2008; Zhang et al. 2017; Hawthorne and Miniat 2018) (i.e., position of sand dunes in the present study). The leaf area index was estimated based on the five hemispherical photographs obtained using automatic exposure with the Nikon Coolpix 995 camera equipped with an FC-E8 fisheye lens at each position of sand dune. The images were upward facing at 1.0 m from the ground and obtained avoiding midday hours. Four trees each at TS and BS were randomly selected for sap flux density measurements (Table 2).

Meteorological data and soil moisture measurement

Meteorological variables were monitored using an automatic meteorological station installed in open areas of flat sandy land near the bottom of stabilized sand dunes. Ambient temperature (T_a, °C) and relative humidity (RH, %) were measured using a thermosensor (3688WD1; Spectrum Technologies, Inc., Aurora, USA) at 2.0 m above the ground. Photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) was measured using a silicon pyranometer sensor (3670I; Spectrum Technologies, Inc., Aurora, USA) at 2.0 m above the ground. Precipitation (mm) and wind speed (m s^{-1}) were measured using a tipping bucket rain gauge (3655R, Spectrum Technologies, Inc., Aurora, USA) and an anemometer, respectively. These measurements were obtained at 60 s intervals and recorded as 10 min averages in a data logger (Watchdog 1000 Series, Spectrum Technologies, Inc. USA). Because of small differences in the height of the canopy surface between TS and BS (approximately 2.0 m; Table 1, Fig. 1), we assumed that the radiative energy received by the canopies and the ambient temperature and relative humidity above them to be similar (Kumagai et al. 2008). Vapor pressure deficit (VPD) was calculated as described by Campbell and Norman (1998).

Table 1 Characteristics of studied plots at the top (TS) and bottom (BS) of sand dunes in 2018

Characteristics	Topographic position	
	TS	BS
Age	38	38
Density (trees ha^{-1})	867	533
Mean diameter at breast height (cm)	16.7 ± 2.7	24.0 ± 2.3
Mean height (m)	7.0 ± 1.2	12.0 ± 1.2
Leaf area index (m^2 m^{-2})	0.8 ± 0.2	1.1 ± 0.3
Sap flux density measurement (trees)	4	4

The data are expressed as mean ± 1SD for diameter at breast height, height, and leaf area index

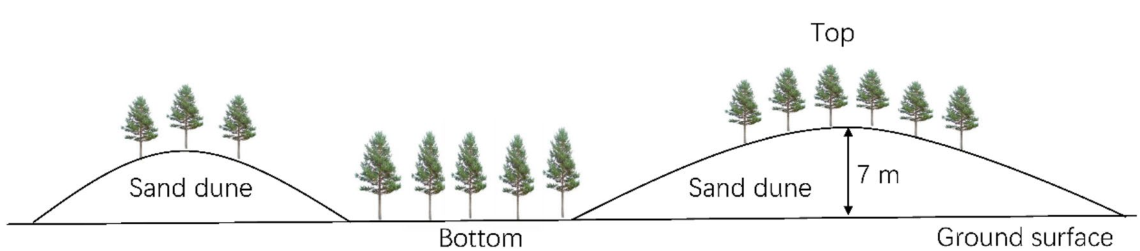


Fig. 1 Schematic diagram of a typical stabilized sand dune terrain

Table 2 Characteristics of sampling trees at the top (TS) and bottom (BS) of sand dunes in 2018 and 2019

Topographic position	No	2018				2019			
		DBH (cm)	H (m)	Sapwood area (cm^2)	Leaf area (m^2)	DBH (cm)	H (m)	Sapwood area (cm^2)	Leaf area (m^2)
TS	1	16.2	5.5	155.4	38.6	16.4	5.7	159.7	39.8
	2	18.0	7.9	196.2	52.2	18.3	8.1	203.5	53.8
	3	17.8	7.7	191.4	50.9	18.0	8.0	196.2	52.5
	4	18.1	8.1	198.6	53.1	18.3	8.4	203.5	54.8
BS	5	26.2	11.2	449.7	92.9	26.6	11.5	465.1	95.7
	6	20.7	10.9	267.2	71.5	21.1	11.3	278.7	74.4
	7	28.9	11.1	558.6	102.5	29.2	11.4	571.5	105.1
	8	20.9	10.7	272.9	71.5	21.3	11.2	284.6	74.7

DBH diameter at breast height; *H* height

At TS and BS, volumetric soil water content (θ) was monitored using time–domain reflectometry (TDR; Trime-T3, Ettlingen/Baden-Württemberg, Germany). To measure θ at each position, a probe was inserted into a 100 cm plastic tube, buried vertically in the field in advance, and readings were recorded at the soil depth of 0–100 cm at 20 cm intervals. Because the TRIME-T3 probe was unable to connect with the data logger, θ was measured twice a month at each position of the sand dune (beginning and end of each month). Generally, there were over 3 bright days before each sampling date; therefore, the two measurements in each month were considered to reliably represent the monthly status of soil moisture (Zhang et al. 2015). Previous studies measuring the root distribution of Mongolian pine trees of various ages in the study area have shown that it is a shallow-root tree species, with 98% of the roots being distributed within the soil depth of 100 cm below the ground (Zhu et al. 2008; Zhang et al. 2021). Therefore, soil moisture at the depth of 100 cm was measured in the present study. Although most of the roots were distributed within the soil depth of 100 cm, several roots could reach up to several meters deep (Zhu et al. 2005; Song et al. 2016). The maximum height of the capillary rise from shallow groundwater was approximately 1.0 m in the study area (Song et al. 2016). Therefore, the water table did not affect soil moisture within the soil depth of 100 cm.

Sap flux density measurement and tree transpiration calculation

In the present study, Granier-type thermal dissipation probes (TDPs) (Granier 1987) were used to measure the sap flux density of Mongolian pine trees at TS and BS during two consecutive growing seasons (May–September) in 2018 and 2019. Each sensor comprised a pair of probes (length, 20 mm; diameter, 2 mm) and a copper constantan thermocouple. The probes were inserted into the north-facing side of the trunk at a height of 1.3 m to minimize radiation effects (Liu and Biondi 2020; Lyu et al. 2020). To install the probes, the bark of the sample tree was removed until the cambium was exposed. The distance between the two probes was approximately 15 cm. The temperature difference between the two probes was measured every 10 s, and 10 min averages were recorded in a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA) and a multiplexer (AM16/32A, Campbell Scientific). The sap flux density (J_s) was calculated using a previously published empirical calibration equation for the TDP method (Granier 1987):

$$J_s = 0.0119\left[\frac{\Delta T_m - \Delta T}{\Delta T}\right]^{1.231} \quad (1)$$

where J_s (g cm^{-2} s^{-1}) is the sap flux density, ΔT (°C) is the temperature difference between the two probes at any given time, and ΔT_m (°C) is the maximum temperature difference between the sensors during a day, which was determined based on the maximum ΔT of 7–10 successive days (Lu et al. 2004).

During the 2018 and 2019 growing seasons, the sap flux density of the same trees was measured. The accuracy of the sensor readings was regularly controlled, and, if necessary, the sensors were replaced with fresh drilling. As only one sensor was installed on each sampled tree, we did not consider the azimuthal and radial variations in sap flux density within the sampled trees, as they would be low (Leo et al. 2013; Song et al. 2020). Guo et al. (2008) measured sap flux density at four depths in the xylem (i.e., 10, 20, 30, and 40 mm) of Mongolian pine at the study site and found that no significant differences in the estimates of tree transpiration between a single sensor installed at 20 mm and four integrated sensors at different depths. Dang et al. (2020) investigated the sap flux density of Mongolian pine in different directions (east, south, west, and north) of the stem at 1.3 m above the ground at the study site and observed that the estimate of tree transpiration from the north was near equal to the values from the four integrated directions. Therefore, we assumed that our installation represented the overall water flux of this conifer in the present study (Wieser et al. 2014). Based on the above assumption, tree water consumption (Q_t) was calculated using the following equation:

$$Q_t = J_s \times A_s \tag{2}$$

where A_s is the sapwood area (cm^2), calculated based on the exponential regression between A_s and diameter at breast height, of Mongolian pines at the study site ($A_s = 0.33$ DBH$^{2.21}$, $R^2 = 0.98$, $P < 0.001$; Song et al. 2020).

To compare the transpiration rate between different positions of sand dune, tree transpiration per unit leaf area (E_L) was calculated by dividing tree water consumption (Q_t) by leaf area (A_L) as follows:

$$E_L = \frac{Q_t}{A_L} \tag{3}$$

where A_L is leaf area (cm^2), calculated using Eqs. (4) and (5), of Mongolian pines at the study site (Jiao 1989):

$$A_L = 2.28 + 0.0595W \tag{4}$$

$$\log W = -0.84648 + 0.5249 \log(DBH^2 H) \tag{5}$$

where W is leaf biomass (mg), DBH is the diameter at breast height (cm), and H is the tree height (m).

Tree canopy conductance

Mean tree canopy conductance per unit leaf area (G_L, mm s^{-1}) was calculated by multiplying the conductance coefficient (K_G) with E_L divided by VPD, as described by Luis et al. (2005) and Hawthorne and Miniat (2018) using the following equation:

$$G_L = \frac{K_G E_L}{\text{VPD}} \tag{6}$$

where K_G is the conductance coefficient as the function of temperature (115.8 + 0.4236 T, kPa m^3 kg^{-1}), which accounts for the temperature effect on the psychometric constant, latent heat of vaporization, and specific heat and density of air (Ewers et al. 2001; McDowell et al. 2008).

This equation assumes that leaf temperature is equal to ambient temperature, VPD is relatively homogeneous within the canopy, and stem capacitance is minor during the period used for calculation (Ewers and Oren 2000). Given the relationship between leaf size and boundary layer conductance, conifers (e.g., Mongolian pine in the present study) are assumed to exhibit high boundary layer conductance, indicating that transpiration is primarily controlled by stomatal conductance (Martin et al. 1999). In the present study, we calculated daily mean G_L when VPD was ≥ 0.6 kPa to maximize the likelihood of meeting the above assumptions (Ewers and Oren 2000; Wieser et al. 2014).

To quantify the degree of coupling between the canopy and atmosphere, we estimated the decoupling coefficient (Ω, 0–1) in the present study. Canopies are aerodynamically well coupled to the atmosphere when the value of Ω is near zero, which indicates that the boundary layer conductance is high and that transpiration is therefore primarily controlled via stomatal opening (Jarvis and McNaughton 1986). Stomata exert weak control on canopy transpiration as the value of Ω approaches 1; as a result, transpiration depends not only on stomatal opening but also on boundary layer conductance, which is mainly dependent on wind speed (Martin et al. 1999). Ω can be calculated as follows (Kumagai et al. 2004):

$$\Omega = \frac{1}{1 + \left[\gamma/(\Delta + \gamma)\right](g_a/G_L)} \tag{7}$$

where γ is the psychrometer constant (0.067 kPa °C^{-1}) and g_a is the aerodynamic conductance (m s^{-1}), calculated as follows:

$$g_a = \frac{1 + 0.54Uz}{\left[\ln \frac{z-d}{z_o}\right]^2} \tag{8}$$

where Uz is the wind speed above the canopy (m s^{-1}), calculated based on the wind speed measured at the height of 2.0 m, z is the wind speed measurement height (canopy height, m), z_o is the roughness height (usually 0.1·H, where H is the canopy heights), and d is the displacement height (0.75·H) (Sommer et al. 2002).

Data analysis

In the present study, two-way repeated measures ANOVA was performed to determine the effects of positions on sand dunes and years on mean monthly θ, mean daily E_L, mean daily G_L, and mean daily Ω for all sampling trees. All data were tested for normality and homogeneity of variance and then transformed, if necessary, to meet the statistical assumptions. In addition, the exponential threshold model was applied to analyze the relationships of E_L, VPD, and PAR, as follows:

$$E_L = \beta(1 - e^{-\beta_0 x}) \tag{9}$$

where β and β_0 are the fitting parameters, E_L is the daily canopy transpiration per unit leaf area, and x is the corresponding meteorological variable.

The relationship between E_L and VPD or PAR was analyzed when the value of PAR exceeded 200 μmol·m^{-2} s^{-1} or the value of VPD exceeded 0.6 kPa and the soil moisture was relatively high (June, July, and September of 2018 and May, June, July, August, and September of 2019). In fact, Zhu et al. (2005) reported that Mongolian pine seedlings suffered from severe drought stress when the soil moisture dropped below 30% of the field capacity (24.9% in volumetric soil water content) in the study region. Therefore, the monthly volumetric soil moisture content above 7.5% (30% of the field capacity) was considered relatively high. In addition, Zhang and Liu (2012) reported that in sandy land, the net photosynthetic rate of Mongolian pine trees increased sharply with an increase PAR below 200 μmol m^{-2} s^{-1} and increased slowly until leveling off thereafter. Song et al. (2020) found that the E_L of Mongolian pine plantations in the study region increased rapidly when the daily mean VPD was below 0.6 kPa, but increased slowly until leveling off when VPD was above 0.6 kPa. Therefore, we considered the daily mean PAR > 200 μmol m^{-2} s^{-1} and VPD > 0.6 kPa to be relatively high. In addition, analysis of covariance (ANCOVA) (Wu et al. 2018b) was used to test the differences in slope and intercept of the fitting curve between E_L and VPD or PAR at TS and BS. ANCOVA can identify regression lines that are different from one another in terms of either slope or intercept and has been widely used to compare two or more regression lines.

In addition, the responses of G_L to VPD was described using the following linear equation (Oren et al. 1999; Ewers et al. 2005):

$$G_L = G_R - m \ln \mathrm{VPD} \tag{10}$$

where G_R and m are the fitted parameters representing the reference value of G_L at VPD = 1 kPa and the sensitivity of G_L to lnVPD, respectively. Significant differences in m and G_R between TS and BS were tested using ANCOVA.

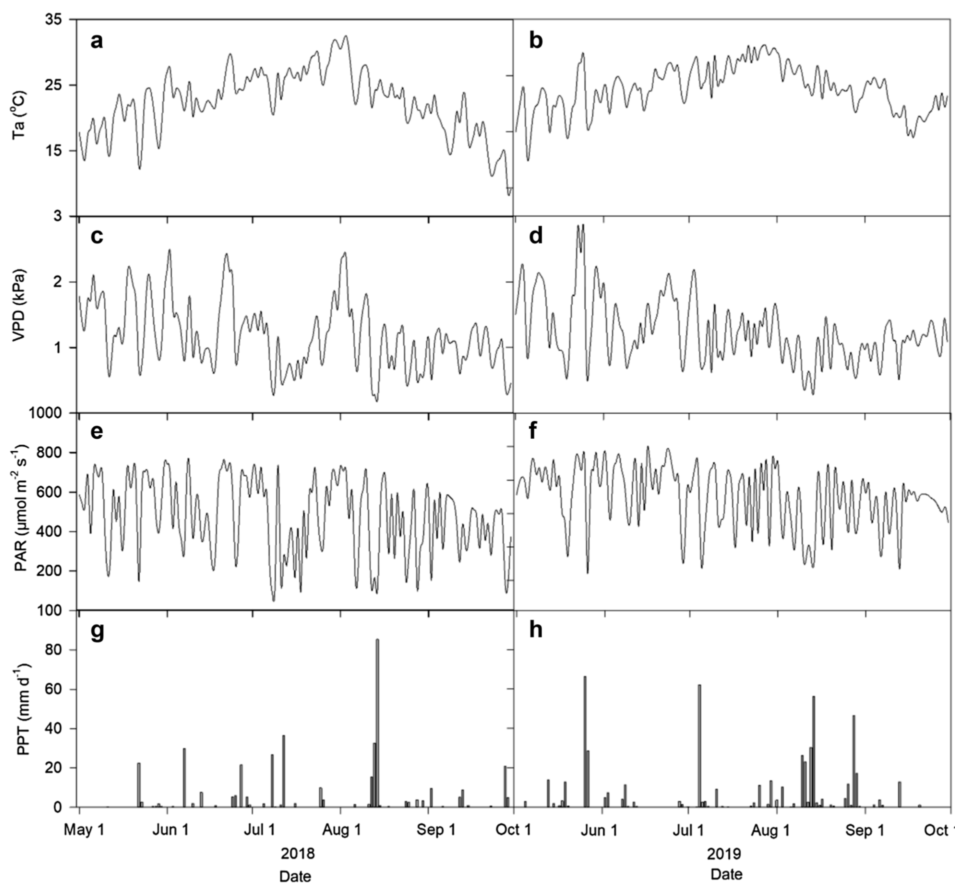
All statistical analyses were performed using SPSS (version 16.0; SPSS Inc., Chicago, IL, USA). The significance level was set at $P < 0.05$.

Results

Meteorological variables and soil moisture

The mean daily ambient temperature (T_a) was respectively 22.4 ± 4.8 °C (standard deviation, the same as below) and 21.6 ± 4.0 °C (Fig. 2a) and mean daily VPD was respectively 1.2 ± 0.5 and 1.1 ± 0.5 kPa during the growing seasons of 2018 and 2019 (Fig. 2b). The mean daily PAR was 479.4 ± 188.0 and 500.7 ± 177.7 μmol·m^{-2} s^{-1}

Fig. 2 Seasonal variations in daily ambient temperature (T_a, **a** and **b**), vapor pressure deficit (VPD, **c** and **d**), photosynthetically active radiation (PAR, **e** and **f**), and precipitation (PPT, **g** and **h**) during the growing seasons of 2018 and 2019



during the growing seasons of 2018 and 2019, respectively (Fig. 2c). Total precipitation during the growing season (May–September) of 2018 and 2019 was 391.2 and 533.2 mm, respectively, accounting for 98% and 133% of long-term mean precipitation over the same period (401 mm; Fig. 2d). Based on these values, 2018 was a normal year, whereas 2019 was a wet year. In addition, mean θ across soil layers significantly differed between TS and BS ($F = 17.279$, $P < 0.05$; Fig. 3), with higher values at BS (10.8%) than at TS (8.4%). Furthermore, mean θ across soil layers was significantly higher in 2019 than in 2018 ($F = 32.947$, $P < 0.05$; Fig. 3). There was no interaction between the positions on sand dunes and years for mean θ ($F = 1.468$, $P > 0.05$; Fig. 3).

Sap flux density and tree transpiration

Diurnal patterns of sap flux density at both positions of sand dune exhibited a bell-shaped curve, indicating that J_s was lower at night, increased sharply around 6:00 h, reached the maximum value at around 12:00 h, and decreased thereafter (Fig. 4a). Daily variations in J_s were primarily related to variations in T_a, VPD, and PAR. For instance, J_s increased rapidly after sunrise as T_a, VPD, and PAR increased, reached the maximum at the same as PAR but before T_a and VPD, and decreased thereafter (Fig. 4a, b).

Throughout the measurement period, E_L at TS ranged from 0.03 to 0.80 mm d^{-1}, with the mean values of 0.45 and 0.53 mm d^{-1} in 2018 and 2019, respectively (Fig. 5). Meanwhile, at BS, E_L ranged from 0.02 to 0.85 mm d^{-1}, with the mean values of 0.51 and 0.59 mm d^{-1} in 2018 and 2019,

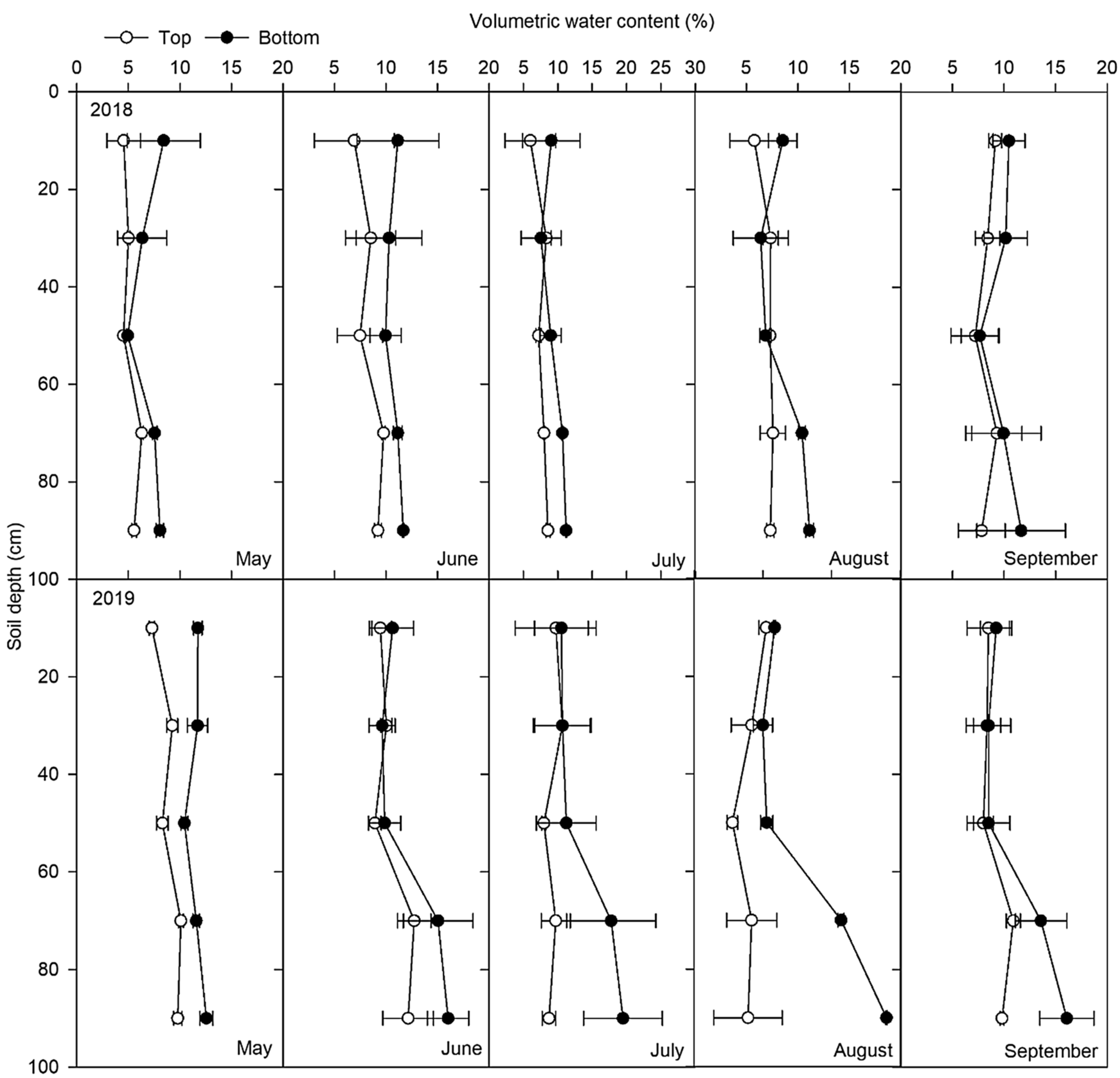


Fig. 3 Monthly variations in volumetric water content at the soil depth of 0–100 cm during the growing seasons of 2018 and 2019. The data are expressed as mean ± 1SD

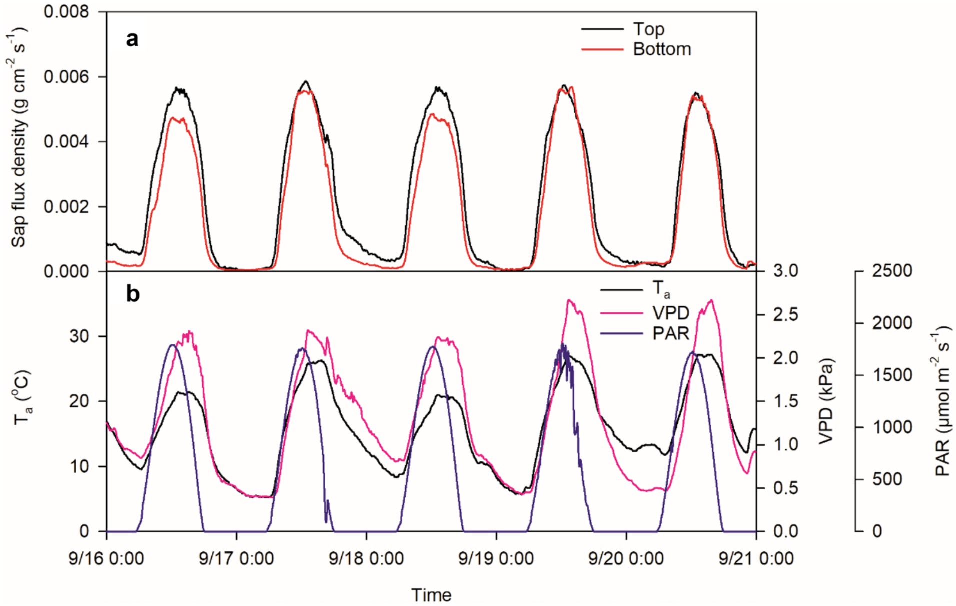


Fig. 4 Diurnal course of the weighted mean sap flux density (J_s) of sampled trees over five consecutive sunny days (from September 16 to 20, 2019) and the corresponding ambient temperature (T_a), vapor pressure deficit (VPD), and photosynthetically active radiation (PAR) at the top (TS) and bottom (BS) of sand dunes

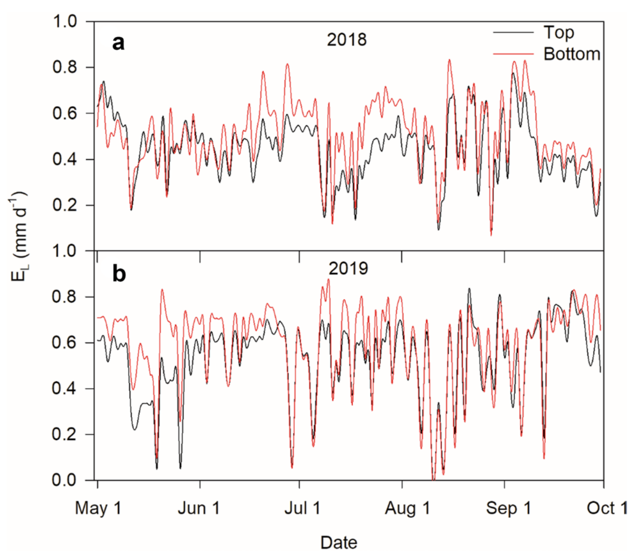


Fig. 5 Seasonal variations in the daily mean canopy transpiration per unit leaf area (E_L) of sampled trees at the top (TS) and bottom (BS) of sand dunes during the growing seasons of 2018 (**a**) and 2019 (**b**)

respectively (Fig. 5). The mean E_L was significantly higher at BS than at TS ($F=19.829$, $P<0.05$; Fig. 5). In addition, the mean E_L significantly differed between the two years, with higher values in 2019 ($F=40.568$, $P<0.05$). However, there was no interaction between the positions on sand dunes and years for mean E_L ($F=0.000$, $P>0.05$).

Response of tree transpiration per unit leaf area to environmental variables

The E_L of Mongolian pine trees increased sharply at low VPD and tended to saturate at high VPD values (e.g., > 1.5 kPa) at different positions on sand dune during the growing seasons of 2018 and 2019 (Fig. 6a, b). VPD explained, respectively, 37% and 22% total variation in E_L at TS and BS in 2018 (Fig. 6a) and, respectively, 16% and 38% of total variation in E_L at TS and BS in 2019 (Fig. 6b). ANCOVA revealed that the intercept of the relationship between E_L and VPD was significantly higher at TS than at BS in both years ($F=33.650$, $P<0.05$ in 2018 and $F=19.027$, $P<0.05$ in 2019), but the slope was significantly higher at BS than at TS in 2019 ($F=6.144$, $P<0.05$ in 2019; Fig. 6a, b). In addition, E_L increased significantly with increase in PAR at different positions on sand dunes in both 2018 and 2019 (Fig. 6c, d). PAR explained, respectively, 38% and 29% of total variation in E_L at TS and BS in 2018 (Fig. 6c) and, respectively, 43% and 65% of total variation in E_L at TS and BS in 2019 (Fig. 6d). ANCOVA revealed that the intercept of the relationship between E_L and PAR was significantly higher at TS than at BS in both years ($F=45.573$, $P<0.05$ in 2018 and $F=8.249$, $P<0.05$ in 2019), but the slope was significantly higher at BS than at TS only in 2019 ($F=21.858$, $P<0.05$). Furthermore, monthly E_L significantly and linearly increased with increasing θ at TS over the 2 years, whereas there was no significant relationship between monthly E_L and θ at BS (Fig. 7).

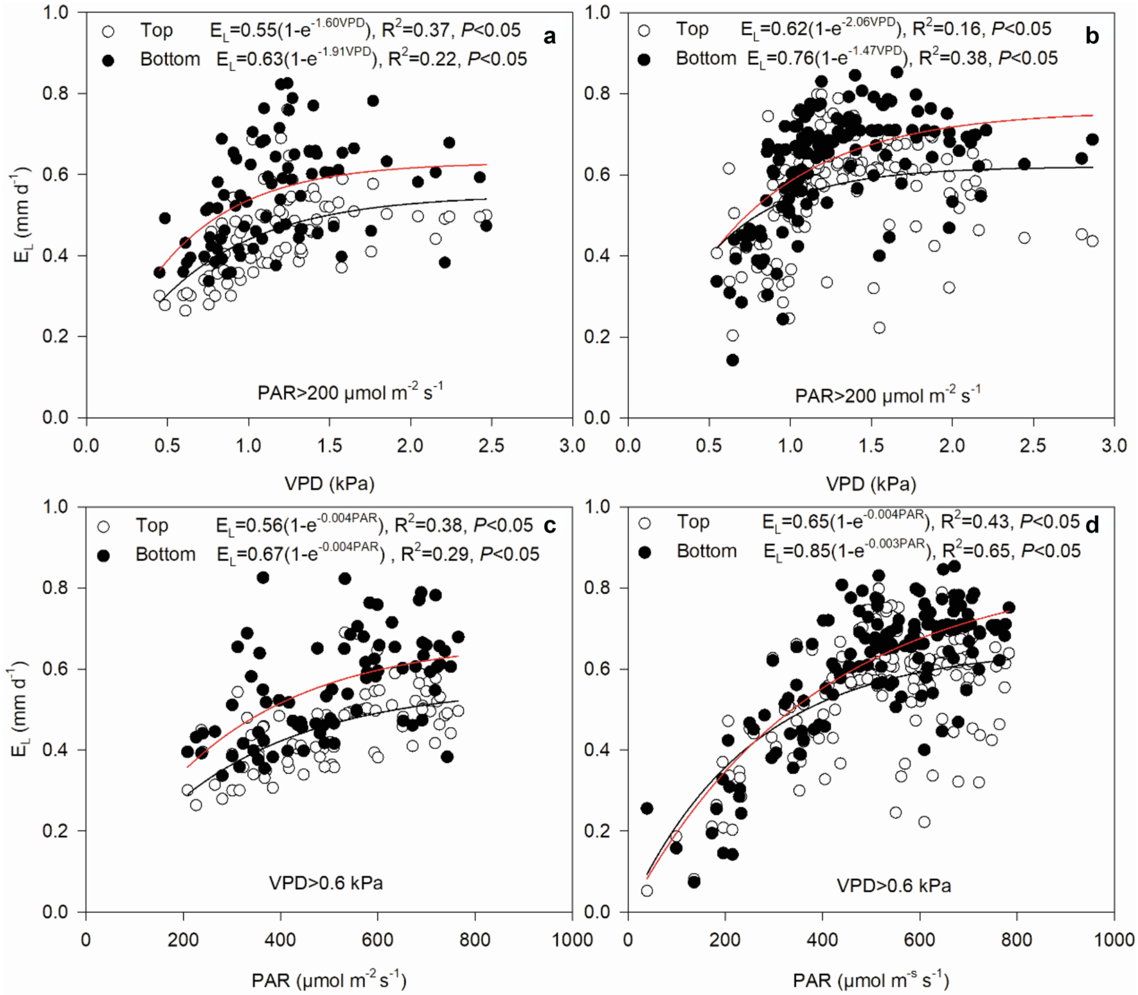


Fig. 6 Relationship of daily mean canopy transpiration per unit leaf area (E_L) with vapor pressure deficit (VPD, **a** and **b**) and photosynthetically active radiation (PAR, **c** and **d**) at the top (TS) and bottom (BS) of sand dunes during the growing seasons of 2018 and 2019. The black and red lines represent regression lines for trees at TS and BS, respectively

Response of canopy conductance to environmental variables

Throughout the measurement period, the G_L of trees at TS ranged from 0.11 to 1.24 mm s^{-1}, with the mean values of 0.58 and 0.66 mm s^{-1} in 2018 and 2019, respectively. Meanwhile, the G_L of trees at BS ranged from 0.17 to 1.37 mm s^{-1}, with the mean values of 0.66 and 0.72 mm s^{-1} in 2018 and 2019, respectively (Fig. 8). In addition, the mean G_L was significantly higher at BS than at TS ($F = 14.034$, $P < 0.05$; Fig. 8). Moreover, the mean G_L was significantly higher in 2019 than in 2018 ($F = 12.254$, $P < 0.05$), but the magnitude of increase in mean G_L from 2018 to 2019 was greater at TS than at BS (Fig. 8). Furthermore, there was no interaction between the positions on sand dunes and years for mean G_L ($F = 0.368$, $P > 0.05$).

In both years, G_L significantly decreased with increasing VPD at different positions on sand dunes (Fig. 9). VPD explained, respectively, 48% and 50% of total variation in G_L at TS and BS in 2018 and, respectively, 25% and 19% of total variation in G_L at TS and BS in 2019. In addition, m (the sensitivity of G_L to lnVPD) was significantly higher at BS than at TS in 2018 ($F = 5.384$, $P < 0.05$), whereas no significant difference in m was observed between the two positions on sand dunes in 2019 ($F = 0.727$, $P > 0.05$; Fig. 9). Furthermore, during both years, G_R (reference canopy conductance at VPD = 1 kPa) was significantly higher at BS than at TS ($F = 21.336$, $P < 0.05$ in 2018 and $F = 10.964$, $P < 0.05$ in 2019; Fig. 9). Moreover, there was no significant difference in m at TS between the two years ($F = 0.104$, $P > 0.05$), but m at BS was significantly higher in 2018 than in 2019 ($F = 10.259$, $P < 0.05$; Fig. 9).

Throughout the measurement period, the daily Ω of trees at TS ranged from 0.75×10^{-4} to 15.65×10^{-4}, with the mean values of 6.33×10^{-4} and 7.58×10^{-4} in 2018 and 2019, respectively (Fig. 10). Meanwhile, the Ω of trees

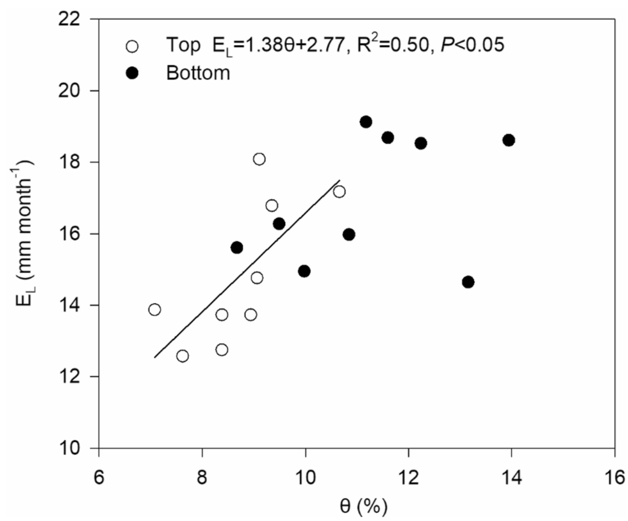


Fig. 7 Relationship between monthly canopy transpiration per unit leaf area (E_L) and monthly mean volumetric soil water content (θ) at the top (TS) and bottom (BS) of sand dunes during the growing seasons of 2018 and 2019. The values of θ in May of 2018 were not included as the plastic tube was not in close contact with the soil and/or the soil near the tube was disturbed soon after installation

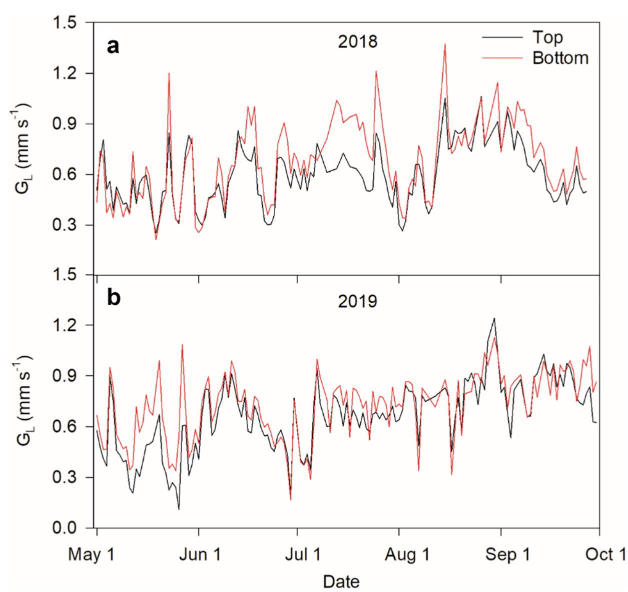


Fig. 8 Seasonal variations in the daily mean canopy conductance per unit leaf area (E_L) of sampled trees at the top (TS) and bottom (BS) of sand dunes during the growing seasons of 2018 (**a**) and 2019 (**b**)

at BS ranged from 1.74×10^{-4} to 15.99×10^{-4}, with the mean values of 7.34×10^{-4} and 8.33×10^{-4} in 2018 and 2019, respectively (Fig. 10). Two-way repeated measures ANOVA revealed that the positions on sand dunes and years significantly affected mean Ω throughout the measurement period ($F = 6.462$, $P > 0.05$ for positions on sand dunes and $F = 23.084$, $P > 0.05$ for years); however, there was no significant interaction between the positions on sand dunes and years for mean daily Ω ($F = 0.465$, $P < 0.05$).

Discussion

Canopy transpiration of Mongolian pines growing at different positions on sand dunes

In the present study, the higher E_L of Mongolian pines growing at BS than that of pines growing at TS indicated the significant effect of topography on the canopy transpiration rate of trees, supporting our first hypothesis. Several studies have shown that the canopy transpiration rate of trees is lower at higher topographic positions than at lower topographic positions (Hardanto et al. 2017; Wang et al. 2019), which is consistent with our findings. The higher transpiration rate of pines at BS may be associated with the higher canopy conductance of trees and higher moisture content of soil (Figs. 3, 8). Under these environmental conditions, the canopy transpiration rate is primarily controlled by stomatal conductance, and higher canopy stomatal conductance generally indicates a higher transpiration rate (Yan et al. 2016; Monje and Bugbee 2019). In addition, reduced soil moisture increases the hydraulic resistance between the soil and root system, preventing the water movement from soil to plant leaves and triggering stomatal closure, which ultimately decreases the transpiration rate (Ghimire et al. 2018).

Environmental control on Mongolian pine transpiration growing at different positions on sand dunes

Daily E_L of Mongolian pines saturated under high VPD conditions (e.g., > 1.5 kPa) at both TS and BS (Fig. 6), which is consistent with previous findings in *Pinus sylvestris* and other tree species in different regions (Wieser et al. 2014; Urban et al. 2019). This may primarily be attributed to the decrease in canopy conductance with increase in VPD (Fig. 9). Under high VPD conditions, the stomata of trees must be promptly closed to prevent the dropping of water potential below the threshold at which xylem cavitation occurs, resulting in the inhibition of transpiration (Ambrose et al. 2010; Grossiord et al. 2020). In addition, the greater contribution of PAR than of VPD in explaining the total variation in E_L at both TS and BS in both years indicates that transpiration was limited to a greater extent by radiation than by VPD at the daily scale. Furthermore, under the relatively low soil moisture conditions of 2018, the contribution of climatic variables (VPD and PAR) in explaining the variation in E_L was lower at BS than at TS, whereas these trends were reversed under the relatively high soil moisture conditions of 2019 (Figs. 3, 6). Therefore, soil moisture affects

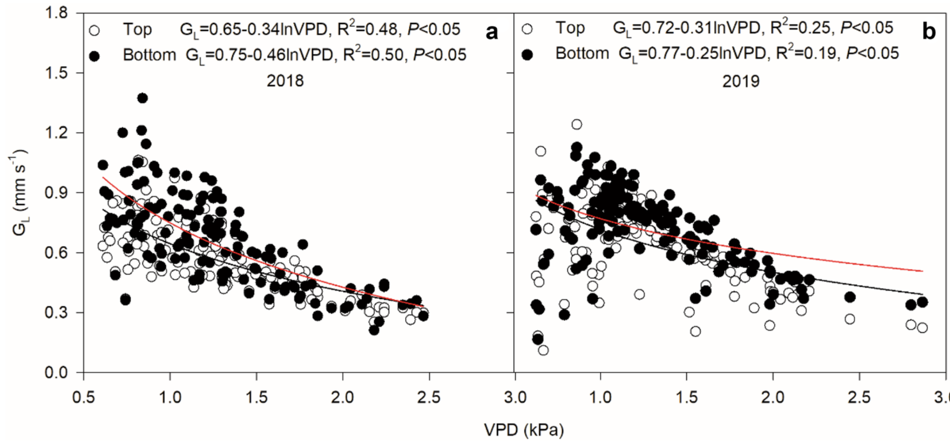


Fig. 9 Relationships between daily canopy conductance per unit leaf area (E_L) and daily vapor pressure deficit (VPD) at the top (TS) and bottom (BS) of sand dunes during the growing seasons of 2018 (**a**) and 2019 (**b**). The black and red lines represent regression lines for trees at TS and BS, respectively

the sensitivity of canopy transpiration to environmental variables. These findings were further supported by the lack of significant differences and significant differences in the slope of relationship of E_L with climate variables between BS and TS in 2018 and 2019, respectively (Fig. 6). Similar to our findings, several studies reports that soil moisture significantly affected the sensitivity of canopy transpiration to climatic variables (McDowell et al. 2005; Gu et al. 2017).

Canopy conductance of Mongolian pines growing at different positions on sand dunes

In the present study, G_L at BS was 11.5% higher than that at TS over the two study years, indicating that topography significantly affected the canopy conductance of pine trees, which supported our first hypothesis. Similar trends have been reported in other tree species (Zhang et al. 2017; Hardanto et al. 2017). For instance, Kumagai et al. (2008) reported that due to hydraulic limitations, the canopy conductance of *Cryptomeria japonica* D. Don was higher in a lower-slope plot than in an upper-slope plot on the Kyushu Island of Japan. Because we assumed that the climatic conditions were the same at TS as at BS, the significantly higher G_L at BS than at TS may be associated with the higher soil moisture at the former position on sand dunes (Fig. 3). In addition, the vertical distance between TS and BS may also contribute to reduced canopy conductance at TS (Schäfer et al. 2000). Furthermore, at the same study site, the leaf $\delta^{13}C$ value was higher at TS (indicative of low stomatal conductance) than at BS (Song et al. 2019). In addition, the increase in canopy conductance from 2018 to 2019 was higher at TS than at BS (Fig. 8), indicating a greater effect of soil water limitation on canopy conductance at TS. These results were partly supported by the significant linear relationship between monthly E_L and soil moisture at TS (Fig. 7).

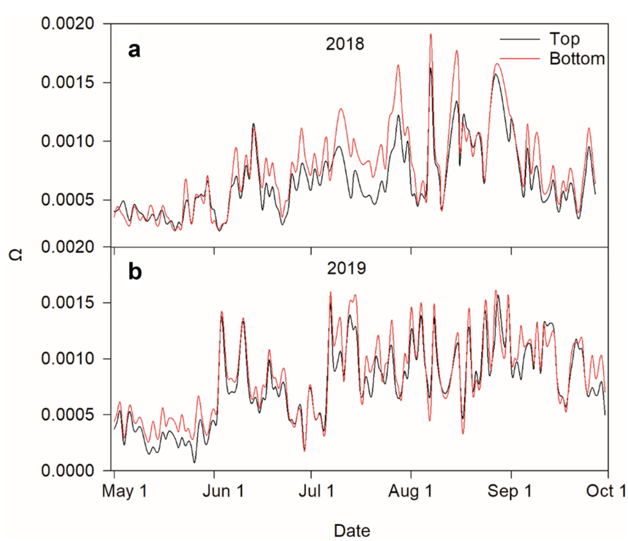


Fig. 10 Seasonal variations in the daily mean decoupling coefficient (Ω) of sampled trees at the top (TS) and bottom (BS) of sand dunes during the growing seasons of 2018 (**a**) and 2019 (**b**)

Trees regulate transpiration through the control of stomatal conductance (Jarvis and McNaughton 1986). The significant negative relationship between G_L and VPD in Mongolian pines at both positions on sand dunes (Fig. 9) indicates that G_L is controlled by evaporative demand. Stronger stomatal regulation of canopy transpiration responds to higher atmospheric VPD, playing pivotal roles in conserving water and maintaining water status to prevent the catastrophic loss of xylem function (Oren et al. 1999; Grossiord et al. 2020). In addition, stomatal sensitivity to VPD was greater at BS than at TS in 2018, but there was no significant difference in sensitivity between the two positions in 2019; these trends partly support our second hypothesis. Higher stomatal sensitivity to VPD at BS than at TS in 2018 indicates that the stomatal conductance was more sensitive to soil moisture than to VPD at TS under relatively low soil moisture conditions (Renninger et al. 2015). This result was further supported by the lack of significant difference in stomatal sensitivity to VPD between the two years (Fig. 9). The lower to sensitivity of stomatal conductance to

VDP may be a disadvantage for trees at TS for preventing excess water loss under drought conditions. Conversely, in 2019, there was no significant difference in stomatal sensitivity to VPD between BS and TS (Fig. 9), indicating that stomatal sensitivity to soil moisture was greater at BS than at TS under relatively high soil moisture conditions. This result was further supported by the lower sensitivity of canopy conductance to VPD in 2019 than in 2018 at BS, indicating a weaker VPD control of gas exchange under relatively high soil moisture conditions. Similar results have been reported in previous studies on various other tree species (Huntingford et al. 2015; Grossiord et al. 2020). Overall, the higher stomatal sensitivity to VPD in 2018 and to soil moisture in 2019 of pine trees at BS is an important mechanism to balance the maximization of carbon uptake when soil moisture is ample and to maintain hydraulic security when soil moisture is limited (McDowell et al. 2008; Wu et al. 2018a). These findings were further supported by the greater magnitude of increase in Ω from 2018 to 2019 at BS than at TS (Fig. 10).

Implications for forest management

The present study revealed that the transpiration of Mongolian pines is primarily driven by soil water availability at TS and by VPD at BS, which are further modulated by inter-annual variability in water availability. However, precipitation exhibits large interannual variations, and extreme droughts have become more frequent in the study region (Song et al. 2016). Therefore, the predicted increase in the frequency and severity of drought events would render Mongolian pines at TS more vulnerable to dieback than trees at BS due to the stronger control of their transpiration by soil moisture under dry conditions. To ensure long-term survival of Mongolian pines growing on sand dune, tree density at TS should be reduced (i.e., thinning), which would increase soil water availability for plants (Song et al. 2019). In addition, for the ecological restoration of sand dunes, Mongolian pines should be planted at the top in sparse wood grasslands and at the bottom in pure Mongolian pine plantations, because their transpiration is primarily driven by VPD under dry conditions. However, in the present study, the frequency of soil moisture measurements at the monthly scale was low and the environmental variables were estimated at BS alone. Therefore, more frequent (e.g., 10 min) measurements of soil moisture and estimation of environmental variables above the canopy at both TS and BS are warranted in future studies.

Conclusion

In the present study, Mongolian pines exhibited higher canopy transpiration and conductance at BS. Moreover, the transpiration of pines at BS was primarily driven by VPD under relatively low soil moisture conditions and by soil moisture under relatively higher soil moisture conditions. Meanwhile, Mongolian pines at TS exhibited lower transpiration and canopy conductance, but their transpiration was mainly driven by soil moisture under relatively low soil moisture conditions, which would render them more susceptible to dieback under drought conditions. To ensure the long-term survival of Mongolian pine plantations in sand dunes, thinning should be adopted at the top to increase soil moisture availability for plants. In addition, for the ecological restoration of sand dunes in semiarid and arid sandy regions, Mongolian pines should be planted at the top in sparse wood grasslands and at the bottom in pure plantations.

Author contribution statement LS: formal analysis, methodology, writing original draft. JZ: project administration, designing the experiment, and writing—review and editing. XL and KW: data curation, formal analysis. GW and HS: Investigation.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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