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Intra-Annual Variation of Stem Radius of *Larix principis-rupprechtii* and Its Response to Environmental Factors in Liupan Mountains of Northwest China

Zebin Liu, Yanhui Wang *, Ao Tian, Pengtao Yu, Wei Xiong, Lihong Xu and Yarui Wang

Key Laboratory of Forestry Ecology and Environment of the State Forestry Administration of China, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China; binarystar1989@163.com (Z.L.); tianao640249@126.com (A.T.); yupt@caf.ac.cn (P.Y.); xwcaf@163.com (W.X.); xulh@caf.ac.cn (L.X.); wangyaruio@163.com (Y.W.)

* Correspondence: wangyh@caf.ac.cn; Tel.: +86-10-6288-9531

Academic Editor: Ignacio García-González

Received: 15 August 2017; Accepted: 2 October 2017; Published: 7 October 2017

Abstract: Fine-resolution studies on the stem radius variation at short timescale can provide useful information about the tree growth process and the major environmental variables that trigger and drive stem radius variation. This study investigated the stem radius variation of *Larix principis-rupprechtii* Mayr growing in the semi-humid Liupan Mountains of Northwest China at daily and seasonal scales using high-resolution automatic band dendrometers from May to October in 2015. The results showed that the stem radius variation of *Larix principis-rupprechtii* has a clear diurnal pattern which can be divided into contraction, recovery, and increment phases; and also a seasonal pattern which can be divided into three stages: (1) the rapid growth stage in spring (stage 1) with the radius increment of 94.0% of the total in the entire growing period; (2) the persistent shrinkage stage in the dry summer (stage 2) with a negative diurnal radius increment for most days, and a significantly larger amplitude of stem contraction and recovery than other stages; (3) the minimal growth stage in autumn (stage 3), mainly caused by the lowering temperature and leaf area. The amplitude of stem contraction was significantly correlated with air temperature (both the mean and highest value) in all three stages: vapor pressure deficit (VPD) in stage 1; relative humidity (RH), VPD and soil moisture (M_s) in stage 2; and soil temperature (T_s) in stage 3. This indicates that the stem radius contraction was mainly controlled by the factors influencing tree transpiration rate in spring and autumn stages, but jointly controlled by the factors influencing both the tree transpiration rate and the soil moisture availability in the dry summer stage. The factors controlling the stem radius recovery was similar to the stem contraction. The amplitude of stem increment was significantly correlated with the rainfall amount and air temperature (both the mean and highest value) in stage 1 and 3, M_s in stage 2, and the lowest air temperature and T_s in stage 3. This indicates that temperature and precipitation were the key factors controlling the stem radius increment in the spring and autumn stages, and soil moisture was the main factor limiting the stem radius increment in the dry summer stage at the study site with semi-humid climate in Northwest China.

Keywords: stem radius variation; diurnal pattern; seasonal pattern; drought effect; environmental factors; *Larix principis-rupprechtii*

1. Introduction

Under the increasing influence of global climate change, the growth of trees has been affected not only by the change of annual values of meteorological parameters, but also by the variation of environmental factors in short timescale, such as the hourly or daily values of soil moisture and weather parameters, and especially the extreme weather events (i.e., high temperature, drought, freeze injury) [1–6]. However, the current knowledge about climate-growth relationships was mostly based on annual dendroclimatological studies and cannot completely reflect the effect of short-term environment on tree growth [7,8]. In fact, the annual effect on tree growth is an accumulated effect on the cambial cell division and cell enlargement in many small time periods [9]. The understanding of influence in short timescales can help to explain and predict the influence across larger timescales. Therefore, studies at short-term timescale (i.e., diurnal and seasonal) are required for a more precise assessment, interpretation, and prediction of tree growth response to environmental stresses at larger timescales [10].

The dendrometer can automatically and continually record intra-annual stem radius variation with high temporal resolution [11], thus providing a possibility to study the diurnal and seasonal dynamics of stem radius and their response to environmental factors at shorter timescales. Based on such dendrometer data, several studies were reported in recent years [12–14]. For example, Vieira et al. [15] reported that the continuous positive stem radius increment of *Pinus pinaster* Ait. under the Mediterranean climate began in spring and reached its maximum by the end of June; subsequently, marked radius shrinkage occurred due to drought. Dong et al. [16] reported that soil temperature is the key factor limiting stem radius growth of *Picea meyeri* Rehd. et Wils. during the growing period at alpine timberlines of North China. Bräuning et al. [17] reported that daily radius changes of *Cedrela montana* Moritz ex Turcz from Ecuador were related to moisture availability, with precipitation and vapor pressure deficit being the most important controlling factors. These studies provide a scientific basis for understanding intra-annual stem growth dynamics and its response to environmental variables, and for the prediction of future climate change impact on tree growth.

The native range of *Larix principis-rupprechtii* is distributed in the area of North China (38°–41° N, 112°–117° E) [18], but this tree species has been successfully afforested in a much wider area (32°–46° N, 85°–127° E), with an elevation range of 800–2800 m above sea level (a.s.l.), an annual precipitation range of 350–1000 mm, and an annual air temperature range from −1.2 to 13.0 °C [19–21]. Therefore, it plays an important role in afforestation. In the Liupan Mountains, the forest cover of *Larix principis-rupprechtii* plantation amounts to 31.3%, thus accounting for 90.0% of the total plantation area in this region, and plays an important role in soil and water conservation, wood production, and environment protection [22]. Therefore, understanding the growth response of *Larix principis-rupprechtii* to environmental variation is crucially important for understanding, designing, and managing the stability of such plantations and their multiple services. Although there were few studies on the stem radius variation of *Larix principis-rupprechtii* [23], there is still no report on the response of stem radius variation to environmental factors in short timescales within a whole growing season. Therefore, we want to describe the diurnal and seasonal variation patterns of stem radius of *Larix principis-rupprechtii* and their response to environmental factors, with the aim to: (1) reveal the variation patterns of stem radius at daily and seasonal scales, and; (2) determine the major factors controlling the stem radius variation during different growth stages within the growing season.

2. Materials and Methods

2.1. Study Site and Local Climate

The study was conducted in the Xiangshuihe watershed (35°15′–35°41′ N, 106°09′–106°30′ E) with an area of 43.7 km^2, and an elevation range of 2010–2942 m a.s.l. (Figure 1), located in the southern area of the National Natural Reserve of the Liupan Mountains, Ningxia, Northwest China. The climate is temperate semi-humid, with a frost-free period of 100–130 days [23], mean annual air temperature of 6.0 °C, and mean annual precipitation of 632 mm (the mean in 1970–2010 at Jingyuan weather station (35°18′ N, 106°11′ E), close to the study site).

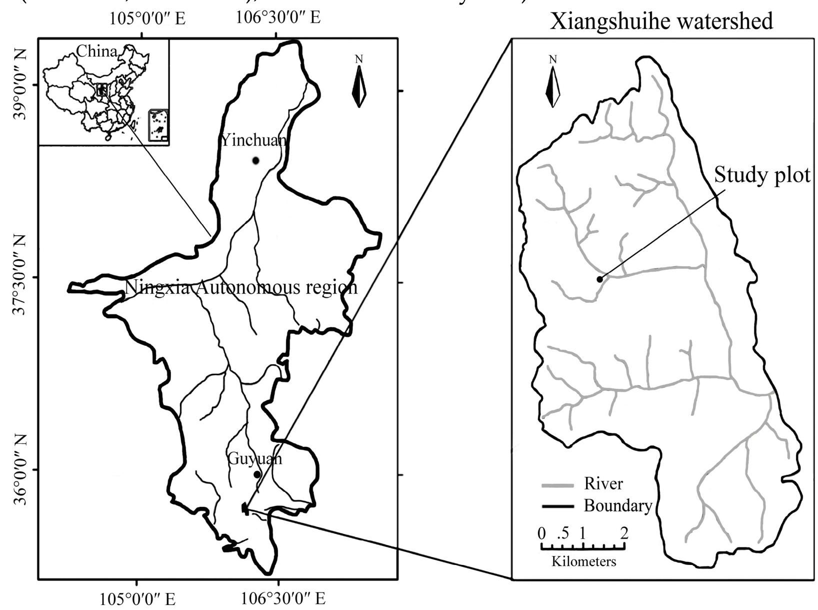


Figure 1. The location of the study site and study plot.

In 2015, a 30 m × 30 m plot was set up in a 34-year-old plantation of *Larix principis-rupprechtii* (35°30′50″ N, 106°13′30″ E; 2278 m a.s.l.) located on a southeast-facing slope with a slope gradient of 34.9°. The soil is sandy loam. The stand characteristics and site conditions are shown in Table 1.

Table 1. The stand characteristics and site conditions of the *Larix principis-rupprechtii* plot. Diameter at breast height (DBH).

Mean DBH (cm)	Mean Tree Height (m)	Stand Density (Tree·hm^{-2})	Crown Density (%)	Mean Crown Diameter (m)	Soil Bulk Density of 0–60 cm Layer (g·cm^{-3})	Field Capacity of 0–60 cm Soil Layer (%)	Total Porosity of 0–60 cm Soil Layer (%)
18.7	16.2	907	65	3.3	0.94	33.1	56.3

2.2. Dendrometer Data Collection

Four trees with different diameters at breast height (DBHs) within the plot of *Larix principis-rupprechtii* were selected for this study. The mean DBH (19.1 ± 3.4 cm) and mean tree height (H, 15.8 ± 2.4 m) of the sample trees are close to the mean DBH and H of the stand. From 10 May to 21 October 2015, the band dendrometers (DC2, Ecomatik, Munich, Germany), with a resolution of 2 μm and a temperature coefficient <0.1 μm/K, were installed on the stem at breast height to measure stem circumference variation. Before installing the band dendrometers, the outmost dried and dead bark was removed to minimize the effect of hygroscopic swelling and contraction of the bark. Plastic beads were placed around the dendrometer wire to avoid friction between the wire and the tree stem, and weatherproof rubber bands were used to hold the dendrometer onto the tree. Data were collected every 5 min and stored in a data logger (DL15, Ecomatik, Munich, Germany).

2.3. Meteorological and Soil Moisture Measurements

An automatic weather station (WeatherHawk232, WeatherHawk, Logan, UT, USA) was installed on an open area, 100 m from the plot, to collect weather data such as air temperature (°C), relative humidity (%), precipitation (mm), radiation (w·m^{-2}), and wind speed (m·s^{-1}).

The soil temperature and the volumetric soil moisture were monitored at depths of 0–20, 20–40, and 40–60 cm at a place close to the sample trees by soil moisture, temperature, and electrical conductivity sensors (5TE, Decagon, Washington, DC, USA), the data were stored in data logger (Em50, Decagon, Washington, DC, USA). Owing to the roots of *Larix principis-rupprechtii* were mainly distributed in the 0–60 cm soil layer, the volumetric soil moisture and soil temperature in the 0–60 cm soil layer were calculated as the average of the measured data in the 0–20, 20–40, and 40–60 cm soil layer, to reflect the overall dynamic of root-zone soil moisture and temperature.

All above environmental variables were recorded every 5 min to keep pace with the dendrometer measurement. The vapor pressure deficit (VPD, kpa) was calculated by the following equation [24]:

$$VPD = 0.611 \times (1 - RH/100) \times EXP(17.502T/(T + 240.97)) \quad (1)$$

where RH is the relative humidity (%) and T is the mean air temperature (°C).

2.4. Data Analysis

The circumference data obtained by dendrometers were further converted to the radii data for clearly reflecting the variation of stem growth and easily comparing with similar studies. The stem radius variation phases were extracted using the stem cycle approach developed by Downes et al. [25] and modified by Deslauries et al. [26]. This method divides the daily stem radius variation into three distinct phases: (1) contraction phase, the period between the first maximum radius and subsequent minimum; (2) recovery phase, the period from the minimum radius to the position of previous maximum radius; (3) radius increment phase, which can be positive or negative, relying on whether the previous maximum radius was achieved or not (Figure 2). According to these definitions, the amplitudes and relative duration of contraction, recovery, and increment for each cycle can be calculated, and the corresponding environmental factors of three phases in each circadian cycle can also be calculated [20,27]. All of these calculations were performed using the "dendrometeR" package specially developed to disentangle the different cyclic phases of trees from dendrometer data [28] by R 3.3.3 software (R Development Core Team, Vienna, Austria).

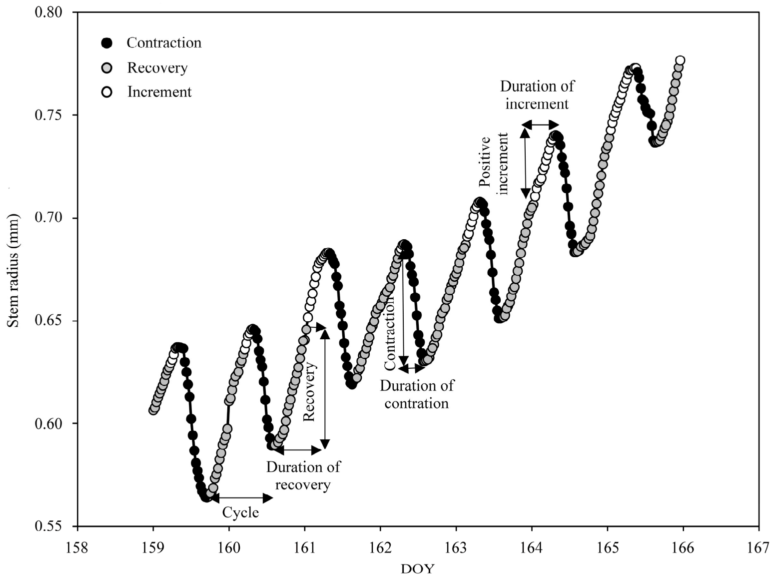


Figure 2. Cycles of stem radius of *Larix principis-rupprechtii* and its three phases: contraction; recovery, and; increment. The values are the mean stem radius of four trees (DOY 159–166, 2015).

Spearman correlations were conducted using the Statistical Product and Service Solutions (SPSS), version 19.0 (IBM Inc., Chicago, IL, USA) for each growth stage, which was divided according to seasonal radius variation pattern, to determine the influence of environmental factors on the contraction, recovery, and positive increment in different growth stages. The difference in the amplitude and duration of three distinct phases of stem radius among different growth stages were analyzed by one-way analysis of variance (ANOVA) and further by multiple comparisons (LSD) at $p < 0.05$ using SPSS 19.0.

3. Results

3.1. Meteorological Conditions

In the period from 10 May to 21 October 2015, the total precipitation was 536 mm, with the highest daily precipitation of 48 mm on 3 September (Figure 3A). The daily mean, maximum, and minimum air temperature varied in the range of 1.3–19.0 °C, 8.1–30.0 °C, and −6.7–14.3 °C, respectively, with the highest daily mean air temperature of 19.0 °C on 29 June (Figure 3B). The daily relative humidity ranged from 27.6% to 100%, with an average of 69.2% (Figure 3C). The daily VPD varied in the range of 0–1.51 kpa, with an average of 0.55 kpa (Figure 3D). Affected by precipitation, the soil moisture showed a large fluctuation: the mean volumetric soil moisture in 0–60 cm soil layer during the whole study period was 20.7%, but decreased to 19.0% during the dry period from 22 July to 2 September, with a minimum of 16.1% in the period from 20 August to 2 September (Figure 3E). The variation pattern of daily soil temperature was similar to the daily mean air temperature, only with a smaller fluctuation within the range of 2.5–14.5 °C (Figure 3F).

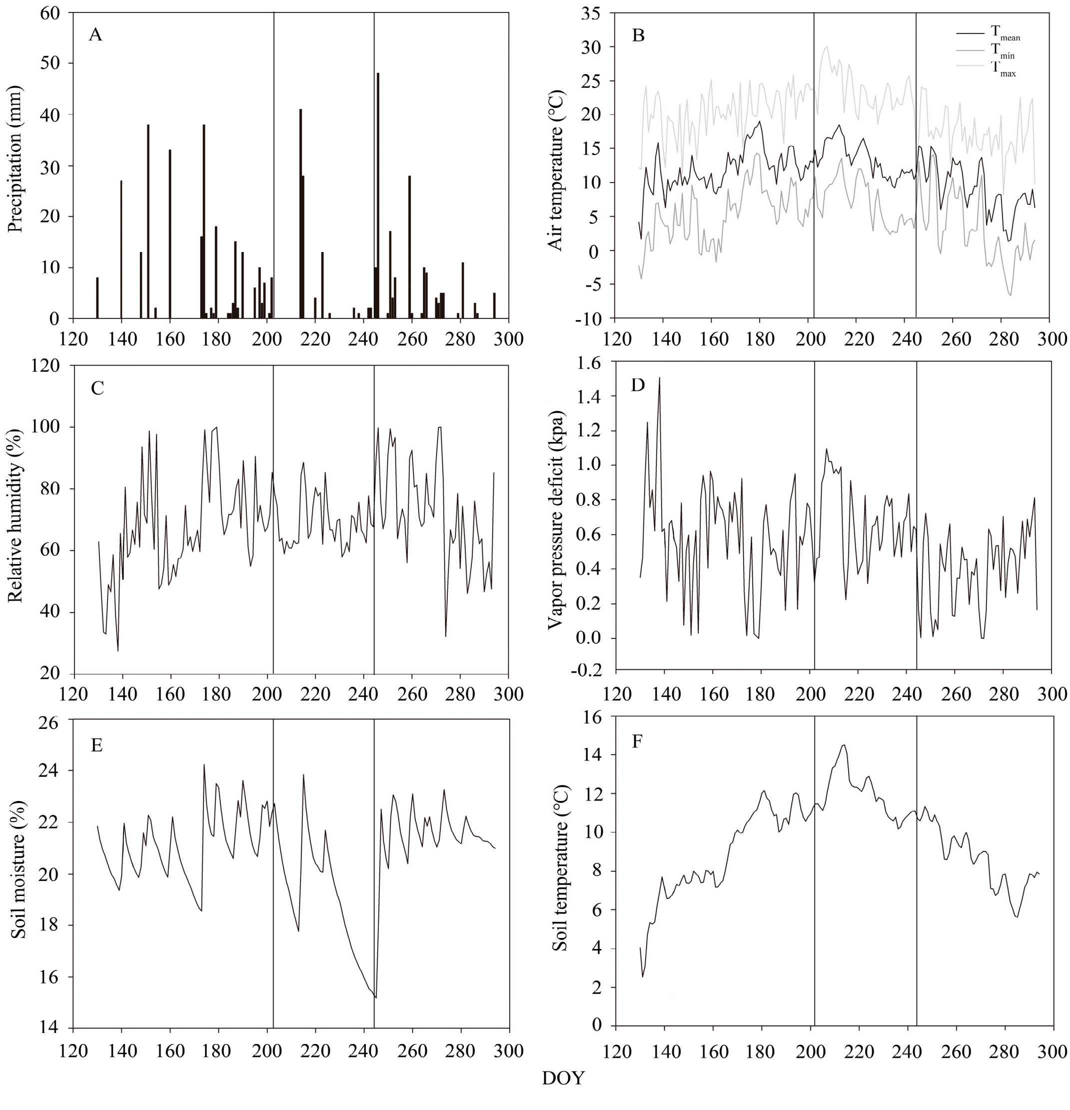


Figure 3. Daily variation of precipitation (**A**), mean and maximum and minimum of air temperature (**B**), relative humidity (**C**), vapor pressure deficit (VPD) (**D**), volumetric soil moisture (**E**), and soil temperature (**F**) during the study period. The vertical lines delimit the three growth stages of stem radius.

3.2. Stem Radius Variations

Considerable diurnal variation in stem radius was observed (Figure 2). The stem radius showed a daytime contraction and a nighttime swelling. The maximum stem radius appeared in the early morning (5:00 to 8:00), and subsequently, the stem radius contracted until the minimum stem radius was reached in the afternoon (14:00 to 16:30).

Besides the daily variation of the stem radius, a clear seasonal variation pattern during the study period can be seen in Figure 4. It can be divided into three distinct stages according to the amplitude of the cycles and net radius increment [15]. Stage 1 (day of the year (DOY) of 130–203) represented the most rapid, vigorous, and continuous positive radius increment. Stage 2 (DOY 204–244) represented a persistent radius shrinkage, particularly obvious from 12 to 30 August; the amplitude of stem shrinkage was 0.15 mm from 12 to 30 August. Stage 3 (DOY 245–294) presented the minimal stem radius growth, the stem radius variation started to stabilize, except three larger fluctuations caused by precipitation events.

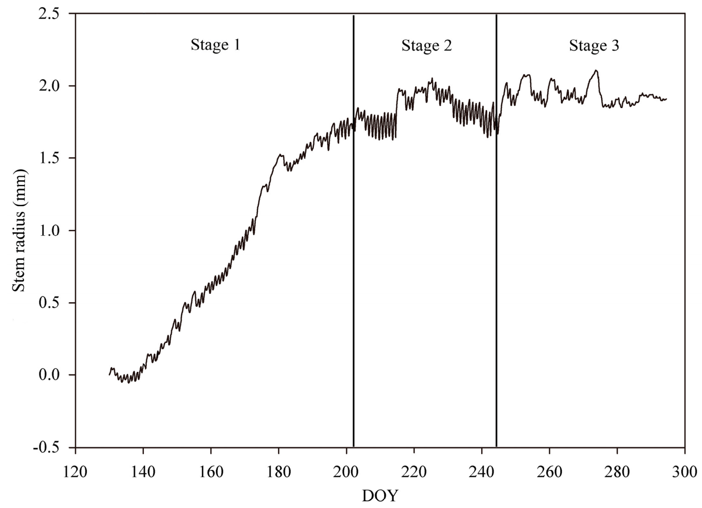


Figure 4. Mean stem radius of four trees during the whole study period, and the three stages: stage 1 with the most rapid growth; stage 2 with persistent shrinkage; and stage 3 with minimal growth. The values are the mean stem radius of four trees.

3.3. Seasonal Changes in the Amplitude and Duration of Radius Variation Phases

The mean amplitudes and duration of the three stem radius variation phases showed a marked seasonal difference (Figure 5). The amplitudes of contraction and recovery in stage 2 was significantly ($p < 0.01$) larger than in stages 1 and 3. The mean amplitude of contraction and recovery were 0.044 and 0.040 mm for stage 1, 0.124 mm and 0.111 mm for stage 2, and 0.035 mm and 0.020 mm for stage 3, respectively. The duration of contraction in stage 2 (8.7 h) and 3 (8.4 h) was significantly ($p < 0.01$) longer than in stage 1 (6.1 h). The duration of recovery in stage 2 (13.9 h) was significantly ($p < 0.01$) longer than in stage 1 (9.9 h) and 3 (10.3 h). The duration of recovery was significantly ($p < 0.01$) longer than that of contraction in every stage. The longest duration of recovery and contraction appeared in stage 2, of 13.9 h and 8.7 h, respectively. The increment mainly occurred in stage 1 (0.025 mm), and was significantly ($p < 0.01$) higher than in stages 2 (−0.001 mm) and 3 (0.004 mm). The duration of increment in stage 1 (7.8 h) was significantly ($p < 0.01$) longer than in stages 2 (2.7 h) and 3 (5.7 h).

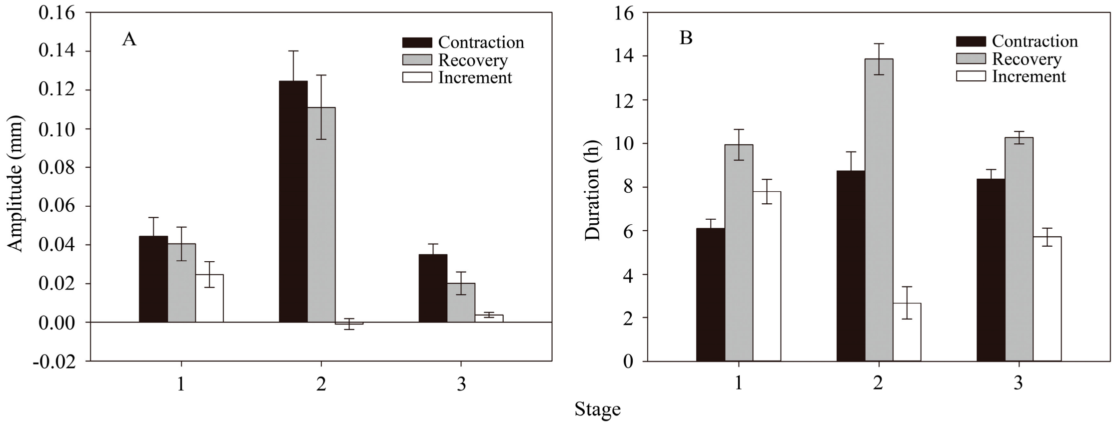
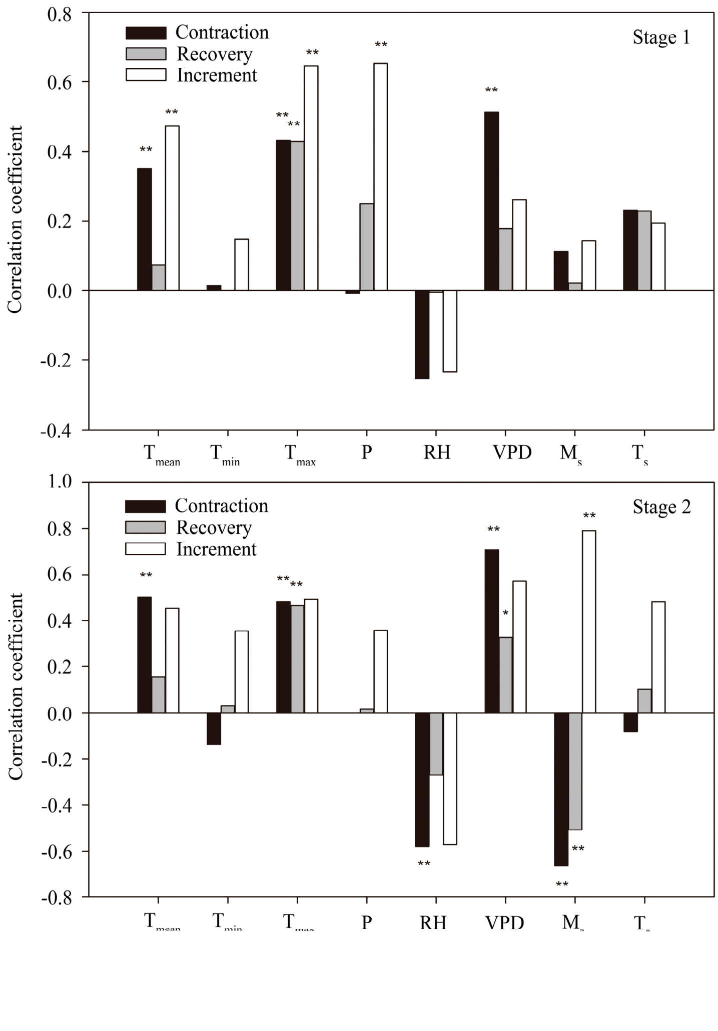


Figure 5. Mean amplitude (**A**) and duration (**B**) of contraction, recovery, and increment phase of four trees in three stages. Values are means ± standard error (n = 4).

3.4. Correlation between Stem Radius and Environmental Factors

The correlation of amplitude of stem radius variation and environmental factors varied with growth stages (Figure 6). The amplitude of contraction was significantly correlated with T_{mean} and T_{max} in all three stages, VPD in stages 1 and 2, RH and soil moisture (M_s) in stage 2, and soil temperature (T_s) in stage 3. The amplitude of recovery was significantly correlated with T_{max} in stages 1 and 2, VPD and M_s in stage 2, and T_s in stage 3. The amplitude of increment was significantly correlated with T_{mean} and T_{max} in stages 1 and 3, P in stages 1 and 3, M_s in stage 2, and T_{min} and T_s in stage 3.



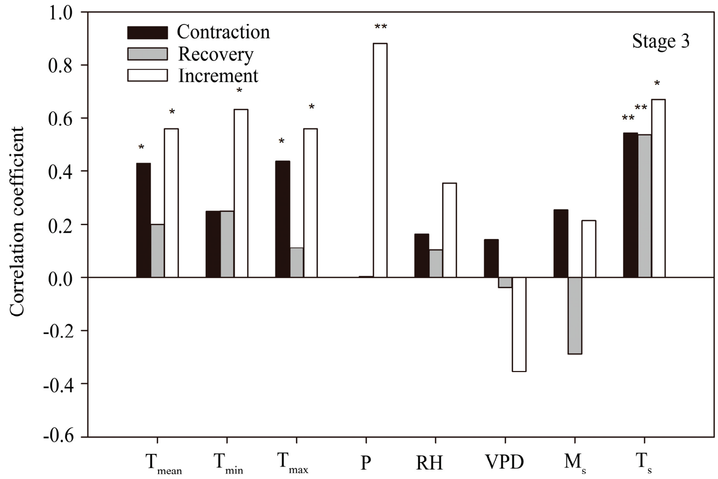


Figure 6. Spearman correlations of amplitude of stem radius variation and air temperature (mean, T_{mean}; minimum, T_{min}; and maximum, T_{max}), precipitation (P), relative humidity (RH), vapor pressure deficit (VPD), soil moisture (M_s), and soil temperature (T_s) during stages 1, 2, and 3. * $p < 0.05$; ** $p < 0.01$.

4. Discussion

4.1. Intra-Annual Variations of Stem Radius

On a diurnal basis, stems of trees contract during daytime and swelled during nighttime owing to the change of tree cell water content and its own growth [15,16,29–31]. Our results showed that stems of *Larix principis-rupprechtii* also undergo this basic pattern. However, several other studies also found the stem radius diurnal variation in stems of some tree species, such as *Picea abies* (L.) H. Karst. [32] and *Juglans regia* (L.) [33], showed an inverted day/night cycle in cold season, with contraction during the night and swelling during the day, caused by low temperatures rather than transpiration [15]. The formation of inverted day/night cycles was a direct consequence of stem tissues reaching freezing temperatures [32]. There was no such inverted day/night cycle in our study, since the sap did not reach the freezing point during the growing season.

Although the radius diurnal variation of *Larix principis-rupprechtii* showed the same pattern of daytime contraction and nighttime swelling in each stage, the amplitude of stem radius variation differed among the three stages. The contraction amplitude in stage 2 was significantly higher than in other stages, probably due to the strong transpiration but insufficient water uptake by roots in the summer drought period [34]. In this study, for the drought days in stage 2, the mean volumetric soil moisture of 19.0% was lower than in other stages, whereas the mean maximum air temperature of 23.7 °C was higher. Therefore, we speculated that the deficiency of soil water reserves and high transpiration resulted in the increase of amplitude of stem contraction. A similar result was also found by Vieira et al. [15] in Portugal. They observed that the diurnal cycles of stem contraction of *Pinus pinaster* during a summer drought were 10 times higher than that in the rest of year. In our study, the stage 3 showed low amplitude of stem contraction compared with stages 1 and 2. Li et al. [35] reported that the amplitude of stem contraction in late growing season was low because of low transpiration caused by low leaf biomass and temperature. In our study, *Larix principis-rupprechtii* is a deciduous tree, and the needles begin to fall in September, which is reflected by the decreased leaf area index [36]. Meanwhile, the temperature gradually decreased in this stage (Figure 3B). Therefore, low transpiration might be the direct reason leading to the low amplitude of stem contraction.

The rapid stem radius growth in this study was observed in the time from May to July (stage 1), coincident with the most rapid division rate of cambial cells [37]. The rapid growth stage is considered as a critical stage for the formation of early wood cell and stem radius growth. For example, Vieira et al. [15] observed that approximately 75.0% of stem radius growth in *Pinus pinaster* growing at Perimetro Florestal Dunas de Cantanhede of Portugal was formed during the rapid stem radius growth stage from May to June. Oberhuber et al. [38] also reported that approximately 80.0% of stem radius growth in *Picea abies* growing at inner Alpine site of Austria was observed during the rapid stem radius growth stage from May to June. In our study, approximately 94.0% of the total radius growth was observed from mid-May to late July, the most productive period for *Larix principis-rupprechtii* in Liupan Mountains.

Marked stem shrinkage was observed in this study after late July (stage 2) when the amplitude of stem shrinkage from 12 to 30 August reached 0.15 mm. Since tree growth is an irreversible process, the persistent stem shrinkage does not mean that the trees were not growing in the stage 2, but can be explained as a result of bigger stem shrinkage due to net loss of stem water content compared with the real stem radius growth. The stem shrinkage corresponded to the decrease of soil moisture (Figures 3E and 4), indicating that the stem shrinkage was caused by the soil water deficits resulting from low precipitation and strong transpiration driven by high temperature and VPD. Replenishing the stem from the water lost during the daytime was difficult because of the decreased soil moisture and the increased day length in summer. This phenomenon was also found for *Pinus pinaster* [15], *Fitzroya cupressoides* (Mol.) I. M. Johnst. [12], *Pinus sylvestris* (L.) [39], and *Picea abies* [40], indicating that the marked stem shrinkage during drought period is a widespread characteristic of trees and might be in relation to internal physiological mechanisms of trees to tolerate short-term water stress. After the drought period, a rapid stem radius increment was observed in response to a precipitation event (48 mm, DOY 246). This result supports the conclusion by Drew et al. [41] that continuous rapid stem radius increment for days can be measured immediately when drought ends after sufficient rainfall and soil moisture recovery. Zweifel et al. [42] suggested that 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 to their mature stage.

In stage 3 (September to October) of this study, the stem radius grew slower as the result of slowed or even stopped cambium division under lowered temperatures. Although this stage is critical to the formation of late wood [43], it contributed very little to radius growth (Figure 4). Thus, the stem radius presented a plateau over this period as a whole, except three larger fluctuations caused by precipitation events. This variation pattern of stem radius during the late growing period was observed in many forest trees, such as *Picea crassifolia* Kom. [44], *Picea schrenkiana* Fisch. et Mey [43], and *Platycladus orientalis* (L.) Franco [45]. On a diurnal basis, although the stem radius maintained the diurnal pattern of daytime contraction and nighttime swelling in this stage, this daily fluctuation was mainly controlled by the variation of stem internal water content caused by meteorological factors because of the lowered daily radius increment.

4.2. Controlling Factors for Stem Radius Variation

4.2.1. Stem Radius Contraction

Stem contraction was caused by the changes of stem internal water balance between the water consumption through tree transpiration and the water uptake by root system from soil [46]. Thus, the amplitude of stem contraction was closely related to the factors influencing the tree transpiration and the soil water availability. The variation of the related environmental factors in short timescale can affect the stem contraction. Li et al. [47] reported that the factors controlling daily stem contraction of *Pinus koraiensis* Sieb. et Zucc. in the Xiaoxinganling Mountains were relative humidity, VPD, and soil temperature. Devine and Harrington [46] pointed out that the daily stem contraction of *Pseudotsuga menziesii* (Mirb.) Franco was correlated with mean air temperature, VPD, and potential evapotranspiration (PET). Similarly, in our study, the daily contraction of *Larix principis-rupprechtii* was significantly correlated with the factors influencing tree transpiration rate (air temperature (mean and maximum), relative humidity, VPD, soil temperature) or the soil water availability (soil moisture), and finally influencing the stem water content and diurnal contraction [15,48]. It is noted that the factors controlling stem contraction varied among different growth stages, the daily contraction was mainly correlated with air temperature (mean and maximum) and VPD in stage 1; air temperature (mean and maximum), VPD, relative humidity and soil moisture in stage 2; and air temperature (mean and maximum) and soil temperature in stage 3. This indicates that the stem contraction can rapidly respond to the changes of environmental conditions. Moreover, the air temperature was correlated with daily contraction in all stages, indicating that air temperature played an important role in stem contraction of *Larix principis-rupprechtii* in our study.

The significant correlations between stem contraction and air temperature (mean and maximum), relative humidity, VPD, and soil moisture in stage 2 confirm our previous speculation that the deficiency of soil water reserves and high transpiration may increase the amplitude of stem contraction. It should be noted that the positive correlation between maximum air temperature and stem contraction during drought stress (stage 2) was contrary to that observed by Vieira et al. [15], who found a negative correlation for *Pinus pinaster* during summer drought period. This contradiction may be explained by the stomatal regulation, which is important for avoiding a hydraulic failure under the Mediterranean climate with pronounced summer drought [15,49]. As temperature rises and soil moisture decreases, stomata close, resulting in a reduced transpiration rate [50] and thus a lowered stem contraction. In our site under a semi-humid climate with relatively low temperature due to the high elevation, the drought is transient and temporary, thus the stomatal regulation of *Larix principis-rupprechtiiis* might be relatively weak. Besides, Sun et al. [51] reported that the stomatal conductance of *Larix principis-rupprechtii* could maintain at a relatively high level when the VPD was lower than 0.80 kpa in Liupan Mountains. In our study, the VPD in stage 2 was less than 0.80 kpa in most days, indicating that the stomata of *Larix principis-rupprechtii* might be in an open state in this stage. Thus, stem contraction increased as the temperature increased.

4.2.2. Stem Radius Recovery

Typically, as shown in Figure 2, the amplitude of recovery is determined or driven by the magnitude of the contraction phase, since the amplitude of recovery is defined as the same of the amplitude of contraction in most days when the soil moisture is not too low to prohibit full recovery. This means that the larger amplitude of contraction at daytime will be accompanied by the larger amplitude of recovery at nighttime. This relation can be maintained even under drought conditions, beacuse the stem can make up the lost water in daytime by increasing the recovery duration when there are soil water deficits (Figure 5B). Thus, they are interdependent in most days, and this phenomen is less affected by the soil moisture level. Therefore, the factors affecting stem contraction might also control the stem recovery. In our study, a positive correlation between stem recovery and maximum air temperature was observed in stages 1 and 2. Air temperature can affect water uptake capacity of the root system and thus control the stem recovery by changing soil temperature [47]. However, soil temperature was not significantly correlated with stem recovery. This indicates that air temperature controlled the stem recovery not by affecting the water uptake by root system in nighttime but by controlling the stem contraction in daytime. Moreover, a negatively significant correlation between the amplitude of recovery was observed in stage 2 because the amplitude of contraction increased under decreased soil moisture in stage 2 (Figure 6), and the corresponding recovery phase would replenish the lost water from stem during contraction phase as much as possible by increasing the recovery duration (Figure 5B), and thus the amplitude of recovery also increased. This indicates that the environmental factors might control the stem recovery through affecting the stem contraction. Vieira et al. [15] reported that climatic responses of stem contraction and recovery are similar because they are interdependent. This is in accordance with our result. Based on that, the significant correlation between soil temperature and stem recovery in stage 3 cannot be explained to a direct effect of soil temperature on stem recovery, but an effect of soil temperature on stem contraction.

4.2.3. Stem Radius Increment

Air temperature had a positive effect on the daily stem radial increment of *Larix principis-rupprechtii* during the rapid stem growth time (stage 1). Early season increase of air temperature promotes the stem radius growth by inducing the cambial activity and xylem differentiation [52]. Several studies reported that the warm spring caused by global warming resulted in an earlier timing of stem growth [53–55]. Our results also showed that the radius growth during early growing season was related to air temperature. Precipitation can cause the reduction of leaf water potential, leading to a release of the low pressure conditions in the cambium, thereby allowing existing cells to enlarge [42]. In our study, the stem radius increment was positively correlated to precipitation in stage 1, indicating that precipitation played an important role in stem radius increment for *Larix principis-rupprechtii* during the early growing season (stage 1). This stage (mid-May to late July) is the rapid growth period and is also the main period for tree-ring formation. From this point of view, the significance of precipitation in this stage and its effect on annual stem growth or tree-ring growth of *Larix principis-rupprechtii* is clear. The significance of precipitation during the rapid growth period to annual stem growth was also reported in other species, such as *Picea schrenkiana* [43] and *Picea crassifolia* [56]. Under the increasing influence of global climate change, the distribution of precipitation will become more uneven within a given year and vary greatly across years [57]. Therefore, the decrease or increase of precipitation during the rapid growth period of trees will have an important influence on annual stem growth. Furthermore, our result showing the dependence of stem radius increment on air temperature and precipitation further confirms the results of previous dendroclimatological studies in a bigger timescale showing that tree-ring growth is positively correlated with the precipitation and temperature in early summer [58,59].

Water deficit limited the radius increment of *Larix principis-rupprechtii* during the drought period (stage 2), as shown by the positive correlation between soil moisture and stem radial increment. The soil water deficit directly affects the cambial activity and cell expansion [42,60]. In addition, the decrease of photosynthetic activity under dry soil conditions will lead to the decrease of availability and allocation of carbohydrates for cell division, thereby inhibiting radius growth [61]. Several studies examining the effects of environmental factors on stem radius growth during a drought period got similar results for other tree species, such as *Pinus hartwegii* Lindl. [62], *Fagus sylvatica (*L.) [63] and *P. sylvestris* (L.) [61]. Besides, several studies reported that the water deficit in summer can lead to earlier cessation of cambial activity and xylem formation [38,64]. Thus, the decrease or earlier cessation of cambial activity and cell division during the mid-growing season will reduce the annual stem radius growth. Drought is a common phenomenon during summer in the semi-arid and semi-humid areas [65,66]. The increased heating from global warming will strengthen the drought frequency and intensity [67], and thus increase the influence of drought on annual radius growth. Therefore, more attention should be given to the influence of drought stress on tree growth in dry mid-growing season in the context of global change.

Temperature plays the most important role in constraining the radius growth in cold environments [46,68–70]. These facts were in line with our findings that a positive correlation exists between stem radius increment of *Larix principis-rupprechtii* and the air and soil temperature in stage 3, indicating that the gradually decreasing temperature led to a reduced physiological and cambial cell activity, and then limit the stem radius growth [15,71]. Although the stem radius increment rate was low in stage 3, precipitation can also induce a radius growth, especially early in stage 3. The abundant precipitation in early stage 3 can replenish the soil moisture and increase the water content of the stem, thereby inducing the cell turgor pressure and stem radius growth [42]. The late growing season is the main period for the formation of late wood. Zhang et al. [43] reported that the radius increment during late growing season has limited contribution to annual radius growth of *Picea schrenkiana*. In our study, no obvious increase of stem radius during this stage was also observed, indicating the changing environment conditions (i.e., temperature and precipitation) during the late growing season might have relatively low direct effect on the magnitude of annual radius growth.

4.3. Implications for Climate-Growth Relationship Studies

The major environmental factors and their influence on stem radius increment varied along with growth stages. However, we did not get quantitative relations describing these varying influences to annual radius growth in this study because of the limited data. Under growing influence of global climate change, the changing environmental conditions especially the occurrence of extreme weather events (i.e., high temperature, flooding, drought, and freeze injury) will have critical influence on the intra-annual and annual stem radius growth. Further studies to combine dendrometer measurement, cell analysis, and model simulations should be encouraged to define the crucial weather events (e.g., high temperature, drought) occurring in radius growth process, and to quantify the effects of short-term variation of environmental conditions on tree stem radius growth.

In our study, the main stage of stem radius growth of the studied tree species was observed in the short period from May to July, which is a critical period for tree-ring formation [43]. Thus, the variation of environmental conditions in this short period will has a more important impact on the stem radius growth than the variation of the annual values of environmental factors. Determining the main growing stage of different tree species at different regions and clarifying the relations between environmental factors and stem radius growth should be encouraged in future studies, to overcome the limitation of the usual studies based on annual scale, and to provide a better understanding of the fine-time growth process of the annual growth and the corresponding controlling mechanism.

5. Conclusions

The variation of stem radius of *Larix principis-rupprechtii* has a clear diurnal pattern, which is generally composed of three phases, namely, daytime contraction, nighttime recovery and increment; and a clear growing seasonal pattern which can be divided into three stages: a spring stage with the most rapid growth (stage 1); a summer drought stage with the persistent shrinkage (stage 2); and an autumn stage with the minimal growth (stage 3). The stem radius increment mainly occurred in stage 1. The amplitude of diurnal stem radius contraction and recovery in stage 2 was larger than in other stages. The major factors controlling the variation/increment of stem radius differed along with growth stages. The diurnal contraction and recovery of stem radius was mainly controlled by the factors influencing the tree transpiration rate in the spring and autumn stages, but jointly controlled by the factors influencing both the tree transpiration rate and the soil moisture availability in the dry summer stage. Diurnal stem radius increment was mainly controlled by the temperature and precipitation in the spring and autumn stages since their relative higher soil water availability, and by the soil moisture in the summer stage due to its heavy soil drought stress.

Acknowledgments: This work was supported by National Natural Science Foundation of China (No. 41390461, 41230852, 41671025). Sincerely thanks for the assistance during field experiments by Xiuxiu Deng, Yu Liu, Xiao Wang and Haijun Zuo.

Author Contributions: Z.L. and Y.W. conceived and designed the experiments, analyzed the data and wrote the paper; Z.L., A.T. and Y.W. performed the experiments; Y.W., P.Y., W.X. and L.X. reviewed and edited the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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