



Species-specific coupling of tree-ring width and litter production in a temperate mixed forest

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ABSTRACT

Tree growth is delineated into multiple processes, such as foliar growth, stem growth, and reproductive growth; however, only stem growth can store carbon in forests at a relatively long time scale. Understanding how these processes interact in response to climate change is of utmost importance for predicting the future carbon fixation ability of forests. However, it largely remains an unresolved question. To bridge this knowledge gap, we collected litter and tree-ring samples of two deciduous tree species, i.e. *Larix principis-rupprechtii* and *Quercus liaotungensis*, in a temperate mixed forest on Dongling Mountain in northern China. The influence of climate and the coupling characteristics between leaf/needle litter, fruit/cone litter, and tree-ring width (TRW) were analysed. The results highlighted that leaf/needle production was significantly and positively coupled with TRW for both species, but with one-year time lag for larch. Path analysis revealed that climate changes directly and significantly affected fruit production, which in turn indirectly affected TRW for oak trees, but such effect of cone production on TRW was not significant for larch trees. Additionally, we found that the radial growth of oak trees is more sensitive to drought stress than larch, possibly due to the close coupling between leaf biomass and TRW. Our results demonstrated that the coupling characteristics between different components of tree growth are species-specific, and understanding these relationships is of great significance for improving the tree growth model of forest ecosystems.

1. Introduction

Tree growth is a key determinant of the dynamics of forest ecosystems at various timescales under climate change. Tree stem growth, in particular, as a long-term storage mechanism of carbon in forests, is important for mitigating anthropogenic warming via CO₂ fixation (Pan et al., 2011). However, the response of tree growth to climate change is not well understood; the relationship between climate and growth is not always consistent across time and space and is not reproduced well by vegetation models (Rammig et al., 2015). One major source of such uncertainty is the lack of knowledge of the key processes and underlying mechanisms of tree growth. Tree growth can be broken down into multiple processes, such as foliar development, stem growth (Huang et al., 2014), and reproductive growth (Martínez-Alonso et al., 2007; Bonser and Aarssen, 2009). These processes may show coupling changes to climatic drivers due to common constraints (Waring, 1983; Makela, 1997), but may also respond to climate change differently and exhibit uncoupling patterns (Solberg, 1999; Seidling et al., 2012; Tallieu et al.,

2020). Elucidating the links between these processes is important for an accurate assessment of resource allocation strategies for trees and for developing models to predict changes in forest ecosystem productivity under climate change.

Previous studies on the relationship between foliar development and tree-ring width (TRW) revealed the lack of a clear pattern. Foliar conditions and TRW have different maintaining organisms and may be regulated by different stressors, leading to uncoupling patterns in response to climate variation. For example, defoliation induced by insects was shown to lead to a delayed TRW reaction in several examples (Dobbertin, 2005). Canopy duration (i.e. time between leaf unfolding and colouring) was also shown to have no significant effect on variation in radial growth of beech trees (Cufar et al., 2015). In contrast, in boreal conifers, xylem formation could be modelled as a function of shoot and needle growth (Huang et al., 2014). Similarly, another study showed that changes in annual TRW and needle litterfall were significantly correlated, although with possible lags of up to 4 years in Scots pine (Aleksi et al., 2008). The coupling relationship can also be negative, as

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evidenced by a trade-off between leaf production and TRW at a stand level during and following drought (Kannenberg et al., 2019).

In addition to crown conditions, reproductive growth may also be linked to TRW (Bonser and Aarssen, 2009). For instance, allocation of resources for reproductive growth was proven to be a key factor in regulating tree growth in European beech (Hackett-Pain et al., 2018). Another study on young olive trees also indicated that resource investment in reproductive growth proportionately limited the investment in whole-tree vegetative growth (Rosati et al., 2018). Generally, a trade-off between growth and reproduction (the cost of reproduction) exists and strengthens in more stressful growing conditions (Hackett-Pain et al., 2017). However, decoupling and inverse relationships between reproductive and TRW also exist. Interannual variation in reproduction were not found to be associated with growth in a tropical forest (Alfaro-Sánchez et al., 2017) and the radial growth of white bark pines were not affected by masting events (Sala et al., 2012).

Although extensive research has been performed to elucidate the interactions between radial growth, reproduction, and crown development in response to climate, the outcomes remain to be debated. In some cases, climatic changes resulted in an uncoupling of litter production, secondary growth, and reproduction. However, it has been found that a decrease in carbohydrate supply under defoliation may not counterbalance the carbon used for mineral and water uptake, or their transport to other tissues (Jacquet et al., 2014; Vilà-Cabrera et al., 2014; Oddou-Muratorio et al., 2018). Therefore, the relationship between canopy dynamics, stem growth, and cone production as influenced by climate is likely to be highly variable across species and functional plant types (Cufar et al., 2008; Sala et al., 2012; Richardson et al., 2013; Delpierre et al., 2016). Thus, it is problematic to predict the response of tree growth and carbon sequestration capability to climate change without considering the coupling characteristics of these components (Iqbal et al., 2012).

To address these issues, we selected *Larix principis-rupprechtii* (Prince Rupprecht's larch) and *Quercus liaotungensis* (Mongolian oak), found in warm temperate mixed forests in northern China, as our research subjects. For deciduous tree species, annual leaf litter production is a reliable indicator of annual foliar biomass. The continuous observation of forest litter at our study site enabled bridging the data gap between different components of tree growth, including leaf production, TRW, and reproduction biomass, as well as their coupling characteristics. Our study focused on three key parameters: leaf/needle production, cone production, and TRW. We hypothesized that: (H1) TRW and foliar production are positively coupled and (H2) reproduction is negatively coupled with TRW for both deciduous species. We aimed to improve our understanding of different growth processes to better predict the response of tree growth to climate change.

2. Materials and methods

2.1. Study area

The study was carried out on Dongling Mountain (40°00'–40°02'N, 115°26'–115°30'E) in Mentougou District, Beijing, at an average elevation of 1100 m (Fig. 1). This location has a warm, temperate monsoon climate with four distinct seasons; it is cold and dry in the winter, and warm and humid in the summer. In the study area, annual precipitation ranged from 329 to 766 mm (over the 2005–2018 study period), which was concentrated in the summer. Mean monthly temperatures ranged from 20 °C in July to –14 °C in January (Fig. 2).

The studied forest belongs to a long-term field monitoring base, Beijing Forest Ecosystem Research Station, established in 1991. We used two experimental forest plots on the eastern slope of Dongling Mountain. The landform was mainly a mountain erosion structure and the soil was brown earth.

The larch plot (39°57'36.36"N, 115°25'32.16"E; 1250 m a.s.l.) was a permanent plot (30 m × 40 m) located in a *Larix principis-rupprechtii*

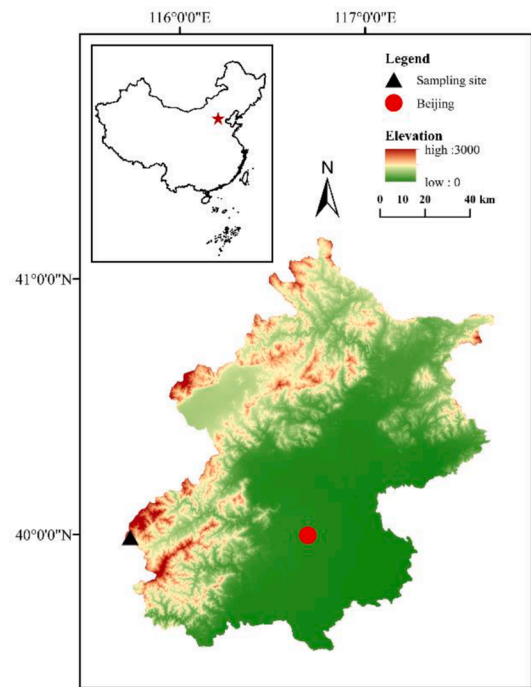


Fig. 1. Map of the sampling site in Beijing, China.

forest, mixed with a small amount of *Betula dahurica* Pall. Tree diameter at breast height (DBH, 1.3 m) ranged from 17 to 23 cm (Fig. S1a). The dominant species was larch with an average height of 10 m. In this plot, nine square litter traps (1 m × 1 m) were installed at a height of 0.50 m from the ground. The traps were evenly distributed across the plot.

The oak plot (39°57'28.44" N, 115°25'30.36" E; 1250 m a.s.l.) was a permanent plot (30 m × 40 m) located in a broad-leaved mixed forest with *Quercus liaotungensis* as the constructive species, approximately 1 km away from the larch plot. The dominant tree species was oak with an average height of 7.2 m and DBH ranged from 22 to 41 cm (Fig. S1b). We evenly distributed 11 square litter traps (1 m × 1 m) across the plot.

2.2. Sampling and laboratory method

We built two temporary plots of the same size next to the two permanent plots in order to obtain dendrochronological cores, which was not allowed in the permanent plots. At least 30 trees per species, without heavy insect or other damage, were sampled in the autumn of 2019. For each tree, a sample core was extracted with a hand increment borer (5.14 mm diameter) at 1.4 m above the ground from the southern side of the tree. Cores were dried, mounted on wooden plates, and sanded using successively finer sandpaper, until the core was polished up to 600 grid polishing band. We measured the TRW to the nearest 0.001 mm using the LINTAB 6 measuring instrument system (Frank Rinntech Company; Heidelberg, Germany). Tree-ring crossdating was further validated using COFECHA computer software (Holmes, 1983). Cores that failed the crossdating check were excluded from further analysis.

Litter production was evaluated through the analysis of crown defoliation over a 14-year period (2005–2018). The growing season of plants in the Dongling Mountain area starts in May and ends in October each year based on the leaf phenology observation, so the contents of the litter traps were collected at the end of each month from May to October. The litter frames were cleaned at the end of April every year, which were the accumulation of litter from November of the previous year. The monthly contents of the litters were collected and separated into five categories: leaves/needles, branches, fruits/cones, bark, and others (shoots, seeds, insects, and their faeces). These were then dried in an

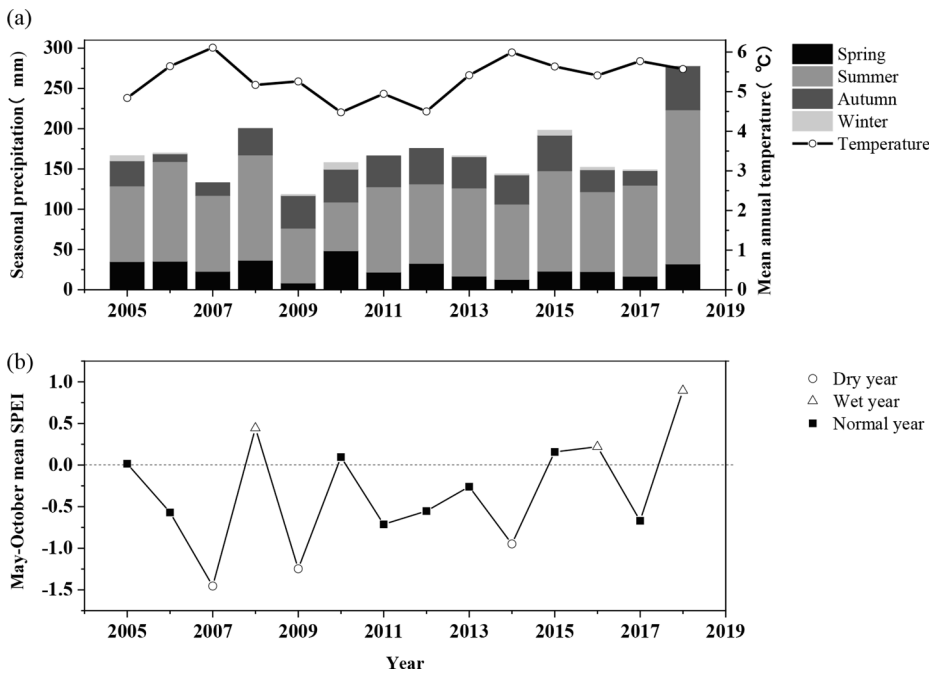


Fig. 2. Seasonal precipitation and annual mean temperature of the study area over the 2005–2018 period (a) and the growing season (May–October) mean Standardized Precipitation–Evapotranspiration Index (SPEI) (b) for the Dongling Mountain. The seasonal precipitation means total precipitation over each of the four seasons defined as spring (March, April and May), summer (June, July and August), autumn (September, October and November) and winter (December, January and February). Open triangles and circles represent the three wettest (2008, 2016, 2018) and driest (2007, 2009, 2014) years used in plant growth comparisons.

oven at 65 °C for approximately 48 h. Finally, the samples were weighed to the nearest 0.01 g separately.

2.3. Development of TRW chronology

In general, detrending on tree-ring series is supposed to remove the age related growth trend as well as short to medium period signals from stand dynamics or canopy-scale variations, in order to manifest the climate signals. We detrended each of the cross-dated raw tree-ring width series by using a cubic spline of 50% frequency–response cut-off at a 30-year window and then subjected the detrended series to an autoregressive model to remove the autocorrelations (Cook et al., 1990). At last, the resultant series were averaged using bi-weight robust mean method (Cook et al., 1990) to obtain two residual tree-ring width chronologies for the two studied tree species, separately. The TRW chronologies were calculated by using the ARSTAN software (Cook, 1985).

To evaluate the quality of the TRW chronologies, several statistics were calculated. Mean sensitivity (MS) and standard deviation (SD) were used as a measure of the variability of TRW chronologies. The strength of common signal of the TRW index were accessed by the mean correlation (Rbar), signal to noise ratio (SNR) and expressed population signal (EPS). These three statistics were calculated over the common period defined for each tree species according to the series lengths. A higher Rbar means higher similarity between TRW index series. The EPS and SNR are indicative of the point at which replication within the chronology is high enough to ensure reliability. An EPS value > 0.85 indicates chronology reliability in dendroclimatic studies (Wigley et al., 1984).

2.4. Meteorological data and growth–climate relationships

Air temperature and precipitation data were obtained from the nearest automatic weather station at the Beijing Forest Ecosystem Research Station of the Chinese Academy of Sciences (39°57'N, 115°25'E; 1150 m a.s.l.), at the edge of the *Quercus liaotungensis* forest. Besides, we calculated standardized precipitation–evapotranspiration index (SPEI) to measure drought severity according to intensity and duration. The SPEI was calculated based on the climate data obtained

from the above weather station by using the SPEI package (Beguería et al., 2014) in R (R program version 3.4.3).

To investigate the tree growth–climate relationships, the residual TRW chronologies were correlated to the climate variables including monthly mean temperatures, monthly mean maximum temperatures, monthly mean minimum temperatures, monthly precipitation and monthly SPEI. The climate data from previous October to current October were used for the analysis, as the climate conditions of the previous year may have effects on tree-ring growth of the current year (Fritts, 1976).

2.5. Comparisons based on extreme years

To further elucidate the sensitivity of TRW and litter productions to the main climate factor (SPEI in this study). Three driest (2007, 2009, 2014) and three wettest years (2008, 2016, 2018) as judged by the SPEI values were selected for comparisons with TRW and litter production in the years from 2005 to 2018 (Fig. 2). Then, we calculated an average TRW for the three dry years and for the three wet years, and further calculated the ratio of the mean TRWs in wet years to dry years (W:D) for each tree (Fekedulegn et al., 2003). We compared W:D between the species using two-tailed T-test. The ratio of leaf and cone litter in wet years to dry years (W:D) was calculated in the same way for comparison between species.

Since detrending may result in loss of growth signal associated with short-term changes in crown status (Drobyshev et al., 2007), raw tree-ring width data were used W:D ratios here and for the following analyses. To avoid the potential bias caused by the internal trends of raw TRW, we checked the raw TRW data series for each core over the period 2005–2018. Fortunately, no clear trends were found in the raw TRW series (Fig. S2).

2.6. Synchronization analyses between TRW and litter

We used the first-order difference of different components of tree growth (TRW, leaf/needle production, and fruit/cone production) in both species to remove first-order autocorrelation and then used the Gleichläufigkeit score (G) as a measure of similarity between TRW and litter productivities (Schweingruber, 1988). The G-scores were

calculated using following equation:

$$\Delta_i = (x_{i+1} - x_i) \quad (1)$$

$$\text{When } \Delta_i > 0 : G_{ix} = +1/2$$

$$\Delta_i = 0 : G_{ix} = 0$$

$$\Delta_i < 0 : G_{ix} = -1/2$$

then

$$G(x, y) = \frac{1}{n-1} \sum_{i=1}^{n-1} |G_{ix} + G_{iy}| \quad (2)$$

where x_i is the TRW/litter in year i ; x_{i+1} is TRW/litter in the following year; G_{ix} is the value added to the G-score reflecting whether TRW/litter is increasing, staying the same, or decreasing in each interval for series x ; G_{iy} is the value added to the G-score for series y ; and n is the number of years being compared.

2.7. Path analysis

Path analysis was used to statistically explore the mechanistic pathways between the climate variables and different components of tree growth. Path analysis (AMOS Graphics) is advantageous as it can indicate the extent to which the predictors are affected by the underlying variables and provide estimates of the relative importance of direct and indirect factors. The initial model was recursively saturated. It evolved into a simplified model when the insignificant paths were deleted and all indexes were fitted within the acceptable range, which indicated that the goodness of fit between the model and the data was reasonably acceptable (Pijnappels et al., 2009). To assess the reliability of the model, we examined several goodness-of-fit indicators, including chi square (χ^2) / degrees of freedom (DF), root mean square error of approximation (RMSEA), standardized root mean residual (SRMR), comparative fit index (CFI), and the adjusted goodness-of-fit index (AGFI). In general, when the $\chi^2/DF < 3$, $P > 0.05$, $RMSEA < 0.08$, $SRMR < 0.05$, $CFI > 0.90$, and $AGFI > 0.90$, the model would be considered to fit the data well (Byrne, 2004).

3. Results

3.1. Climate analysis

Mean annual precipitation during the 2005–2018 period in this study area was 504 mm. The driest years were 2007 and 2009 and the rainiest year was 2018. The season with the highest precipitation was summer, with rainfall exceeding 323 mm. The mean annual temperature of the experimental plots was 5 ± 0.5 °C. The coldest years were 2010 and 2012 and the hottest were 2007 and 2014 (Fig. 2a). Based on the SPEI values, the dry years include 2007, 2009, and 2014, whereas wet years include 2008, 2016, and 2018 (Fig. 2b).

3.2. TRW chronologies and the TRW-climate relationships

At last, 28 and 30 tree cores were successfully crossdated for larch and oak, respectively (Table 1). The mean TRW of larch is 2.01 mm and

Table 1

Statistic characteristics of residual tree-ring width chronologies for the two studied species larch (*Larix principis-rupprechtii*) and oak (*Quercus liaotungensis*) in the Dongling Mountain.

Species	Chronology span	Crossdated/total cores	Mean TRW(mm)	MS	SD	Rbar [#]	SNR [#]	EPS [#]
Larch	1982–2018	28/30	2.01	0.30	0.15	0.52	27.81	0.97
Oak	1933–2018	30/30	1.49	0.30	0.17	0.51	28.06	0.97

Note: Mean sensitivity (MS), standard deviation (SD), mean correlation (Rbar), signal to noise ratio (SNR), expressed population signal (EPS). [#] Common period for larch (*Larix principis-rupprechtii*) is 1990–2018, common period for oak (*Quercus liaotungensis*) is 1960–2018.

oak is 1.49 mm. The residual chronologies length of larch is 37 years (1982–2018) and oak is 86 years (1933–2018) (Fig. 3). The mean inter-series correlation coefficients (Rbar) were larger than 0.5, indicating the common signals of TRW variations were strong. The high EPS values (0.97 for both species) suggested well replication and reliability of the chronologies (Table 1).

The results of the climate-growth relationships showed that the residual TRW chronologies were generally positively correlated to SPEI and precipitation whilst negatively correlated to monthly temperatures, suggesting a moisture limitation on the TRW variations (Fig. 4). Nevertheless, the months with peak correlations showed species-specific patterns. Specifically, significant negative correlations ($P < 0.05$) with the mean temperatures in January and February whilst a significant positive correlation occurred with SPEI in May in the year of tree ring formation were found for larch (Fig. 4a). For oak, significant negative correlations with the monthly temperatures were observed in June and September ($P < 0.05$), whilst a significant positive correlation occurred with SPEI in August (Fig. 4b). Furthermore, the growing-season (May–October) mean SPEI showed well agreement with TRW chronologies for both tree species (larch: $r = 0.32$, $P = 0.1$; oak: $r = 0.4$, $P < 0.05$), particularly in extreme dry/wet years (Fig. S3). Therefore, the sensitivities of TRW and litters to drought stress were presented based on these extreme years in the subsequent analysis.

3.3. Climate sensitivity of TRW and litters

Oak trees had a higher W:D ratio for both total litterfall and TRW than that of larch trees ($P < 0.05$, Fig. 5a). Cone litterfall from oak trees had a higher W:D ratio than leaf litterfall ($P < 0.001$, Fig. 5b); however there was no significant difference of tree growth variables in the W:D ratio in larch. Average TRW of oak in wet years was greater than in dry years ($F = 2.010$, $P < 0.05$; Fig. S4).

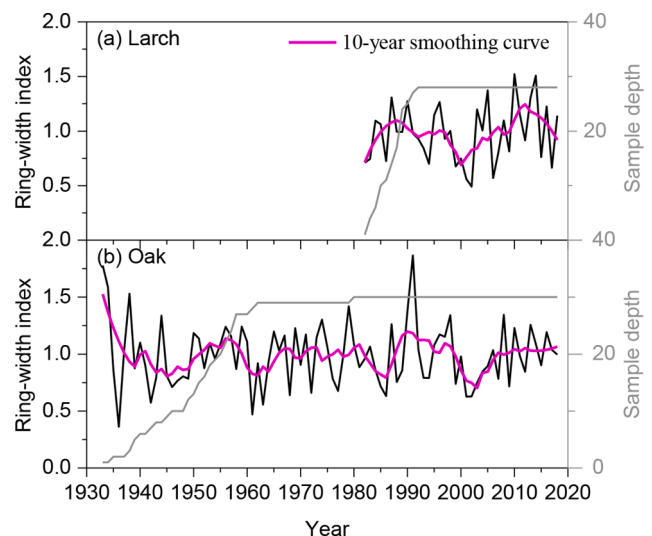


Fig. 3. Tree-ring width chronologies for the two species larch (*Larix principis-rupprechtii*) and oak (*Quercus liaotungensis*) in the Dongling Mountain. The margarita curve is 10-year Savitzky-Golay low-pass filter.

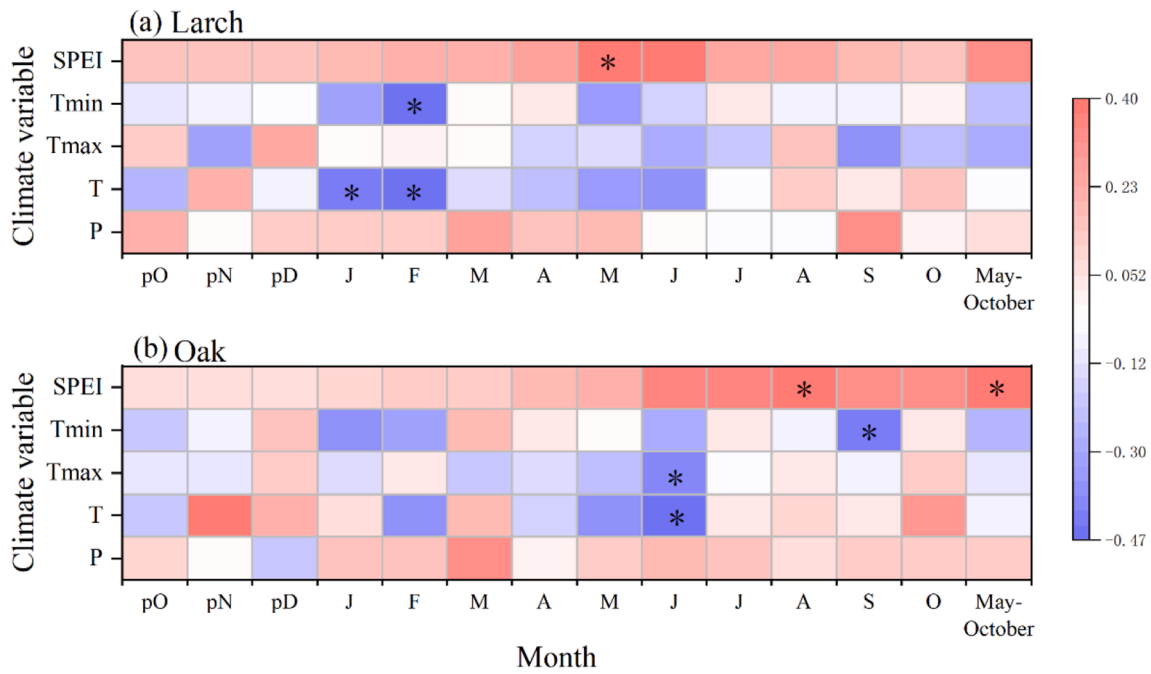


Fig. 4. Correlation coefficients between the tree-ring width chronologies of larch (*Larix principis-rupprechtii*) and oak (*Quercus liaotungensis*) and monthly or growing season (from May to October) climatic factors over the period 1993–2018 in the Dongling Mountain. The prefix “p” of the month indicates previous calendar year. * indicates $p < 0.05$.

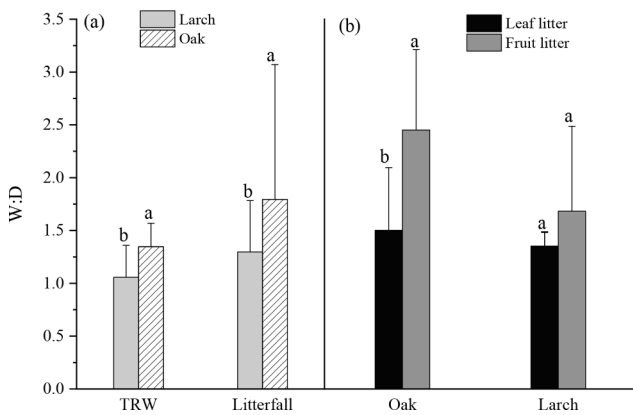


Fig. 5. (a) Mean ratio of tree-ring width (TRW) and total litter from wet years to dry years (W:D) for *Larix principis-rupprechtii* (larch) and *Quercus liaotungensis* (oak). (b) Mean ratio of needle/leaf litter or cone/fruit litter from wet years to dry years (W:D) for larch and oak. Lowercase “a” and “b” letters indicate significant differences ($P < 0.05$).

3.4. Synchrony in different components of tree growth

We observed noticeable year-to-year variation of the first-order difference in canopy dynamics and TRW. For larch, the synchronization of needle litter production and TRW within the same year is 17%, but the synchronization of the previous year’s needle litter production and the congruent year’s TRW is 82% (Fig. 6).

For oak trees, the synchronization of leaf litter production and TRW within the same year is 58%. Fruit litter showed a two-year production cycle (Fig. 6).

3.5. Pathways for climate effects on different components of tree growth

Path analysis was performed in larch to evaluate whether the relationship between SPEI and TRW was mediated by the production of

canopy needles and cones. The goodness-of-fit indicators ($\chi^2/DF = 1.346$, $P = 0.260$, $RMSEA < 0.08$, $SRMR = 0.0452$, $CFI = 0.976$, $AGFI = 0.943$) suggested that the final model fit the data well. The model structure showed that TRW was strongly stimulated by the congruent year’s increasing SPEI and the previous year’s needle production (Fig. 7a). Absolute magnitudes of the standardized total effects were 0.25 and 0.35, respectively, but were not affected by cone production (Fig. 7b).

Path analysis was further conducted in oak to assess the relative contribution of changes in SPEI, canopy leaf production, and fruit production on TRW (Fig. 8a). The goodness-of-fit indicators ($\chi^2/DF = 0.395$, $P = 0.530$, $RMSEA < 0.001$, $SRMR = 0.012$, $CFI = 1.000$, $AGFI = 0.992$) revealed that this model had a good fit. The model showed that TRW was predominantly coupled with the positive effects of SPEI, which also enhanced the growth of leaves and fruit, which in turn affected the growth of the tree-ring (Fig. 8a). The standardized total effects of leaf (0.11) and cone production (0.23) on TRW were 21% and 44% of the effects of SPEI (0.53), respectively (Fig. 8b).

4. Discussion

4.1. Species-specific coupling of foliar litter and TRW

The results of the synchronization test revealed strong and positive coupling between foliar litter production and TRW, which supported our first hypothesis (H1), but with species-specific characteristics within the association pattern. Specifically, we found a one-year lag of TRW after needle production for larch, while no time lag was observed for the oak trees.

For the larch trees, the photosynthesis assimilates reserved the year before a given tree ring formation may have enhanced cell differentiation of xylem, and thus increased TRW (Högberg et al., 2001). Moreover, the assimilate leftover of previous year could also help improve whole-tree hydraulic conductivity in the early stage of tree-ring formation without depletion of newly obtained carbohydrates, particularly at the early part of the growing season, which may ultimately transfer to wider TRW of the year (Eilmann et al., 2009). This time lag between foliar

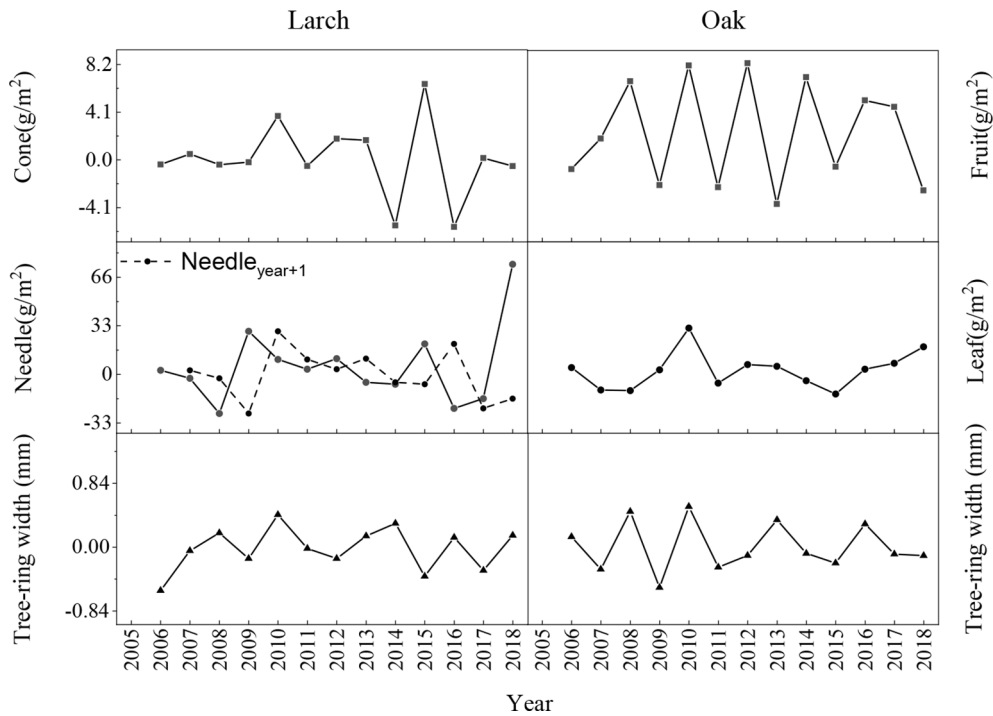


Fig. 6. The first-order difference of tree growth variables for larch (*Larix principis rupprechtii*) and oak (*Quercus liaotungensis*) over the period 2005–2018. Note that tree-ring width showed a one-year lag after needle litter production, so the one-year lagged series (dashed line) of larch needle litter is superposed on for a better visual clarity.

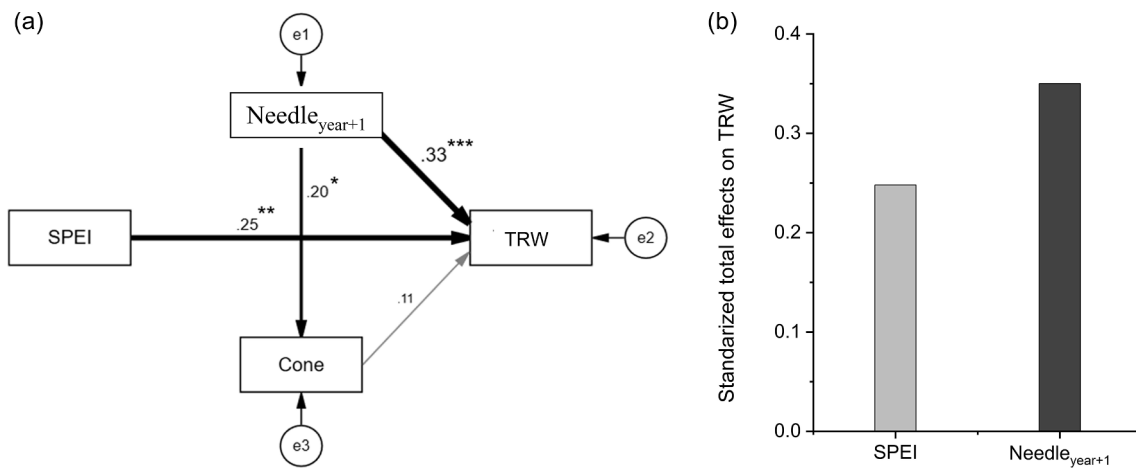


Fig. 7. Final path model of the direct and indirect effects of Standardized Precipitation-Evapotranspiration Index (SPEI) on larch TRW. (a) The path coefficients for larch TRW. Black arrows indicate significant relationships. Grey arrows indicate nonsignificant relationships ($p > 0.05$). The width of the arrow indicates the strength of the relationship. Note that tree-ring width showed a one-year lag after needle litter production, so the one-year lagged larch needle litter was used. Numbers adjacent to arrows are standardized path coefficients and are indicative of the effect size of the relationship. * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p < 0.001$. (b) Standardized total effects of SPEI, needle production, and cone production on larch TRW.

production and TRW was also found in other tree species in previous studies (Maherali and DeLucia, 2000; Sperry, 2003; Eilmann et al., 2009).

For the oak trees, significant synchronization without time lag was found between TRW and leaf litter production, which may be a result of a physiological strategy to adapt to the environment. Formation and transport of resources for the maintenance of the oak stem are strongly dependent on sources (Dickson and Tomlinson, 1996; Nola, 1996) because at least one ring of early wood (EW) vessels is added each spring (Mencuccini et al., 2005). The EW formation is essential for ring-porous trees, like oak, because in the majority older EW vessels tyloses are formed, which block water transport (Kitin and Funada, 2016).

Therefore, the formation of new EW vessels is crucial for survival of ring-porous tree species to regenerate maximal conductivity during spring-time (Ellmore and Ewers, 1985). This is a successful strategy for ring-porous oaks in dry climates (Eckstein, 1974; Eilmann et al., 2009), for the rapid recovery of radial growth after dry years, such as after 2007 and 2009 in this study (Fig. 6). We should acknowledge that higher sensitivity of TRW to drought doesn't mean that oak trees are more prone to drought-related tree mortality, instead, reduction of TRW may help reserve the carbon supposed to be use for structural growth but rather stored as non-structural carbon (NSC) to increase the ability to cope with limitations from seasonal droughts (Jacquet et al., 2014).

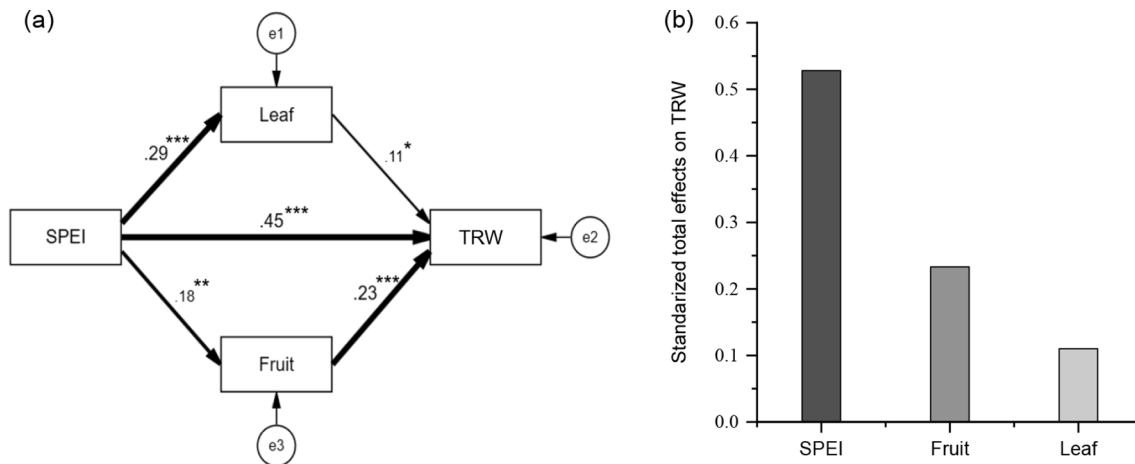


Fig. 8. Final path model of the direct and indirect effects of Standardized Precipitation-Evapotranspiration Index (SPEI) on oak TRW. (a) The path coefficients for oak TRW. Black arrows indicate significant relationships. Grey arrows indicate nonsignificant relationships ($p > 0.05$). The width of the arrow indicates the strength of the relationship. Numbers adjacent to arrows are standardized path coefficients and are indicative of the effect size of the relationship. * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p < 0.001$. (b) Standardized total effects of SPEI, leaf production, and cone production on oak stem annual growth.

4.2. Oak is more sensitive to drought than larch

Analysis of the climate's impact on the radial increment both directly and indirectly revealed the common growth responses of larch and oak to change in climate. There was a strong common positive response of radial increments and foliar production of both larch and oak to the SPEI. Moreover, both oak and larch reduced their growth increments in the dry years, suggesting drought had a similar direct negative effect on growth. During drought, both species could have low growth rate because of either a low availability of stem assimilates (Mencuccini et al., 2005; Forests, 2008), or of shortened growing season (Bartlett et al., 2012; Peters et al., 2021) or changes in hormone concentrations, such as decreased auxins, gibberellins and cytokinin while increased abscisic acid and ethylene (Farooq et al., 2009).

Further, the W:D ratio of both TRW and total litterfall showed that oak was more responsive to drought (higher W:D value) than larch, possibly due to the direct link between TRW and crown variation, as found in the path analysis. For oak trees, cone litterfall had a higher W:D ratio than leaf litterfall or TRW which is supported by the results of other studies at the physiological level. For example, precipitation preceding acorn maturation was positively related to seed production (Bogdziewicz et al., 2017) and drought can be the main constrain affecting acorn production (Fernández-Martínez et al., 2012).

The first-order difference of the oak TRW series showed significantly decreased in response to drought in 2007 and 2009, but only a moderate reduction in 2014. Drought stress can reduce fruit production directly due to water deficiency and high temperature, which can increase pollen abortion and pollination failure (Hedhly et al., 2009; Zinn et al., 2010; Bykova et al., 2018). However, if the drought does not occur during the induction of buds or flowering years, e.g. 2007 and 2009 in our study, it may not affect the fruit yield (Cremer, 1992; Mutke et al., 2005), but affects TRW instead. Moreover, reproductive allocation is another process that affects TRW (Viñá-Cabrera et al., 2014), e.g. 2014 in our study. However, the climate exerts dominant control.

4.3. Climate and resource allocation together affect TRW

Interannual variation in larch TRW can be adequately explained by a framework of direct climate effects and previous-year crown needle production; this is also the main factor driving interannual variation in TRW according to our path analysis. The one-year time lag between needle production and TRW indirectly affected and can explain the climate-growth relationship which showed "a lagged climate effect" and

explained by a general explanation that the depletion of internal carbohydrate reserves may reduce growth the following year (Skomarkova et al., 2006). The asynchronous time change of crown needle production may be a strategy for nutrient storage for radial growth (Sala et al., 2012), which allows for a more efficient water conducting system that requires a lower investment of carbon under drought conditions (Sperry, 2003).

In oak trees, TRW variations can be explained by both the direct effects of climate and the indirect effects of crown leaf and fruit production (driven by the climate) in the same year. We found a positive response in radial increments of oak to leaf and fruit production, which implies that a change in crown condition is positively related to the ability of the tree to accumulate biomass in the main stem. Several previous studies have confirmed the positive relationship between crown condition and TRW (Dwyer et al., 1995; Eckmüller and Sterba, 2000; Forests, 2008). Cumulative increment increased significantly for trees with healthy crowns, while oaks with defoliation above 60% appeared to reach a threshold in their ability to recover growth (Drobyshev et al., 2007).

Trees may show differential allocation strategies and face trade-offs (negative correlation) between reproduction and growth. In our study, conflicts between these functions were not observed, which contradicted our second hypothesis (H2), suggesting that different components of tree growth are consistently governed by changes in climate. Similar results were also reported by previous studies (Cremer, 1992; Martínez-Alonso et al., 2007). But the strength and even the direction of these associations between TRW and cone/fruit litters observed might change across time or environmental gradients. Here, we want to note that the tree size of the studied trees, particular in larch, was generally small (Fig. S1). As tree size continues to increase, the efficiency of the investment of reproductive output may decrease because a larger size normally incurs a higher cost for maintenance and transport of resources (Mencuccini et al., 2005). Therefore, increased frequency and severity of periods of dry climate, in the long run, may result in limited supply of assimilated carbohydrates, ultimately leading to altered associations between growth and reproduction. Given the associations between different components of tree growth may unstable in time and exhibit species-specific patterns, more endeavours are needed in future studies on the dynamics of forest ecosystems.

5. Conclusions

In this study, we synthesized a unique dataset composing of TRW

data and 14-year field observations of litter productions of *Larix principis-rupprechtii* and *Quercus liaotungensis* at a monthly resolution from two permanent forest plots at a long-term field monitoring base in a warm temperate mixed forest in northern China. We analysed the growth-climate relationships and then investigated the coupling relationships between crown needle/leaf production and TRW for the two tree species. We found that the coupling characteristics between different processes of tree growth were species-specific. For larch trees, the effects of canopy needle production on TRW showed a 1-year lag. In contrast, the leaves and fruits of oaks indirectly affected the stem-climate relationship without a time lag. Furthermore, the sensitivity of oak TRW to drought was stronger than that of larch trees, possibly due to the direct link to variation in leaf biomass. These results demonstrate the holism of the growth of crown, stem and reproductive investments. More similar studies are needed for more tree species in wider environmental domain as our results showed clearly species-specific patterns of the associations between different targets of carbon allocation. Assuming higher intensity and longer duration of drought in the future, the incorporation of coupling characteristics between species-specific processes of foliar development, TRW, and reproductive growth in tree growth models will improve the reliability of predictions on future changes of forest ecosystems.

6. Author statement

W.Z. and L.L. conceived the research, W.Z. performed the statistical analyses, W.Z., J.X. and Y.W. collected TRW samples and litters, W.Z. and L.L. wrote the paper. All authors contributed to the interpretation of the results. All authors have read and agreed to the revised version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119831>.

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