



Comparison of transpiration between different aged black locust (*Robinia pseudoacacia*) trees on the semi-arid Loess Plateau, China

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Abstract: Black locust (*Robinia pseudoacacia*) is widely planted throughout the semi-arid Loess Plateau of China. The spatial distribution of this species at different ages is highly heterogeneous due to restoration and management practices. In this study, we aimed to compare the transpiration levels between different aged black locusts at the tree and stand scales, clarifying the physiological status of this species with different ages. Black locust trees with two representative age classes (12 and 28 years) were selected in the Yangjuangou catchment on the semi-arid Loess Plateau. Sap flux density (F_d) and environmental variables (solar radiation, air temperature, relative humidity and soil water content) were simultaneously monitored throughout the growing season of 2014. Tree transpiration (E_t) was the product of F_d and sapwood area (A_s), and stand transpiration (E_c) was calculated basing on the stand sap flux density (J_s) and stand total sapwood area (A_{ST}). Stomatal conductance (g_s) was measured in a controlled environment and hydraulic conductance was estimated using the relationship between transpiration rate and vapor pressure deficit (VPD). Our results showed that E_t and E_c were higher in the 28-year-old stand than in the 12-year-old stand. The g_s and hydraulic conductance of 28-year-old trees were also higher than those of 12-year-old trees, and the two parameters were thus the causes of variations in transpiration between different age classes. After rainfall, mean F_d increased by 9% in 28-year-old trees and by 5% in 12-year-old trees. This study thus suggests that stand age should be considered for estimating transpiration at the catchment and region scales in this area. These results provide ecophysiological evidences that the older black locust trees had more active physiological status than the younger ones in this area. These findings also provide basic information for the management of water resources and forests on the semi-arid Loess Plateau.

Keywords: sapflow; transpiration; stand age; afforestation; restoration; Loess Plateau

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Forests are potential water consumers which can influence the water balance of ecosystems (Vertessy et al., 2001). Previous studies have shown that stand age is a crucial factor influencing

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the consumption capacity of forests (Alsheimer et al., 1998; Zimmermann et al., 2000; Cornish and Vertessy, 2001; Köstner et al., 2002; Forrester et al., 2010; Röhl et al., 2015). In cases of afforestation after a fire or harvest, annual water yield in watershed initially decreases and then increases to the pre-afforestation level with increasing age of trees over a long-term period. This phenomenon is generally thought to be the result of variations in transpiration along an age series of trees (Roberts et al., 2001; Scott and Prinsloo, 2008). For a watershed with high spatial heterogeneity (due to management practices) in forest classes, investigating variations in transpiration of forests at different ages is thus crucial for assessing water balance (Delzon and Loustau, 2005).

Age-related change in physiological characteristics of trees is a major contributing factor to the variations in transpiration both at the tree and stand scales (Irvine et al., 2004; Delzon and Loustau, 2005; Ewers et al., 2005). Previous studies have shown that both the tree hydraulic redistribution and hydraulic conductance vary as the changes of tree size and height with ages, and the factors that control stomatal conductance (g_s) to maintain an appropriate water potential gradient from soil-to-leaf and so as to avoid hydraulic failure (Ryan and Yoder, 1997; Ryan et al., 2000). Reduction in g_s induced by hydraulic limitations subsequently constrains both transpiration water loss and photosynthesis (Schulze et al., 1994; McDowell et al., 2002; Magnani et al., 2008). Examining hydraulic conductance and g_s , therefore, can provide physiological evidence to interpret transpiration variation among trees with different ages (Ewers et al., 2005). In addition, roots system is another factor that impacts the transpiration of trees and stands (David et al., 2007; David et al., 2013; Thomsen et al., 2013). The effect of drought on younger and smaller trees with shallower roots was higher than that on older and larger trees with deeper roots (Kume et al., 2007). The differences in the roots systems of different aged trees determine the impact degree of soil drought on transpiration of trees (Delzon and Loustau, 2005).

Loess Plateau in China is characterized by severe soil erosion and degraded ecosystems. To control soil erosion and restore ecosystem function, government implemented afforestation projects beginning in the 1950s (Wang et al., 2004; Jin et al., 2011; Chen and Tang, 2016) and carried out afforestation campaign in the later 1980s (Wang et al., 2004). At the end of the 1990s, the “Grain for Green” project was established to protect the environments (Fu et al., 2000; Wang et al., 2011; Liu and Shao, 2016). Black locust (*Robinia pseudoacacia*), an exotic species, was selected as a dominant plant species for afforestation in this area due to its fast growth and drought tolerance (Jin et al., 2011; Li et al., 2014). However, the age of the black locust trees across the Loess Plateau is not uniform, because afforestation is implemented over several decades.

Water shortage is also a serious problem in this region, wherein reduction in water yield after afforestation has become a large concern in recent years (Sun et al., 2006; Feng et al., 2012). Transpiration levels in black locust plantations thus become a central focus due to their potential impact on water resources at the watershed and regional scales (Du et al., 2011; Chen et al., 2014; Jiao et al., 2015). Previous studies mainly focused on the stand transpiration (E_c) within black locust stands at a single age (Wang et al., 2010; Jian et al., 2015; Zhang et al., 2015), and there were few studies on the levels of transpiration variation in trees and stands with different ages. Wang et al. (2010) and Zhang et al. (2015) quantified the E_c of an approximately 30-year-old black locust stand on the Loess Plateau, with the value of 0.32–0.49 mm/d during the growing seasons (accounting for 10%–12% of the potential evapotranspiration (ET_0)), which was rather lower than that of the deciduous forests in the other regions (Bréda et al., 1995; Santiago et al., 2000). Based on field surveys, some researchers believed that the possible reason for lower E_c is the degradation of black locust within approximately 30-year-old trees (Wang et al., 2001; Wang et al., 2004; Wang et al., 2010). Moreover, studies on E_c and ecophysiological characteristics related to water movement among different aged black locust trees are absent. However, such studies would provide useful information for investigating the water requirements of different aged black locust trees and clarify the possible reasons.

This study analyzed the transpiration of black locust stands at two representative age classes (12 and 28 years) on semi-arid area of the Loess Plateau, China. The aim was to investigate the potential differences in transpiration at the tree and stand scales between two different aged black

locust stands as well as analyze their ecophysiological mechanisms. Specifically, this study aimed to: (1) compare transpiration of black locust at the tree and stand scales between 12-year-old and 28-year-old stands; (2) determine the causes of transpiration difference between the two representative ages; and (3) clarify the physiological status of trees between the two ages by comparing transpiration, g_s , hydraulic conductance and response of transpiration to rainfall.

1 Materials and methods

1.1 Study area

This study was conducted in the Yangjuangou catchment (36°42'N, 109°31'E; Fig. 1) within the central Loess Plateau, a typically loess hilly and gully region in China. The catchment comprises an area of 2.02 km² with altitude ranging from 1,050 to 1,295 m (Liu et al., 2012). The annual mean air temperature is 9.8°C. The mean annual precipitation from 1952 to 2012 was 531.0 mm. The growing season is from May to September for most deciduous species, during which the mean air temperature is 20.0°C with the mean precipitation of 421.7 mm (1952–2012).

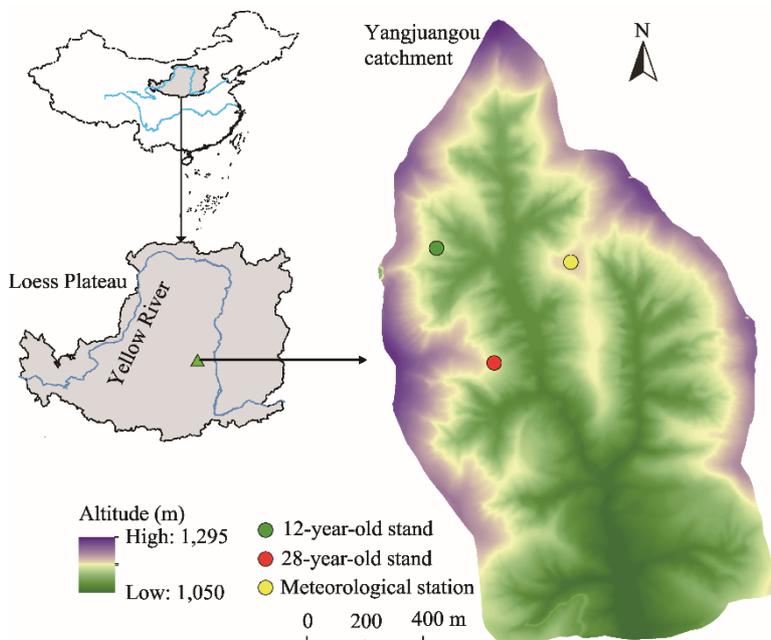


Fig. 1 Geographical locations of the studied black locust stands with different ages and the meteorological station in the Yangjuangou catchment, Loess Plateau of China

1.2 Experimental stands, age determination and sapwood analysis

The study area is the main region for the aforementioned afforestation campaigns, in which black locust was planted in the later 1980s and early 2000s to restore the abandoned hillslope farmlands. Currently, the black locust trees in this area are thus either <15 years or approximately 30 years. The density for afforestation in this catchment is nearly 2,500 trees/hm². No management practices were performed on these trees after planting. In this study, a younger stand and an older stand with similar topographical condition, slope aspect (east), slope degree (approximately 23°), slope position (lower) and altitude (approximately 1,170 m) were selected for the experiment. The area of each stand is 10 m×10 m. Field survey was conducted for each stand at the beginning of the growing season of 2014 (Table 1).

To determine stand age and calculate sapwood area (A_s ; cm²), we selected 26 sample trees beside the younger stand and 28 sample trees beside the older stand. An increment core was taken at breast height (1.3 m aboveground) in each sample tree for determining the age of each tree via

tree-ring analysis. The tree-ring was analyzed in the laboratory after the core was dried, glued and sanded. Then, we determined that the younger stand was 12 years and the older stand was 28 years in 2014.

Table 1 Parameters of the black locust with different ages at the stand and tree scales in the Yangjuangou catchment (mean±SD)

| | Parameter | 12-year-old stand | 28-year-old stand | |
|--------------|--|-------------------|-------------------|--------------|
| Stand | Direction | East | East | |
| | Slope degree (°) | 24 | 26 | |
| | Elevation (m) | 1,169 | 1,172 | |
| | Age (a) | 12 | 28 | |
| | Mean height (m) | 6.94±1.80 | 8.93±1.63 | |
| | Mean <i>DBH</i> (cm) | 5.59±1.66 | 11.76±4.38 | |
| | Density (trees/hm ²) | 2,500 | 1,200 | |
| | LAI (m ² /m ²) | 2.77±0.41 | 2.38±0.42 | |
| | <i>A_{ST}</i> (cm ²) | 373.43 | 314.75 | |
| | Mean <i>A_s</i> (cm ²) | 14.94±9.62 | 22.21±13.53 | |
| | Mean <i>T_s</i> (cm) | 0.89±0.56 | 0.77±0.10 | |
| | Mean <i>T_b</i> (cm) | 0.51±0.22 | 0.92±0.22 | |
| | Mean <i>T_h</i> (cm) | 2.29±1.48 | 4.20±1.87 | |
| | Soil BD at the depth of 0–40 cm (g/cm ³) | 1.23 | 1.21 | |
| | Soil particle composition at the depth of 0–100 cm (%) | | 3.52 (Clay) | 3.42 (Clay) |
| | | | 66.51 (Silt) | 60.67 (Silt) |
| | | 29.97 (Sand) | 35.91 (Sand) | |
| Sample trees | Sample number | 8 | 6 | |
| | Mean height (m) | 8.13±1.18 | 9.50±1.70 | |
| | Mean <i>DBH</i> (cm) | 6.95±1.25 | 14.86±1.99 | |
| | Mean <i>A_s</i> (cm ²) | 22.58±8.55 | 52.46±23.29 | |
| | Mean <i>T_s</i> (cm) | 1.54±0.42 | 0.84±0.04 | |
| | Mean <i>T_h</i> (cm) | 1.99±0.68 | 5.52±0.85 | |

Note: *DBH*, diameter at breast height; LAI, leaf area index; *A_{ST}*, total sapwood area of stand; *A_s*, sapwood area; *T_s*, sapwood depth; *T_b*, bulk thickness; *T_h*, heartwood thickness; BD, bulk density. LAI was derived from the average monthly values from May through September during the growing season of 2014. *A_{ST}*, mean *A_s* and mean *T_s* were measured at breast height of the stem (1.3 m aboveground).

Bulk thickness (*T_b*; cm), sapwood depth (*T_s*; cm) and heartwood thicknesses (*T_h*; cm) were easily distinguished due to different core colors. For trees with a small diameter at breast height (*DBH*; cm) aside from the 12-year-old stand, we conducted a harvest to determine the *T_b*, *T_s* and *T_h*. We used a power regression to establish the relationship of *DBH* and *A_s* (Vertessy et al., 1995). The regressions of *A_s* and *DBH* for 12-year-old and 28-year-old stands were expressed as Eqs. 1 and 2, respectively.

$$A_s = 0.28 \times DBH^{2.25} \quad (R^2 = 0.99, n = 26, P < 0.001), \tag{1}$$

$$A_s = 0.25 \times DBH^{1.81} \quad (R^2 = 0.95, n = 28, P < 0.001). \tag{2}$$

1.3 Climate factors and soil water condition

An automatic meteorological station (Dynamet, Dynamax Inc., Houston, TX, USA), which is located in an open space in the catchment, monitored the climate conditions at a distance of nearly 400 m from the studied stands (Fig. 1). Solar radiation (*R_s*; W/m²) was measured by means of a pyranometer (LI-200, Campbell Scientific, Inc., Logan, UT, USA). Air temperature (*T_a*; °C) and relative humidity (*RH*; %) were measured using a shielded thermistor probe (HMP45, Campbell Scientific Inc., Logan, UT, USA) installed at 2 m aboveground. Precipitation (mm) was measured using a tipping-bucket rain gauge (TE525, Campbell Scientific Inc., Logan, UT, USA). The climate data were collected via a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA). Volumetric soil water content (*SWC*; m³/m³) was measured at depths of 10, 20, 40, 60, 80, 100, 150 and 180 cm in both studied stands using soil moisture sensors (EC-5, Decagon Devices, Pullman,

WA, USA), and recorded by a data logger (HOBO-H21, Onset Computers, Bounce, MA, USA). All data were measured at interval of 60 s and recorded every 30 min. Vapor deficit pressure (VPD ; kPa) was calculated with T_a and RH according to the study of Campbell and Norman (1998).

1.4 Sap flux measurement and calibration

The individual tree sap flux density (F_d ; $\text{kg}/(\text{m}^2\cdot\text{d})$) was measured using the thermal dissipation probes (TDP) from 15 May to 30 September, 2014. Eight trees were selected in the 12-year-old stand and 6 trees were selected in the 28-year-old stand (Table 1). Each sensor consisted of one upper probe and one lower probe, with 10 mm in length and 1.2 mm in diameter. The upper probe contained a heater supplied with 0.15 W of constant power, with the lower probe serving as the reference. The probe contained a copper-constantan thermocouple junction, and the temperature difference between the upper heater probe and the lower reference probe was measured. The probes were inserted in the sapwood at 1.3 m aboveground at the north aspect after first removing the bark. Aluminum-faced foams cover shielded the measuring point in the stem to avoid R_s . The data were measured at intervals of 60 s and recorded at intervals of 30 min in a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA) for each stand. We calculated F_d according to the study of Granier (1987):

$$F_d = 86.4 \times 119 \times \left(\frac{\Delta T_m - \Delta T}{\Delta T} \right)^{1.231}. \quad (3)$$

Where, ΔT ($^{\circ}\text{C}$) is the temperature difference between the upper probe and the lower reference probe; ΔT_m ($^{\circ}\text{C}$) is the maximum value of ΔT when F_d is zero at night.

If the probe length is longer than T_s , calibration is necessary to avoid underestimating F_d . Calibration was conducted according to the following method (Clearwater et al., 1999):

$$\Delta T_{sw} = \Delta T - \frac{b\Delta T_m}{a}. \quad (4)$$

Where, ΔT_{sw} ($^{\circ}\text{C}$) is the temperature difference in the sapwood; a is the proportion of probe in the sapwood; and b is the proportion of probe in the inactive xylem ($b=1-a$). The ΔT in Eq. 3 was replaced with ΔT_{sw} .

To compare the probe length (10 mm) with the T_s of sample trees, we established the relationship of T_s with DBH , T_b and A_s according to the study of Zhang et al. (2015).

$$T_s = \left(\frac{DBH}{2} - T_b \right) \pm \sqrt{\left(\frac{DBH}{2} - T_b \right)^2 - \frac{A_s}{\pi}}. \quad (5)$$

To calculate the T_b of sample trees in each stand, we established the linear regressions of T_b (reading from tree cores) and DBH for 12-year-old and 28-year-old stands (Eqs. 6 and 7, respectively).

$$T_b = 0.054DBH + 0.107 \quad (R^2 = 0.755, n = 26, P < 0.001), \quad (6)$$

$$T_b = 0.05DBH + 0.329 \quad (R^2 = 0.734, n = 28, P < 0.001). \quad (7)$$

1.5 Calculations of tree and stand transpiration

Tree transpiration (E_t ; kg/d) was calculated using F_d and A_s (m^2) measured at breast height of the stem (Eq. 8).

$$E_t = F_d \times A_s. \quad (8)$$

Stand transpiration (E_c ; mm/d) was estimated as Eq. 9 (Kumagai et al., 2008):

$$E_c = J_s \times (A_{ST}/A_G). \quad (9)$$

Where, A_{ST} (m^2) refers to the stand total sapwood area; A_G (m^2) is the ground area; and J_s ($\text{kg}/(\text{m}^2\cdot\text{d})$) indicates the mean stand sap flux density, which can be calculated using Eq. 10.

$$J_s = \frac{\sum_{i=1}^n F_{di} A_{si}}{A_{ST}}. \quad (10)$$

Where, F_{di} ($\text{kg}/(\text{m}^2\cdot\text{d})$) is the mean F_d of the i^{th} DBH class and A_{si} (m^2) is the total A_s of i^{th} DBH class; n is the number of DBH classes. DBH classes was determined at a 2-cm interval according

the frequency distribution of tree *DBH* in each stand (Kumagai et al., 2008).

1.6 g_s measurement

Stands with different structures (e.g. density, tree space and canopy gaps) can modify leaf stomatal conductance (g_s) due to different solar radiations obtained by the trees (Teklehaimanot et al., 1991; Kupper et al., 2006; Sun et al., 2014). To compare the g_s of trees in each stand under similar light conditions, we controlled light intensity in the experiment and measured g_s using a portable infrared gas analyzer (Li-6400, Li-Cor, Lincoln, NE, USA). The light intensity within the leaf chamber was controlled according to the average photosynthetic active radiation (*PAR*; 1,475 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ for this study) from 10:00 to 11:30 on sunny days. In addition, the experiments were conducted from 10:00–11:30 on 21 July for the 28-year-old stand and on 24 July for the 12-year-old stand. On the experimental days, the mean *SWC* was 0.117 m^3/m^3 in the 28-year-old stand and 0.115 m^3/m^3 in the 12-year-old stand. Five trees with different *DBH*s were selected in each stand, wherein five well-expanded leaves were measured from each tree, replicating three measurements for each leaf.

1.7 F_d -*VPD* relationship and response of F_d to rainfall

To analyze the relationship between mean F_d and *VPD*, we used an exponential saturation model (Ewers et al., 2002, 2007):

$$F_d = x \times (1 - e^{-y \times VPD}). \quad (11)$$

Where, x and y are fitting parameters. To examine the responses of F_d in each stand to water recharge from rainfall, we defined an increase in F_d as follows (Kume et al., 2007):

$$\text{Increase in } F_d = \left(\frac{f_{\text{after}(VPD)}}{f_{\text{before}(VPD)}} - 1 \right) \times 100\%. \quad (12)$$

Where, $f_{\text{after}(VPD)}$ is the fitting curve of the mean daily F_d of sample trees versus daily *VPD* after rainfall using an exponential saturation model (Eq. 10); and $f_{\text{before}(VPD)}$ describes the curve of the mean daily F_d of sample trees versus daily *VPD* before rainfall. Rainfalls lower than 3 mm which fell at intervals of <5 d were excluded (Zhao and Liu, 2010). Twelve rainfall events were selected during the study period, and the data of the 2 days before and after rainfall were used for analysis.

1.8 Statistical analysis

A paired *t*-test was used to compare the differences in daily E_t and E_c between the two stands. All statistical analyses were performed with SPSS 16.0 software (SPSS Inc., Chicago, IL, USA).

2 Results

2.1 Climate and soil water conditions

Climate variables and soil water conditions in the study area are shown in Fig. 2. Average daily R_s amounted to $209.9 \pm 91.9 \text{ W}/\text{m}^2$, ranging from 20.5 to $352.6 \text{ W}/\text{m}^2$ (Fig. 2a), and average daily *VPD* was $0.97 \pm 0.55 \text{ kPa}$, ranging from 0.55 to 2.35 kPa (Fig. 2b). During the study period, the stands received a total of 416 mm precipitation, with 87% of which occurring in July, August and September. Rainfall events significantly influenced the variation in daily *SWC* (Fig. 2e). The mean *SWC* in the soil depth of 0–180 cm was significantly higher in the 28-year-old stand than in the 12-year-old stand in May, August and September (paired *t*-test, $P < 0.01$). The mean *SWC* in the entire growing season was 0.115 m^3/m^3 in the 12-year-old stand and 0.120 m^3/m^3 in the 28-year-old stand.

2.2 Tree and stand characteristics

The 12-year-old stand has a higher density than the 28-year-old stand, with 2,500 and 1,200 trees/ hm^2 , respectively (Table 1), possibly resulting from self-thinning during the succession process. The mean height of trees was 6.94 m for the 12-year-old stand and 8.93 m for the 28-year-old stand. The mean A_s was higher in the 28-year-old stand (26.2 cm^2) than in the 12-year-old stand (15.8 cm^2), and higher A_s was usually related to larger *DBH*. The mean T_s of

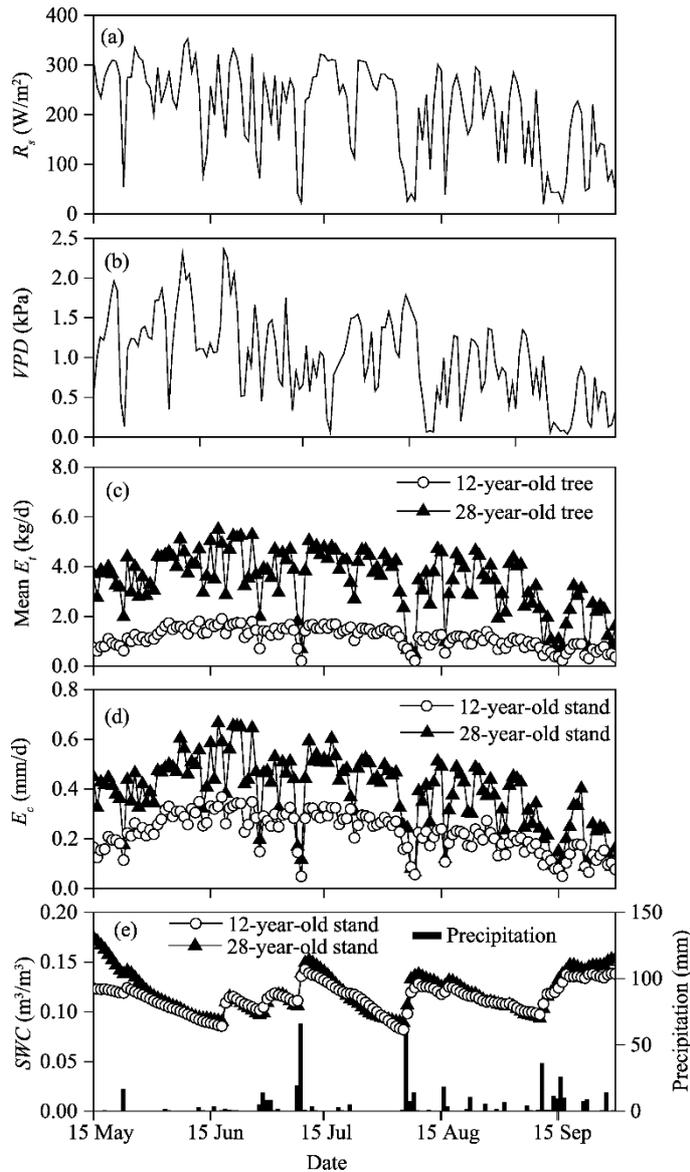


Fig. 2 Climate conditions in the Yangjuangou catchment, transpiration of trees and stands, and soil water content (*SWC*) in each stand from 15 May to 30 September, 2014. (a) Daily solar radiation (R_s); (b) daily vapor pressure deficit (VPD); (c) daily mean tree transpiration (E_t); (d) daily stand transpiration (E_c); (e) daily precipitation (P) as well as mean volumetric soil water content in the soil depth of 0–180 cm within each stand.

28-year-old trees was 0.8 cm, which was lower than that of 12-year-old trees (0.9 cm). The A_{ST} was 314.8 cm² in the 28-year-old stand while it was 394.4 cm² in the 12-year-old stand. The average LAI (leaf area index) was 2.77 for the 12-year-old stand and 2.38 for the 28-year-old stand.

2.3 F_d and E_t

On sunny days (i.e. 20 May and 26 July), the average F_d of sample trees in the two stands showed a similar pattern. For the two stands, F_d was approximately zero from 00:00 to 06:00, reached the peaks approximately at 11:00–12:00, and then decreased in the afternoon (Fig. 3). The diurnal courses of R_s and VPD lagged behind F_d . The daytime mean F_d of sample trees was higher in the older stand than in the younger stand. The maximum diurnal F_d in the older stand was generally double the younger stand. The mean monthly F_d of sample trees was significantly higher in the

28-year-old stand than in the 12-year-old stand (paired *t*-test, $P < 0.01$) (Table 2). Moreover, E_t in the 28-year-old stand was also higher than that in the 12-year-old stand (Fig. 2c).

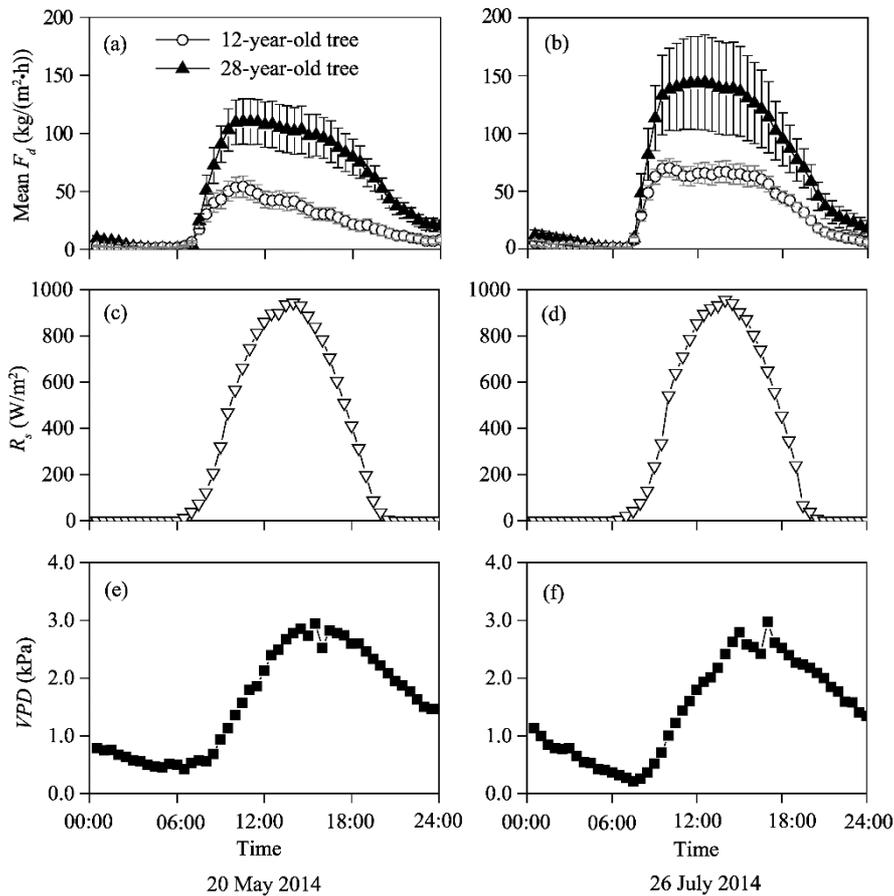


Fig. 3 Diurnal courses of mean sap flux density (F_d) of 12-year-old and 28-year-old sample trees (a, b), solar radiation (R_s ; c, d) and vapor pressure deficit (VPD ; e, f) on 20 May 2014 (a, c, e) and 26 July 2014 (b, d, f). Bars represent standard errors.

Table 2 Mean monthly tree sap flow density (F_d) and stand sap flow density (J_s) in the 12-year-old and 28-year-old stands during the growing season of 2014

| Month | Mean F_d (kg/(m ² ·d)) | | J_s (kg/(m ² ·d)) | |
|-----------|-------------------------------------|-------------------|--------------------------------|-------------------|
| | 12-year-old stand | 28-year-old stand | 12-year-old stand | 28-year-old stand |
| May | 507.5 | 949.3 | 495.3 | 1,207.0 |
| June | 781.4 | 1,204.8 | 752.3 | 1,595.2 |
| July | 725.4 | 1,123.2 | 694.5 | 1,446.9 |
| August | 527.7 | 905.9 | 505.4 | 1,132.6 |
| September | 354.8 | 637.8 | 340.0 | 767.3 |

2.4 J_s and E_c

J_s was higher in the 28-year-old stand than in the 12-year-old stand (Table 2). E_c was also significantly higher in the 28-year-old stand than in the 12-year-old stand (paired *t*-test, $P < 0.001$) with the values of 0.39 and 0.22 mm/d, respectively (Fig. 2d). The dynamic patterns of E_c in both stands were similar, with daily E_c increased at the beginning of the study period. The maximum daily E_c occurred on 17 June for the 28-year-old stand and 18 June for the 12-year-old stand. From then on, daily E_c showed a decreasing trend in the two stands. Cumulative E_c was 54 mm in the 28-year-old stand and 31 mm in the 12-year-old stand during the whole study period.

2.5 Stomatal conductance (g_s)

Under similar light conditions, the g_s value of all sample trees in the different DBH classes was higher in the 28-year-old stand than in the 12-year-old stand (Fig. 4). The mean g_s for sample trees were 0.15 and 0.28 mol/(m²·s) in the 12-year-old and 28-year-old stands, respectively.

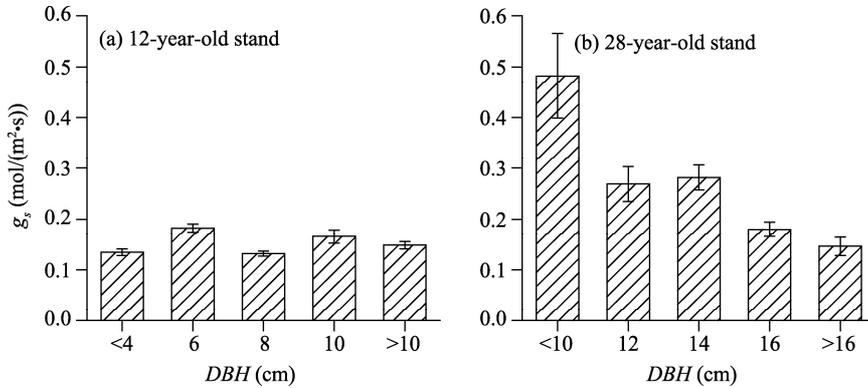


Fig. 4 Leaf stomatal conductance (g_s) of sample trees in the (a) 12-year-old stand and (b) 28-year-old stand under different DBH (diameter at breast height) classes. Bars mean standard errors.

2.6 Relationship between F_d and VPD

Daily mean F_d in both stands showed similar responses to VPD , wherein an exponential saturation model explained the relationships between F_d and VPD for the 12-year-old and 28-year-old stands (Eqs. 13 and 14, respectively). The slope of the F_d - VPD relationship in the 28-year-old stand was higher than that in the 12-year-old stand (Fig. 5).

$$F_d = 1231.93 \times (1 - e^{-2.22 \times VPD}) \quad (R^2 = 0.54, n = 139), \quad (13)$$

$$F_d = 714.92 \times (1 - e^{-2.60 \times VPD}) \quad (R^2 = 0.74, n = 139). \quad (14)$$

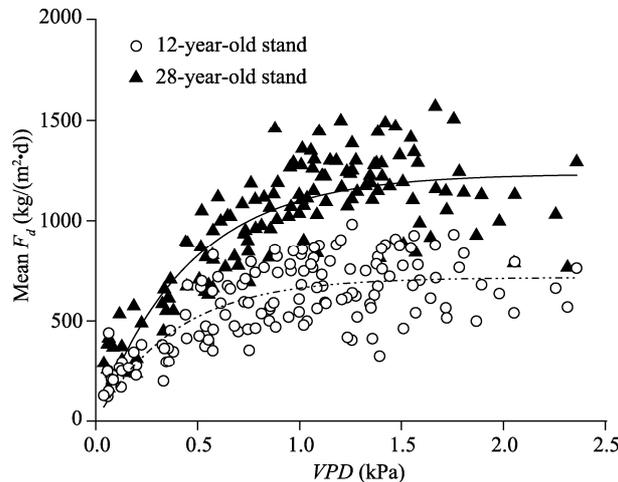


Fig. 5 Relationship of mean F_d and VPD in the 12-year-old and 28-year-old stands

2.7 Increase in F_d after rainfall

The relationship between mean F_d and VPD after rainfall differed from that before rainfall in the 12-year-old stand (Fig. 6a). When VPD remained stable, mean F_d was higher after rainfall compared to before rainfall. Moreover, the same pattern was also found in the 28-year-old stand (Fig. 6b). Compared to before rainfall, the degree of increase in mean F_d for sample trees after rainfall was higher in the 28-year-old (increase by 9%) than in the 12-year-old stand (increase by 5%), where VPD ranged from 0.5 to 2.5 kPa.

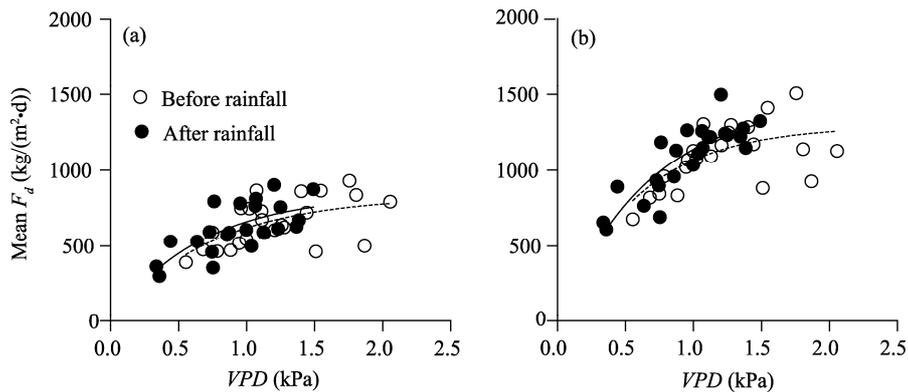


Fig. 6 Daily mean sap flux density (F_d) of sample trees in relation to daily vapor pressure deficit (VPD) before and after rainfall in the (a) 12-year-old stand and (b) 28-year-old stand

3 Discussion

3.1 Transpiration at the tree and stand scales

F_d and A_s are the two main factors for estimating transpiration at the tree and stand scales using thermal dissipation probes (TDPs) (Granier, 1987; Kumagai et al., 2008; Sun et al., 2014). Our results showed that the mean E_t , F_d and A_s in the 28-year-old stand was higher than those in the 12-year-old stand. At the stand scale, E_c in the 12-year-old stand was approximately 40% less than that in the 28-year-old stand, while A_{ST} in the 28-year-old stand was lower than that in the 12-year-old stand. For the 28-year-old stand with a lower A_s , E_c was higher because J_s in this stand was significantly higher than that in the 12-year-old stand. These results suggested that J_s has a major effect on E_c in black locust trees with different ages.

In contrast to some studies on variation in transpiration of tree stands at different ages, other researchers have come to similar conclusion that J_s has a major effect on E_c in different aged forests. For example, Zimmermann et al. (2000) reported that changes in F_d among different aged Siberian pines caused a variation in E_c along a chronosequence. Forrester et al. (2010) indicated that E_c for 2- to 8-year-old *Eucalyptus globules* trees declined due to reductions in J_s in southeastern Australia. However, other studies have suggested that variation in A_{ST} causes the differences in E_c among different ages of trees (Dunn and Connor, 1993; Alsheimer et al., 1998). With increasing age, E_c of Norway spruce stands decreased because A_{ST} decreased (Alsheimer et al., 1998). For the *Eucalyptus regnans* forests in Southeast Australia, mean daily J_s was similar among different ages of forests and A_{ST} decreased with age, resulting in E_c decreasing with stand age (Dunn and Connor, 1993).

3.2 Causes of variation in F_d among different aged trees

The coordination of plant hydraulic conductance and g_s controls transpiration (Yoder et al., 1994; Ryan and Yoder, 1997). The g_s regulates transpiration by decreasing hydraulic conductance to maintain the water potential gradient from soil to leaf above threshold and to avoid hydraulic failure (Zhao, 2011). However, g_s would increase as a result of increasing hydraulic limitation, which boosts the transpiration rate of trees (Ryan et al., 2000). Previous studies have indicated that in older trees, a decrease in g_s consequently results in a decrease in transpiration due to lower hydraulic conductance (Delzon et al., 2004; Delzon and Loustau, 2005).

Oren et al. (1996) suggested that the slope of relationship between F_d and VPD can indicate plant hydraulic conductance from soil to leaf. A steep slope indicates larger hydraulic conductance. By comparing the slopes of relationship between F_d and an integrated index with VPD for different tree species on the Loess Plateau, Du et al. (2011) implied that the changes in hydraulic conductance among black locust trees between pre- and post-rainfall is larger than that among other tree species. In this study, although we did not calculate plant hydraulic conductance

from sap flow and leaf-soil water potential gradient, the relationships between F_d and VPD for trees at different age classes suggested that the 28-year-old trees have greater hydraulic conductance than the 12-year-old trees. Furthermore, the results were also found for g_s in 28-year-old and 12-year-old trees. Therefore, higher hydraulic conductance and g_s resulted in higher F_d for 28-year-old trees than for 12-year-old trees. Meanwhile, stand density is a key factor that impacts sapflow density at the tree and stand scales (Sun et al., 2014). In this study, lower F_d of 12-year-old trees was probably related to higher effect of water stress on F_d due to higher stand density (Bréda et al., 1995).

Rainfall is a key environmental factor determining water availability in arid and semi-arid regions. Rainfall fundamentally influences plant physiological processes, especially transpiration (Oren et al., 1996; Xu and Li, 2006; MacKay et al., 2012). Previous studies have shown that rainfall pulses significantly increase transpiration rate of plants (Zeppel et al., 2007; Zhao and Liu, 2010). In this study, F_d for black locust trees increased in response to water recharge from rainfall. The degree of increase in mean F_d after rainfall, however, was higher for 28-year-old trees than for 12-year-old trees. A possible reason for this is the difference in root systems between different aged trees. Previous studies have indicated that larger trees with higher root biomass and extensive root system can tap more water than smaller trees, thus decreasing the impact of soil water changes on transpiration (Delzon and Loustau, 2005; Kume et al., 2007). A survey of the vertical root distribution showed that the fine roots of black locust trees are concentrated in the 0–100 cm soil profile (Li et al., 2005). As such, root density increases with age along a chronosequence for black locust trees on the Loess Plateau of China (Zhao et al., 2000; Chang et al., 2012). Our study thus suggested that the increase of F_d after rainfall in 28-year-old trees is higher than that in 12-year-old trees due to higher fine root biomass of 28-year-old trees.

Based on field surveys, soil moisture observation and inference, researchers pointed out that the physiological condition and growth rate of approximately 30-year-old black locust trees decreased due to soil water stress on the Loess Plateau, resulting in lower stem growth rate and ratio of E_c to potential evapotranspiration (ET_0) compared to other forests in varied climatic regions (Wang et al., 2004; Wang et al., 2010). However, the present study showed that both transpiration at the tree and stand scales and ecophysiological characteristics related to water movement (i.e. g_s , hydraulic conductance, root system, and response of F_d to rainfall) were higher for the 28-year-old stand than for the 12-year-old stand. These results implied that the 28-year-old trees are physiologically more active than the 12-year-old trees. This might be caused by the more conservative water strategy in the younger trees under water stress in semi-arid area (Delzon and Loustau, 2005; Kume et al., 2007).

3.3 Implications for water resource and forest management

The semi-arid Loess Plateau is a typically loess hilly and gully region characterized by highly spatial heterogeneity of topography. Vegetation (i.e. forest, orchard, shrub, grass and crop) cover differs significantly in this region due to human activity (Liu et al., 2012; Wang et al., 2012). Some studies have focused on transpiration variation in different vegetation and topographical positions, as well as its potential effect on the hydrological cycle in small catchments (Wang et al., 2011; Jian et al., 2015). Due to restoration practices, spatial distribution of forests with different age classes showed heterogeneity at the catchment and regional scales, yet water resource and forest management was neglected in this region (Jin et al., 2011). Our study showed that E_c for black locust trees was significantly different between the two representative ages. Therefore, for accurately estimating vegetation transpiration and evaluating its effect on water yield at the catchment and regional scales, stand age is an essential factor to be considered.

Forest transpiration initially increases until reaching peaks, and then decreases with age along a chronosequence (Forrester et al., 2010; Angstmann et al., 2012). According to this pattern, the forest development process along an age series can be separated into two stages (by the age of peak transpiration): increasing and decreasing stages. Such categorization is useful for predicting transpiration and water requirements of forests with different ages (Dunn and Connor, 1993; Alsheimer et al., 1998). The present study inferred that the 12-year-old trees during the study

period are at the increasing stage. Thus, their water consumption capacity will increase in the coming years. In contrast, it is difficult to determine the development stage of the 28-year-old trees due to the lack of relevant observations along the age series of black locust stand. Therefore, future researches need to establish a relationship between E_c and age for black locust stands on a multi-year scale in this region.

Camarero et al. (2015) predicted that climate becomes warmer and drier. Drought has a negative effect on plants by decreasing both transpiration and productivity (MacKay et al., 2012). The experiment of the present study was conducted during only one growing season, without soil water stressing. Thus, variations in the effects of soil drought on physiological responses, transpiration and growth among different aged trees are needed to be studied in the future.

4 Conclusions

This study investigated the variation in transpiration for black locust stands at two representative age classes on the Loess Plateau of China. Transpiration for black locust at the tree and stand scales was higher for the 28-year-old trees than for the 12-year-old trees. Besides spatial heterogeneities in topographical position and vegetation cover, forest age should be considered to estimate and model the vegetation transpiration accurately at the catchment and regional scales. The 28-year-old trees were more physiologically active than the 12-year-old trees, which contributed to a higher E_c in the 28-year-old stands. Despite having observed only two planting years, these findings provide basic information for water resources and forest management in this semi-arid area. Further researches should thus be conducted to observe the multi-year transpiration and examine the relationship between E_c and age along an age series for black locust stands on the Loess Plateau.

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