

Response of daily stem radial growth of *Platycladus orientalis* to environmental factors in a semi-arid area of North China

Yuan Jiang · Bing-Qin Wang · Man-Yu Dong ·
Yong-Mei Huang · Ming-Chang Wang ·
Biao Wang

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Abstract

Key message The daily stem radial growth of *P. orientalis* during the main growing period in semi-arid areas of North China is mainly limited by moisture availability.

Abstract Finer resolution studies of tree stem radial growth on short temporal scales can be useful for exploring the main environmental variables that trigger radial growth. The objective of this study was to determine the most important environmental factors that impact the intra-annual radial growth of *Platycladus orientalis* (Linn.) Franco in a semi-arid area of North China. The stem radial growth of *P. orientalis* was studied daily during the growing season (May to October 2013) using high-resolution automatic point dendrometers. Our results showed that the daily stem radial increment (SRI) of *P. orientalis* during the main growing period was primarily impacted by relative air humidity, precipitation, vapor pressure deficit and daily maximum air temperature. Those environmental factors mainly influenced the moisture availability to the trees, thereby affecting their daily stem radial growth. The

rapid release of stem radial growth was observed when heavy precipitation events occurred after a drought period. The maximum stem growth rate of *P. orientalis* was observed in early August and was regulated by soil water content in the summer; this was regarded as an adaptation to the local climate conditions. Our results have further implications for sensitivity analyses of tree growth to climate changes in semi-arid areas.

Keywords *Platycladus orientalis* · Dendrometer · Stem radial increment · Climate–growth relations · Semi-arid area

Introduction

Tree growth in semi-arid areas is sensitive to climate change, which has potentially great impacts on vegetation changes, regional climate feedback and the carbon cycle (Rotenberg and Yakir 2010; Williams et al. 2010; Liu et al. 2013). Previous dendroclimatological studies have reported that tree growth in semi-arid areas is generally limited by moisture availability (Liang et al. 2001, 2008; Cherubini et al. 2003; Gebrekirstos et al. 2008; Shi et al. 2008; Dulamsuren et al. 2009). Lebourgeois et al. (2012) reported that spring drought (May–June) is the primary factor limiting conifer growth in the Mediterranean, with narrower tree rings observed in years with a drier spring. A broader study by Liu et al. (2013) showed that tree-ring width at semi-arid forest sites throughout Inner Asia is positively correlated with precipitation from March to June of the growth year, and negatively correlated with vapor pressure deficit (VPD) from April to July of the growth year.

Dendroclimatology aims to establish long-term relationships between radial growth and climatic variables by

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Y. Jiang · B.-Q. Wang (✉) · M.-Y. Dong (✉) · Y.-M. Huang
State Key Laboratory of Earth Surface Process and Resource
Ecology, Beijing Normal University, No.19, Xijiekouwai
Street, Beijing 100875, China
e-mail: wangbq429@qq.com

M.-Y. Dong
e-mail: dongmy@bnu.edu.cn

Y. Jiang · B.-Q. Wang · M.-Y. Dong · Y.-M. Huang ·
M.-C. Wang · B. Wang
College of Resources Science and Technology, Beijing Normal
University, No.19, Xijiekouwai Street, Beijing 100875, China

examining correlations with monthly, seasonal and annual resolution (Fritts and Shatz 1975). The relative low resolution of dendroclimatology limits its interpretation power to the intra-annual short-term radial growth, such as daily stem radial increment and radial growth rate, response to environmental factors (Gutiérrez et al. 2011; Köcher et al. 2012). Finer resolution studies, which address radial growth responses on a daily time scale during the growing season, can be useful to explore the main environmental variables that influence daily stem radial growth (Pérez et al. 2009).

Dendrometer measurements provide a continuous time series of intra-annual stem radial variation with high temporal resolution (minutes to hours) without invasive sampling (Drew and Downes 2009); this technique has been widely used for different tree species and environments to describe the relationship between intra-annual radial growth and climate in the last decade (Downes et al. 1999; Mäkinen et al. 2008; Bräuning et al. 2009; Volland-Voigt et al. 2011; Köcher et al. 2012). For example, Gutiérrez et al. (2011) reported that the seasonal radial increment of *Quercus ilex* L., a dominant evergreen oak species in the Western Mediterranean Basin, is bimodal and characterized by a greater increase in May and a lesser, more variable increase peak in September. Xiao et al. (2014) showed that groundwater depth and the related soil moisture content are key factors potentially limiting the radial growth of *Populus euphratica*, a dominant tree species in desert riparian forests in arid regions of northwest China (Westermann et al. 2008).

Platycladus orientalis is an evergreen tree species with a well-developed root system and a long lifespan that originated in China that is also naturalized in Korea, Japan and Iran (Lei et al. 2010). Due to its resistance to cold, drought and nutrient deficiency, *P. orientalis* has become one of the dominant evergreen tree species in semi-arid areas of North China. Recently, it has been frequently used for afforestation in the semi-arid Loess Plateau of China (Guo et al. 2007). In recent years, a few dendroclimatological studies have examined the stem radial growth of *P. orientalis*. Huang et al. (2006) found that the ring width of *P. orientalis* has a significant positive response to precipitation and a significant negative response to temperature, both from June to August, the current growing season. However, basic studies on the intra-annual daily stem radial growth of *P. orientalis* are still lacking.

In this study, we examined the intra-annual weather response of the stem radial growth of *P. orientalis* in a semi-arid area of North China using high-resolution automatic point dendrometers. We hypothesized that moisture availability throughout the growing season determines its daily stem radial growth. To verify this hypothesis, we aim to (a) test the environmental factors air temperature, relative air humidity, vapor pressure deficit, precipitation, soil

temperature and soil water content in their effect on daily stem radial increment during the main growing period, and (b) identify the most important climatic factors related to the maximum growth rate of *P. orientalis* during the main growing period.

Materials and methods

Study area and local climate

This study was conducted in a pure *P. orientalis* forest with an area of approximately 0.5 ha in Huailai (40°15′37.9″N, 115°36′39.6″E; 495 m a.s.l.), Hebei province, North China (Fig. 1). *P. orientalis* is the dominant forest tree species at the study sites, which were commonly on the tops and slopes of hills. Climatically this area belongs to the temperate semi-arid zone, and it has a temperate, semi-arid, continental monsoonal climate, which is cold and dry in winter and hot and rainy in summer (Tang and Zhang 2003). The mean annual precipitation is 376 mm, most of which

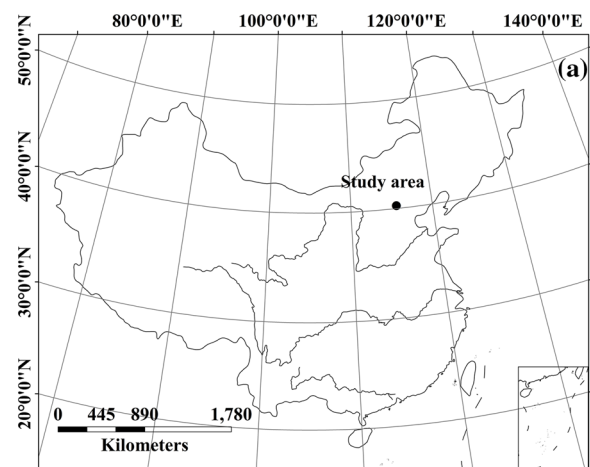


Fig. 1 Study area in North China (a), and the landscape of study area (b)

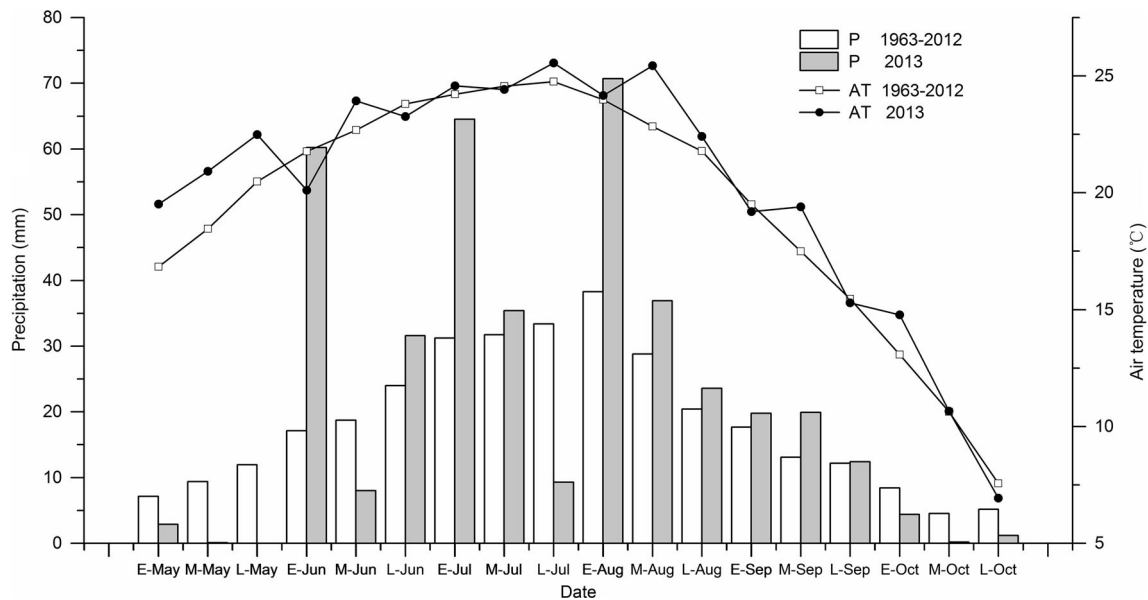


Fig. 2 Comparison of the mean climatic conditions between May and October from 1963 to 2012 and during 2013 (lines 10-day mean air temperature, bars 10-day sum of precipitation). P precipitation, AT average temperature

falls from June to August (65 % of total annual precipitation). The mean annual temperature is 9.6 °C with a warmer period (>24 °C) from late June to early August (Fig. 2). The soil type is sandy loam, according to the United States Department of Agriculture (U.S.D.A.) standards.

Trees and dendrometer measurements

Four sample trees of *P. orientalis*, with stem diameters at breast height of 7.5 ± 0.5 cm and a stem height of 4.0 ± 0.4 m with well-developed crowns and no obvious wounds on the trunk, were selected for this study. From 7 May to 31 October 2013, the stem diameter variation at breast height was continuously monitored using a high-resolution automatic point dendrometer (Type DR, Ecomatic, Munich, Germany) with a resolution of 1 μ m and a temperature coefficient <0.1 μ m/K. The operating principle of the dendrometer is based on the use of a linearly variable differential transformer. As the stem expands and contracts, the sensing rod moves out and in and transmits a signal to the potentiometer (Deslauriers et al. 2003). Before installing the dendrometers, the outer dead bark was peeled off to reduce the influence of hygroscopic swelling and shrinkage of the bark. The radial variation values were recorded every 30 min using a data logger (DL10, Ecomatik, Munich, Germany).

Meteorological measurements

At an altitude of 2 m, air temperature (AT, °C), relative humidity (Rh, %) and precipitation (P, mm) were measured by an automatic weather station (HOBO, Onset, Pocasset,

USA), which was located in a relatively flat area near the research site. The volumetric soil water content (SWC, %; Em50, Decagon, WA, USA) and soil temperature (ST, °C; Em50, Decagon, Washington, USA) were measured at 20-cm depth in close proximity to the trees studied. The vapor pressure deficit (VPD, kPa) was calculated from the values of ST and Rh. The environmental factors were recorded every 30 min, which was synchronous to the dendrometer measurements.

Data analysis

Based on the stem circadian cycle approach described by Downes et al. (1999), the typical diurnal cycle can be divided into three distinct phases as follows: (a) contraction phase, period between the morning maximum and daily minimum; (b) recovery phase, from the daily minimum to the position observed at that morning's maximum; (c) stem radial increment (SRI) phase, from when the stem radius exceeds the morning maximum until the subsequent maximum. According to these definitions, some days did not experience any stem radial increment (SRI) phase (e.g., 23 July in Fig. 3), and those data were treated as missing values in the subsequent analyses (Downes et al. 1999). The daily stem mean value (R) was the average of 48 values measured in 1 day by the dendrometers, and the cumulative radial variation (CRV) was calculated as:

$$CRV_n = R_n - R_1 \quad (1)$$

where CRV_n and R_n are the cumulative radial variation (CRV) and daily stem mean value (R) on the day n ,

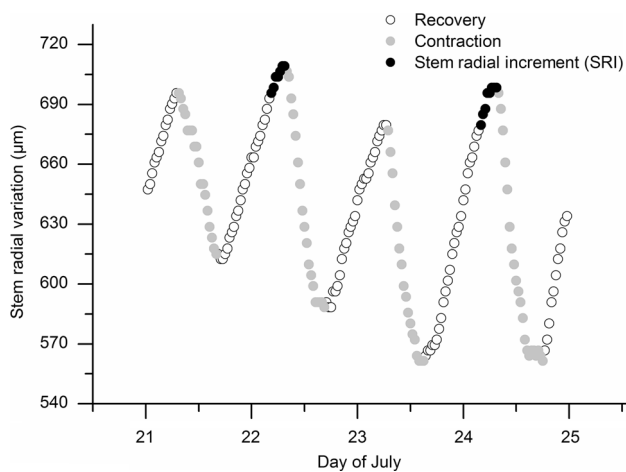


Fig. 3 A stem's circadian cycle divided into three distinct phases, recovery, contraction and stem radial increment (SRI)

respectively, and R_1 is the daily stem mean value (R) on the first day. The RCRV was defined as the running mean of CRV for a time windows of 21 days, and the running means were calculated at the mid-point (days 11) of the 21-day window position. The RCRV was calculated as:

$$\text{RCRV}_n = \sum_{i=n-10}^{n+10} \text{CRV}_i / 21 \quad (2)$$

where RCRV_n is the running mean of cumulative radial variation (CRV) for a time windows of 21 days on the day n . To describe the radial growth rate (RGR) of *P. orientalis* during the main growing season (Fig. 4) with negligible bias from putative stem shrinking and swelling effects, the RGR was determined by calculating the differences between the RCRV values for two consecutive days, according to Köcher's study (2012), and a negative growth rate never occurred during the main growing period by this calculation. The RGR was calculated as:

$$\text{RGR}_n = \text{RCRV}_n - \text{RCRV}_{n-1} = (R_{n+10} - R_{n-11}) / 21 \quad (3)$$

where RGR_n is the radial growth rate on the day n .

Pearson's correlation coefficients were calculated using SPSS 17.0 software (SPSS Inc., Chicago, USA) to quantify the association between the daily stem radial increments (SRI) and the daily environmental variables during the main growing period (Deslauriers et al. 2007).

Results

Environmental variables during the growing season

From May to October 2013, the growing season, it was warmer by 0.7 °C than the long-term mean values (LTM 1963–2012), and the daily mean, maximum and minimum

air temperatures during the growing season ranged from 4.6 to 28.5 °C, −2.5 to 24.1 °C and 11.4 to 39.0 °C, respectively (Fig. 4e). The variation pattern of soil temperature and of mean air temperature was similar with small fluctuations. The precipitation during the study period was higher (67.8 mm) than the LTM, and the highest amount of 10-day precipitation (70.7 mm) was recorded in early August (Fig. 4d). A serious drought period was recorded in May, when the total monthly precipitation was only 3 mm (LTM 28.5 mm), and the mean monthly air temperature was 20.9 °C (LTM 18.6 °C) (Fig. 2). The soil water content (SWC) showed a large fluctuant time course related to the occurrence of precipitation, and the highest SWC was observed in early August (Fig. 4c). The vapor pressure deficit (VPD) reached its highest value in May (Fig. 4h), while the relative air humidity (Rh) exhibited a different course from VPD, varying during the growing season from 20 to 100 % (Fig. 4g).

Dynamics of cumulative stem variation and daily stem radial increment

Serious drought period lasting for about 30 days was observed during the early growing season (in May). Under these drought conditions, the cumulative radial variation (CRV) of *P. orientalis* showed a persistent contraction until the occurrence of heavy precipitation in early June. Then, due to the precipitation, the CRV sharply increased within 4 days and resulted in an increase in soil water content (Fig. 4a). From mid-June to mid-September, the CRV was characterized by rapid growth as shown by an S-shaped growth curve, and this period was regarded as the main growing period for *P. orientalis*. During the late growing season (from late September to October), the CRV plateaued with small fluctuations, suggesting that the radial growth tended to stop at that time. During the main growing period (from mid-June to mid-September), the daily stem radial increment (SRI) was highly variable (Fig. 4b), ranging from 0.9 to 105.7 µm. The daily stem radial increment of *P. orientalis* during the main growing period was 27.6 ± 1.6 µm (mean \pm SE) on average.

Stem radial growth rates

The stem radial growth rate of *P. orientalis* during the main growing period, calculated as the difference between the RCRV values (Fig. 5a) for two consecutive days, decreased from 20 June to 10 July and was followed by a unimodal curve from 10 July to 10 September (Fig. 5b). The radial growth rate reached its highest value (22.9 µm/day) in early August, the time with the best hydrothermal conditions, and its lowest value (0.3 µm/day) in mid-July, which was a short dry period.

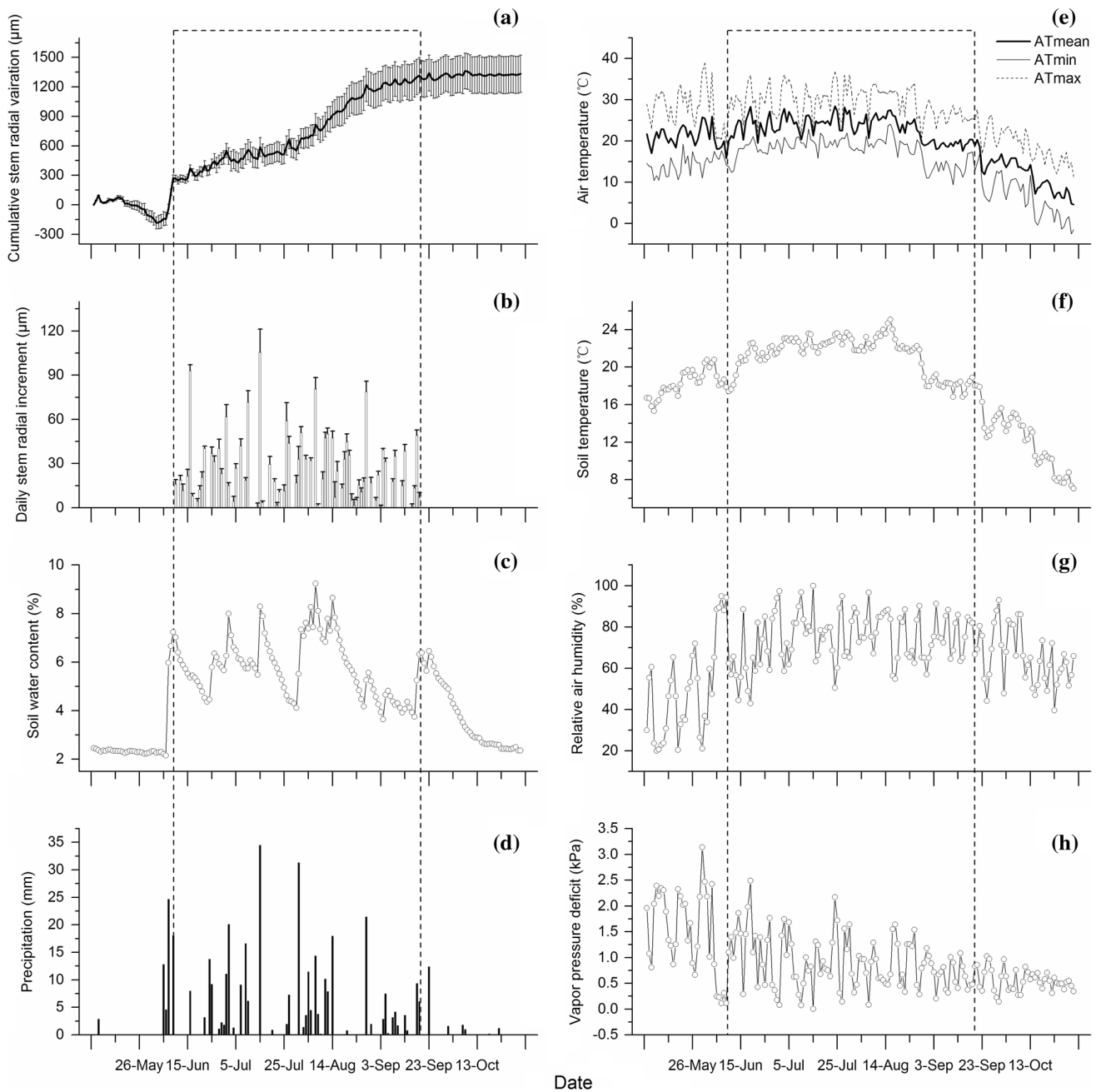


Fig. 4 Daily time series (from 7 May to 31 October 2013) of cumulative radial variation (CRV) of *P. orientalis* (a), daily stem radial increment (SRI) during the main growing period (from 10 June to 20 September) (b), soil water content (c), precipitation (d), daily

mean (AT_{mean}), minimum (AT_{min}) and maximum air temperature (AT_{max}) (e), soil temperature (f), relative air humidity (g), and vapor pressure deficit (h). Rectangular boxes indicate the main growing period for *P. orientalis*, and bars represent the standard error

Daily stem radial increment in relation to environmental factors

The daily stem radial increment (SRI) of *P. orientalis* was analyzed for its relation to environmental factors during the main growing period (Fig. 6). SRI showed the highest direct correlation with relative air humidity (Rh)

($r = 0.675$ $p < 0.001$) and precipitation ($r = 0.572$, $p < 0.001$). A significant indirect relationship was observed between SRI and vapor pressure deficit (VPD) ($r = -0.653$, $p < 0.001$). Non-significant correlations were found between SRI and soil temperature and soil water content. As for air temperature, AT_{mean} and AT_{max} had significantly negative impacts on SRI.

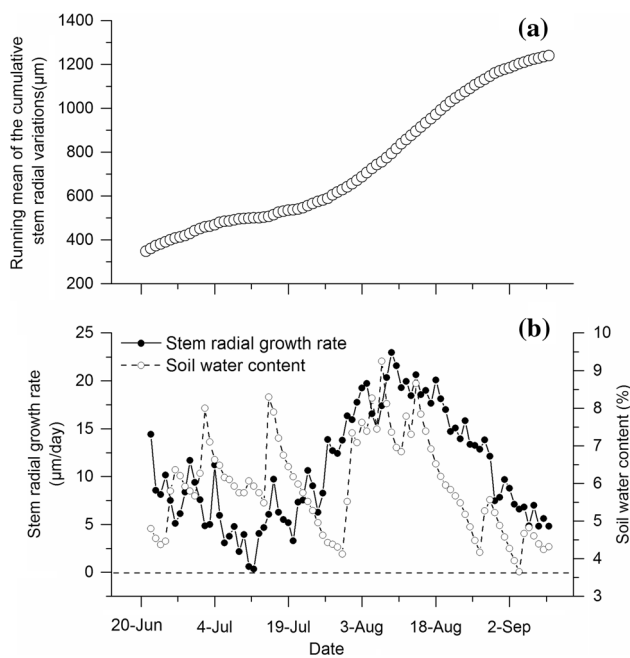


Fig. 5 Running mean of the cumulative radial variations (RCRV) for time windows of 21 days during the main growing period; the running means were calculated at the mid-point (days 11) of the 21-day window position (a), and daily time series of stem radial growth rate and soil water content (b)

Discussion

Response to drought

In our study, a serious drought period was observed in May, and at the same time the stem of *P. orientalis* showed persistent shrinking (Fig. 4a). Zweifel et al. (2006) reported that for a certain period of drought, stem cambial cell division is not inhibited, and only when drought conditions last beyond that period, cell division is stopped. The inhibition of cambial cell expansion with the loss of cell turgor during drought is a well-known phenomenon (Abe and Nakai 1999). When drought ends after certain rainfall events and soil water is replaced, continuous rapid stem growth for days can be measured immediately (Drew et al. 2009). In our study, *P. orientalis* experienced a sharp stem radial increment within 4 days of a precipitation event in early June, and there was an increase in soil water content. To some extent, this rapid growth could be explained by the release of the low-pressure conditions in the cambium by a sudden enlargement of the already existing cells after division to their mature sizes (Zweifel et al. 2006). Although some of this growth was likely to be reversible swelling of phloem and cambial tissue (Zweifel et al. 2001), the stem of *P. orientalis* did not show an obvious contraction when the soil water content sharply decreased after 10 June (Fig. 4a, c), suggesting that irreversible cell

growth resulted in a real net increment, with an increase of approximately 210 μm from early May to early June.

Weather dependence of growth

During the main growth period, the daily stem radial increment (SRI) of *P. orientalis* has been found to be significantly and positively related to relative air humidity (Rh), precipitation and soil water content (SWC) (Fig. 6). Physiological studies have shown that cellular enlargement is basically water dependent, because turgor pressure drives irreversible cell expansion (Proseus and Boyer 2005), and cell enlargement can be considered the major driving force of the net daily radial increase (Deslauriers et al. 2003). In our study, the strong positive effect of Rh on SRI could be the result of high Rh lowering transpiration, which reduces the negative pressure in the conducting system and increases the turgor in the stem cambial cells, thereby favoring cell division and expansion (Köcher et al. 2012). Similarly, Oberhuber and Gruber (2010), using dendrometers and a microsampling method, and Liang et al. (2006), using tree-ring analysis, found that the stem radial growth of *Pinus sylvestris*, *Sabina przewalskii* and *Picea crassifolia* were positively correlated with Rh under dry conditions. With respect to precipitation, on the one hand, large amounts of precipitation (>10 mm) caused an evident soil water content increase (Fig. 4c, d), which increases stem water status and cambial cell turgor, which then influences radial growth (Ryan et al. 1994). With precipitation, reversible variations due to the swelling of extensible tissues outside the cambium inevitably occurs (Deslauriers et al. 2007). On the other hand, small amounts of precipitation (<10 mm) exert a positive effect on cambial activity, not by increasing soil water content (Fig. 4c, d), but through wetting the crown; this leads to a partial release of the low leaf water potential, resulting in an increase in the cambial turgor and, thus, to an enlargement of the cambial cells already produced (Zweifel et al. 2006). This would also explain why there was a decoupling between radial growth and soil water content. Breshears et al. (2008) observed that foliar absorption of intercepted rainfall led to a substantial improvement in the water status of *Juniperus monosperma* during drought. In agreement with our results, a dendroclimatological study by Liang et al. (2008) found that monthly precipitation and relative air humidity in the growing season were major limiting factors for the radial growth of *Pinus tabulaeformis* in semi-arid areas of northern central China. These three environmental factors [relative air humidity (Rh), precipitation and soil water content (SWC)] can influence the moisture availability for the tree and, thereby, the stem radial growth, which also confirms that generally moisture availability is the dominant limiting factor for tree radial

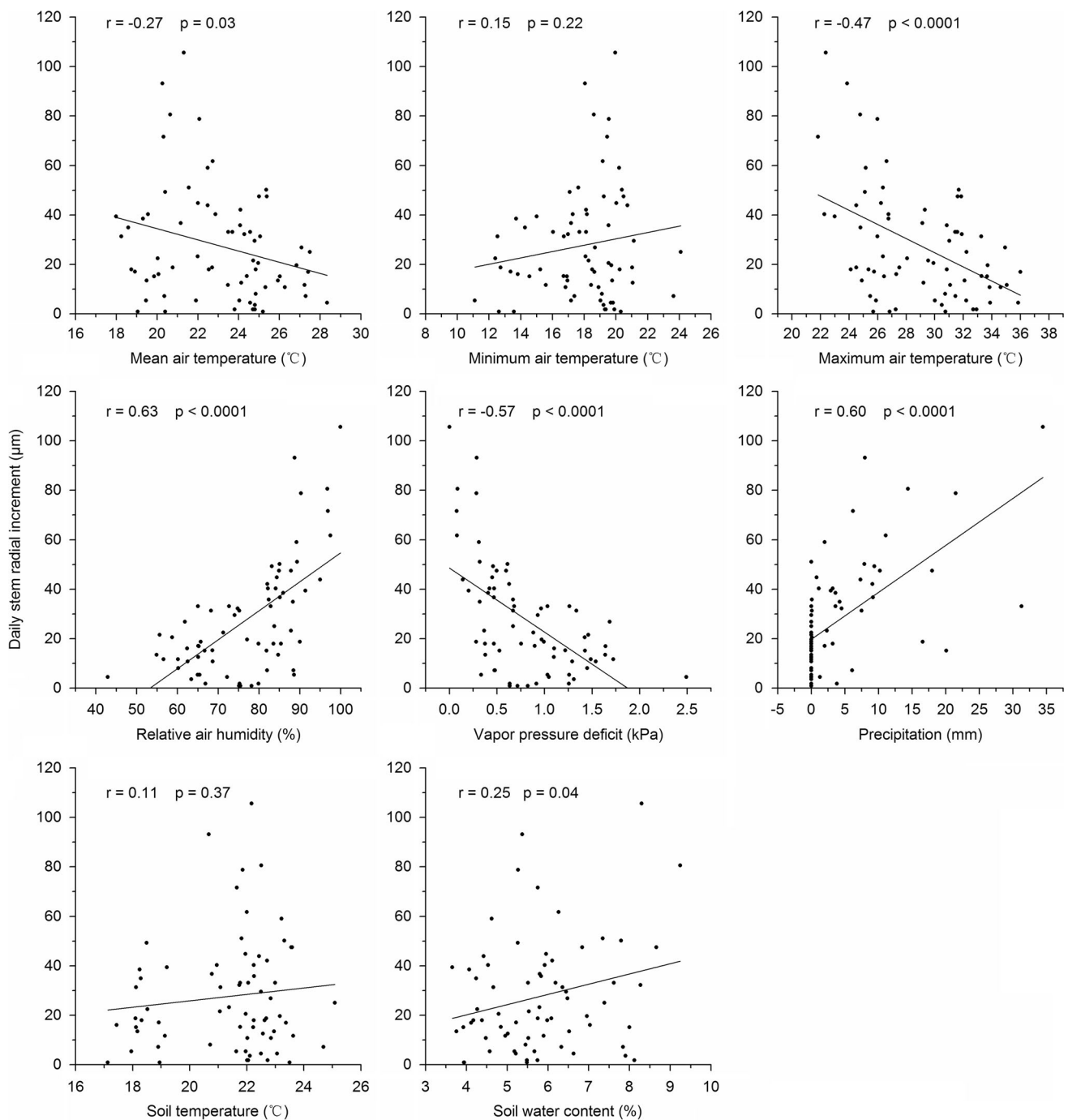


Fig. 6 Pearson's correlations between the daily stem radial increments (SRI) of *P. orientalis* and climate parameters (daily mean air temperature, minimum air temperature, maximum air temperature,

relative air humidity, vapor pressure deficit, precipitation, soil temperature and soil water content) during the main growing period

growth in semi-arid areas of North China based on dendroclimatological studies (Liang et al. 2001, 2008; Shi et al. 2008).

The significant negative response of SRI to vapor pressure deficit (VPD) and, especially, to daily maximum temperature (AT_{\max}) and daily mean air temperature (AT_{mean}) (Fig. 6) also indicates moisture stress. Under the

conjoined influences of high VPD and AT_{\max} , due to the close correlation between them ($r = 0.76, p < 0.0001$), the rate of transpiration of *P. orientalis* is increased. First, the negative pressure in the conducting system is increased, which decreases the turgor in the cambial cells and thereby decreases cell expansion (Köcher et al. 2012); this contrasts with the impact of Rh. Second, the tree closes its stomata to

avoid hydraulic failure (Guehl and Aussenac 1987; Ripullone et al. 2007). By closing the stomata, carbon uptake and photosynthesis are affected, followed by a decrease of carbohydrate availability in the stem and the subsequent inhibition of radial growth (Oribe et al. 2003; Michelot et al. 2012). These results are supported by observations by Tian et al. (2005) who reported that *P. orientalis* showed a mid-day depression of net photosynthesis in a semi-arid region of North China related to high mid-day temperatures, namely the daily maximum temperature (AT_{max}). Moreover, high temperatures lead to higher respiration losses (Kajimoto 1990; Ryan et al. 1995), resulting in a faster consumption of carbohydrates and, hence, in a decreased radial growth; this also decreases the carbohydrate availability for earlywood formation in the next spring (Lebourgeois et al. 2004; Friedrichs et al. 2009). By dendroclimatological study, Huang et al. (2006) found that the ring width of *P. orientalis* has a significant positive response to precipitation and a significant negative response to temperature during the current growing season, which was consistent with our results. Soil temperature and daily minimum temperature did not have significant impacts on the SRI (Fig. 6). In contrast, the stem radial growth of conifers growing in cold conditions, such as at the alpine tree line, may benefit from high soil and air temperatures during the growing season (Rossi et al. 2007; Gruber et al. 2009; Dong et al. 2011), because tree growth is strongly regulated by low temperatures (Körner and Paulsen 2004).

Timing of maximum growth rate

Several authors (Rossi et al. 2006; Seo et al. 2008; Gruber et al. 2009; Duchesne et al. 2012) reported that the maximum daily growth rate of conifers in cold environments, i.e., at the alpine tree line and boreal forests, peaked around the summer solstice, and not during the warmest period of the year. Rossi et al. (2006) hypothesized that the connection of the growth constraint with the maximum photoperiod could be an adaptation of conifers to cold conditions, allowing them enough time to complete cell wall formation and lignification before winter. However, in our study, the maximum growth rate of *P. orientalis* was observed in early August with its favorite growing conditions, i.e., the highest soil water content during the main growing season (Fig. 4c), and a rather steady daily mean air temperature of approximately 24 °C in summer (mid-June to mid-August) (Figs. 2, 4e). There was a significant correlation between the stem radial growth rate and daily soil water content ($r = 0.39$, $p < 0.001$). Zhang et al. (2012) reported that the net photosynthesis rate of *P. orientalis* was closely and positively correlated with

soil water content between 3 and 16 %, which also explains our results with respect to the physiological process. Our results support the conclusion by Henttonen et al. (2009) that the timing of the highest growth rate does not seem to be related to maximum day length as strictly as was suggested by Rossi et al. (2006), and in milder climatic conditions, other environmental variables, such as temperature and water availability, may have an effect on the timing of the maximum growth rate. We suggest that the timing of the maximum growth rate reflects the ability of the species to exploit favorable environmental conditions and could be considered as an adaptation to local climatic conditions. In our study, the maximum radial growth rate of *P. orientalis* in a semi-arid area of North China was regulated by soil water content in summer. This seems to be an adaptation to the local, temperate continental, monsoon climate conditions, with high precipitation and high temperature at the same time in early August simultaneously (Fig. 2). In accordance with our results, Popescu et al. (1968) reported that the maximum increment rate for *Fagus sylvatica* in Romania was reached in late July under conditions of optimal temperature and water availability.

Conclusions

From our analysis, we conclude that the daily stem radial increment (SRI) of *P. orientalis* during the main growing period in a semi-arid area of North China was primarily influenced by relative air humidity, precipitation, vapor pressure deficit and daily air maximum temperature, which mainly influenced the moisture availability for the tree and, thereby, the daily stem radial growth. Daily mean air temperature and soil water content played a secondary role. The stem radial growth was slowed down under drought conditions, but a rapid growth release occurred when water became available. The stem radial growth rate of *P. orientalis* reached its highest value in early August, which was related to soil water content in summer, and this effect appears to be an adaptation to the local, temperate continental, monsoon climate.

Author contribution statement Study conception and design: J.Y. and D.M.Y. Acquisition of data: W.B.Q., W.M.C., H.Y.M. and W.B. Analysis and interpretation of data: W.B.Q. and D.M.Y. Drafting of manuscript: J.Y., W.B.Q. and D.M.Y.

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

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