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Reduced diurnal temperature range mitigates drought impacts on larch tree growth in North China

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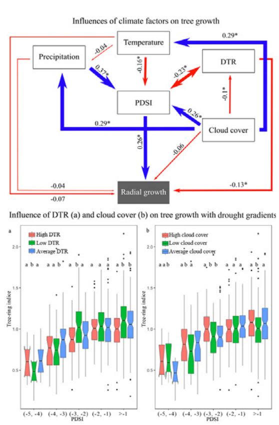
HIGHLIGHTS

- The diurnal temperature range had negative influences on larch tree growth.
- Cloud cover had positive correlation with larch tree growth.
- Reduced diurnal temperature range benefits tree growth during the absence of severe drought.

GRAPHICAL ABSTRACT



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ABSTRACT

干旱与影响之间的联系

Forests are facing climate changes such as warmer temperatures, accelerated snowmelt, increased drought, as well as changing diurnal temperature ranges (DTR) and cloud cover regimes. How tree growth is influenced by the changes in daily to monthly temperatures and its associations with droughts has been extensively investigated, however, few studies have focused on how changes in sub-daily temperatures i.e., DTR, influence tree growth during drought events. Here, we used a network of *Larix principis-rupprechtii* tree-ring data from 1989 to 2018, covering most of the distribution of planted larch across North China, to investigate how DTR, cloud cover and their interactions influence the relationship between drought stress and tree growth. DTR showed a negative correlation with larch growth in 95 % of sites ($r_{mean} = -0.30$, significant in 42 % of sites). Cloud cover was positively correlated with growth in 87 % of sites ($r_{mean} = 0.13$, significant in 5 % of sites). Enhanced tree growth was found at lower DTR in the absence of severe drought. Our findings highlight that in the absence of severe droughts, reduced DTR benefits tree growth, while

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increased cloud cover tended to benefit tree growth only during severe drought periods. Given how DTR influences drought impacts on tree growth, net tree growth was found to be larger in regions with smaller DTR.

1. Introduction

Rising temperatures exacerbate drought stress, causing high risk of growth cessation and decreased tree growth (D'Orangeville et al., 2018; Zhang et al., 2021a; Zhang et al., 2021b). Increasing drought frequency and severity have been shown to cause reduced tree growth and fuel forest die-off (Allen et al., 2015; Allen et al., 2010; McDowell and Allen, 2015), leading to decreased carbon sinks in key forest ecosystems (Ma et al., 2012; Phillips et al., 2010; Zhao and Running, 2010). Drought-induced vascular damage and hydraulic failure through xylem cavitation explains high growth reduction and tree mortality during drought events (Anderegg et al., 2018; Anderegg et al., 2020; Greenwood et al., 2017). Increasingly hot drought events pose high risks of tree growth reduction globally and haves consequently received great attention. However, few studies have investigated how sub-daily changes in temperature, a key small-scale component of rising temperatures, influence the effects of drought on tree growth (McDowell and Allen, 2015).

Forests are being planted across large areas of North China to combat desertification, air pollution and climate change (Zhang et al., 2016). Larch trees are widely used in these afforestation programs. However, planted forests seem to be less resistant to drought stress than natural forests (Domec et al., 2015; Payn et al., 2015; Zhang et al., 2021a), exacerbating the threat posed by the projected increase in drought conditions in the future (Naumann et al., 2018). Tree growth of planted larch nearly ceased under recent extreme drought in North China (Zhang et al., 2021a). However, larch forests have also showed a high capacity for recovery after chronic extreme drought events (Zhang et al., 2021a), and substantial tree mortality has not been found in these sample sites, suggesting that larch trees' responses to drought are complex and influenced by interactions between multiple environmental factors.

Temperature, precipitation, and relative humidity are the main factors assumed to determine tree growth in our study region and have been investigated in the past (e.g. Jiang et al., 2015; Zhang et al., 2021a). However, other less studied factors, such as snowmelt, growing season length, and diurnal temperature range, have also been shown to influence tree growth directly or indirectly (Cox et al., 2020; Zhang et al., 2021a). For example, earlier onset of the growing season allows trees to take advantage of snowmelt, a particularly important water source for tree growth in the early growing season, and indirectly influencing tree growth in Northeast China (Zhang et al., 2019). Understanding complex non-linear relationship between these environmental variables and tree growth is crucial to understand and forecast the potential consequences of a changing climate (Björklund et al., 2019; Peltier and Ogle, 2020; Wilmking et al., 2020; Zhang et al., 2019).

Trees predominantly grow at night, but photosynthesize and transpire during the day, suggesting that diurnal temperature ranges (DTR) and atmospheric water demand (e.g. Vapor Pressure Deficit) are crucial to determine stress and growth responses (Zweifel et al., 2021). Reduced DTR have been observed in large parts of Northern Hemisphere as nighttime temperatures have increased faster than daytime temperatures (Cox et al., 2020; Davy et al., 2017; Vose et al., 2005). Daytime warming can reduce tree growth (Tao et al., 2022), yet consequences for the influence of nighttime warming on tree growth remain uncertain. Increased cloud cover may also reduce DTR (Dai et al., 1997; Sun et al., 2000). Greater night-time than daytime warming, associated with wetter climate, has been shown to be beneficial to plant growth (Cox et al., 2020). Indeed, daytime and night-time warming have been shown to have asymmetric effects on vegetation growth (Peng et al., 2013; Zhu et al., 2020). However, how changes in DTR interact with drought stress to influence tree growth is still poorly known.

Here, we used a tree-ring network from 38 larch plantations spanning from 1989 to 2018 that cover most of the species' distribution in North China to investigate how the interactions between rarely considered environmental factors influence tree growth. We focus on factors with complex interactive effects on tree growth, in particular the interactions of cloud cover, DTR and drought. We tested the hypotheses that (1) reduced DTR alleviate drought stress on tree growth in the absence of severe drought, and (2) increased cloud cover has a beneficial effect on tree growth during severe drought years.

2. Materials and methods

2.1. Study area

Large parts of North China's natural forests have been damaged by human activities, and *Larix principis-rupprechtii* Mayr (abbreviated as larch hereafter) was widely planted in monospecific forests along regular grids to reforest our study region (36°N–43°N, 110°E–120°E, Fig. 1). Although exact planting dates are unfortunately not available for these plantations, most larch trees seem to have been planted at least 25 to 40 years ago (Table S1), with the exception of one site (Wuxiang, CWL), where we found trees younger than 20 years. Larch mainly grows at middle and high elevations (1200–2200 m a.s.l.; Fig. 1), where temperature is lower than at lower elevations. The sample sites were selected to minimize the human influences (i.e., no active management).

The study region has hot wet summers and cold dry winters. The mean annual temperature is 6–13 °C, while the total precipitation is about 380–560 mm. January mean temperatures can be as low as −15 °C, while July mean temperature can reach 27 °C. Most (60–80 %) of the annual precipitation falls between June and August. The study region extends from sub-arid to sub-humid regions, with the northern and mid-eastern parts being more xeric and the southern and northeast parts more mesic.

2.2. Sampling network and ring width measurements

Tree cores from 38 sites were collected throughout the region, mainly in mountain regions (Fig. 1). There were 31 sites that had been used in previous studies to detect the influences of droughts on larch tree growth (Fig. 1; Zhang et al., 2021a). However, how DTR mitigate drought influences on tree growth was not investigated in previous work. To expand the scale of our network, seven new sites in the eastern parts were added to form a larger network that covers most larch plantations in North China. At each site, 20 to 34 living larch trees were chosen randomly and two dendrochronological samples were taken at breast height (1.3 m) using a standard increment borer (5.15 mm diameter, Haglöf, Sweden). In total, 1975 cores from 1000 trees were collected (Table S1). Tree cores were dried, stabilized to wood sticks, and then sanded until ring boundaries and wood structure were clearly visible to ensure the quality of ring measurement. Cores were visually cross-dated, and then measured to the nearest 0.01 mm using the LINTAB 6 measuring system (Rinntech Heidelberg, Germany). The accuracy of the dating and measurements was verified using the program COFECHA (Holmes, 1983).

Each tree ring width series was detrended to develop a site-level chronology using a Friedman curve with alpha = 5 to remove the influence of tree age, competition, and topography (Friedman, 1984). Site chronologies were developed using the program ARSTAN (Cook and Holmes, 1986). The low-frequency growth trend of each tree was removed and high-frequency signals were kept (Fig. S1). In total, 38 tree-ring width chronologies were developed. The subsample signal strength (SSS, Wigley et al., 1984) was above 0.85 after the year 1987 for most sites (Table S1).

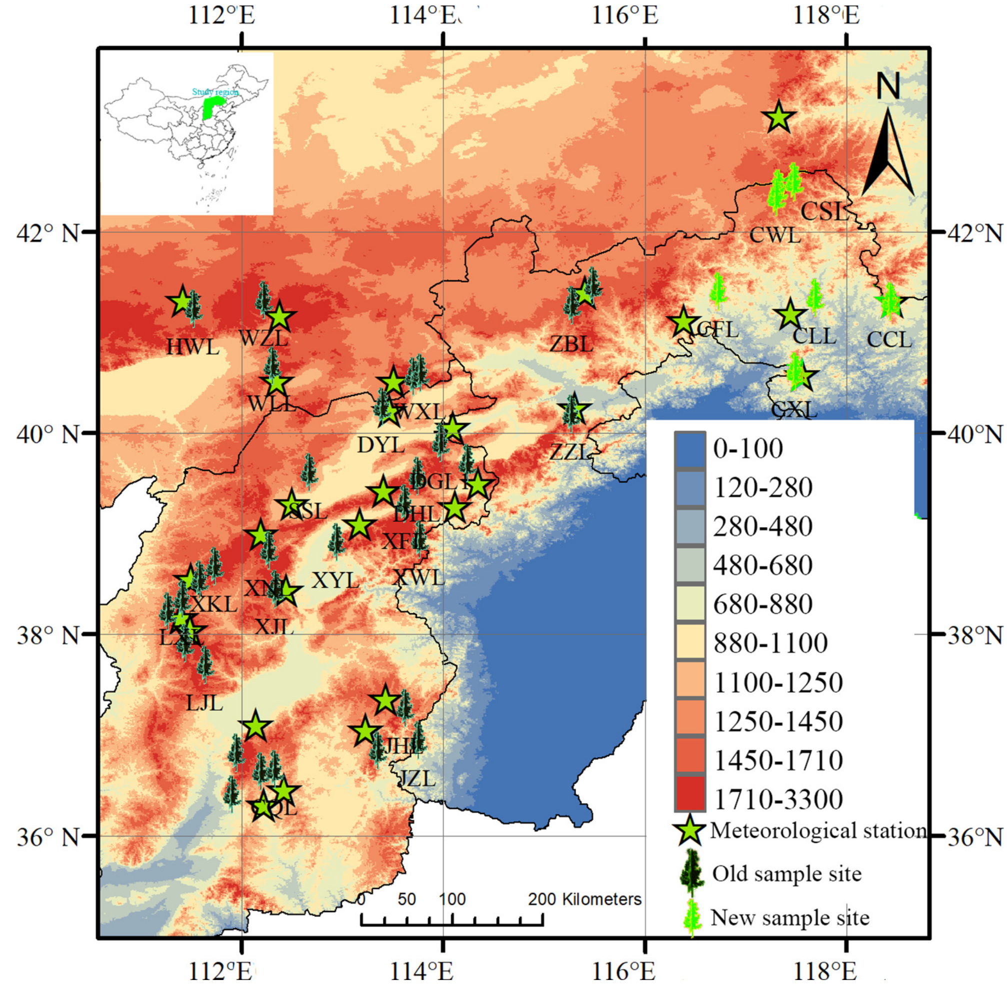

Fig. 1. Topographical map of our sampling network, including 38 sampling sites and their nearest meteorological stations. The seven newly added sites (grouped as CWL, CFL, CLL, CCL, CXL, CSL) are highlighted with bright green tree symbols. For further site information see Table S1.

2.3. Climatic data

We obtained climate data (daily values of minimum, maximum, and mean temperature, monthly total precipitation, snow depth, and maximum wind speed) from the nearest meteorological station to each sampling site, from the China meteorological administration (http://data.cma.cn). We selected climate data from within the same climate zone of a sample site to avoid selection bias (Zhang et al., 2021c). In total, we used climate records from 38 meteorological stations, spanning from 1989 to 2018. Consequently, a maximal common period from 1989 to 2018 was used for analysis.

The Self-calibrating Palmer Drought Severity Index (PDSI) was used as drought metric, as PDSI is a widely used index in investigations of tree growth-climate relationships. PDSI was calculated based on the monthly temperature and precipitation using the method of (Thornthwaite, 1948) as implemented in the R package 'scPDSI' (Zhong et al., 2018) for the common period 1989–2018. Cloud cover data with a resolution of 0.5° × 0.5° was retrieved from the CRU TS4.01 dataset (http://badc.nerc.ac.uk/data/cru/). Daily diurnal temperature range (DTR) was calculated as the difference between maximum and minimum daily temperatures. The monthly DTR refers to the mean of daily DTR for each month.

2.4. Data analysis

We calculated the Pearson correlation between site chronologies and monthly climate variables (temperature, precipitation, DTR, PDSI, could cover, wind speed, and snow depth) from previous October to current

相对重要性的定量

September, as well as seasonally averaged climatic variables to detect the influences of climate on tree growth for the common period 1989–2018. The relationship between site averaged DTR and drought-growth correlation was detected using linear regression. A linear mixed model was used to assess the relative importance of different variables on tree growth. DTR, PDSI, temperature, precipitation and the interaction 'DTR × PDSI' were selected as fixed effect variables, and the year was integrated as a random factor. The model was fit with the R package 'lme4' (Bates et al., 2015).

The interaction effects of multiple seasonal climate variables on tree growth were investigated using structural equation model (SEM). SEM models were used to explore the interactions between multiple climate variables influencing tree growth, including the less studied variables of snow cover, wind speed, cloud cover and DTR, which substantially influenced tree growth. Direct and indirect contributions of different climate variables on tree growth can be detected using SEM. Due to sample size limitations, we focused on current year climate variables only in our SEM modelling approach, meaning no lagged effects were considered. Models with different interactions were tested and the final model with the best fitness indices was used ($\chi 2$, p-value, Normed Fit Index (NFI), Comparative Fit Index (CFI), and root mean square error of approximation (RMSEA), with NFI > 0.9, CFI > 0.9, p > 0.05 and, lower $\chi 2$ and RMSEA indicate satisfactory fit). The SEM was fitted over merged data from all sites. SEM considered the interactions between different variables, while correlation analysis only considers the relationship between two variables.

Extreme events of cloud cover and DTR were identified as those with values more than one standard deviation away from the mean. Tree growth under high DTR and/or cloud cover was compared to tree growth under low DTR and/or cloud cover for similar drought levels (based on PDSI) to investigate whether DTR and cloud cover can alleviate drought stress. Analysis of variance (ANOVA) with Dunnett's multiple comparisons test was used to compare the tree growth under different DTR/cloud cover for the same drought stress.

Finally, a commonality analysis was used to partition the explained variance in our models between unique and common effects of PDSI, DTR, temperature and precipitation in explaining the variation of tree growth (Ray-Mukherjee et al., 2014). The model decomposes explained variance into unique and common variance components of every predictor based on a regression function, separating the marginal effect of a single predictor, from those explained by the interactions between two or more predictors. The commonality analysis was conducted separately for drought (PDSI > −3) and extreme drought (PDSI < −3) conditions. The commonality analysis was performed using R package 'yhat' (Nimon and Oswald, 2013).

3. Results

3.1. Climate-growth correlation

The analyses of correlation with single climate variables showed that all seven factors influenced tree growth (Fig. 2). Monthly mean temperature negatively influenced larch tree growth in 36 out of 38 sites. Significant correlations between summer (June–August) mean temperatures and tree growth were found in 7 sites ($p < 0.05$). Summer precipitation had positive correlations with tree growth in 29 out of 38 sites. Compared to temperature and precipitation, tree growth was even more strongly related to Summer PDSI. Summer PDSI had a significantly positive correlation with tree growth in 15 sites ($p < 0.05$). Snow depth was the least consistent environmental factor, as it had a negative influence on tree growth in 17 sites but a positive one in 19 sites. However, tree growth was significantly influenced by snow depth in only two sites ($p < 0.05$). May–July DTR had a nearly universal (36 out of 38 sites) negative influence on tree

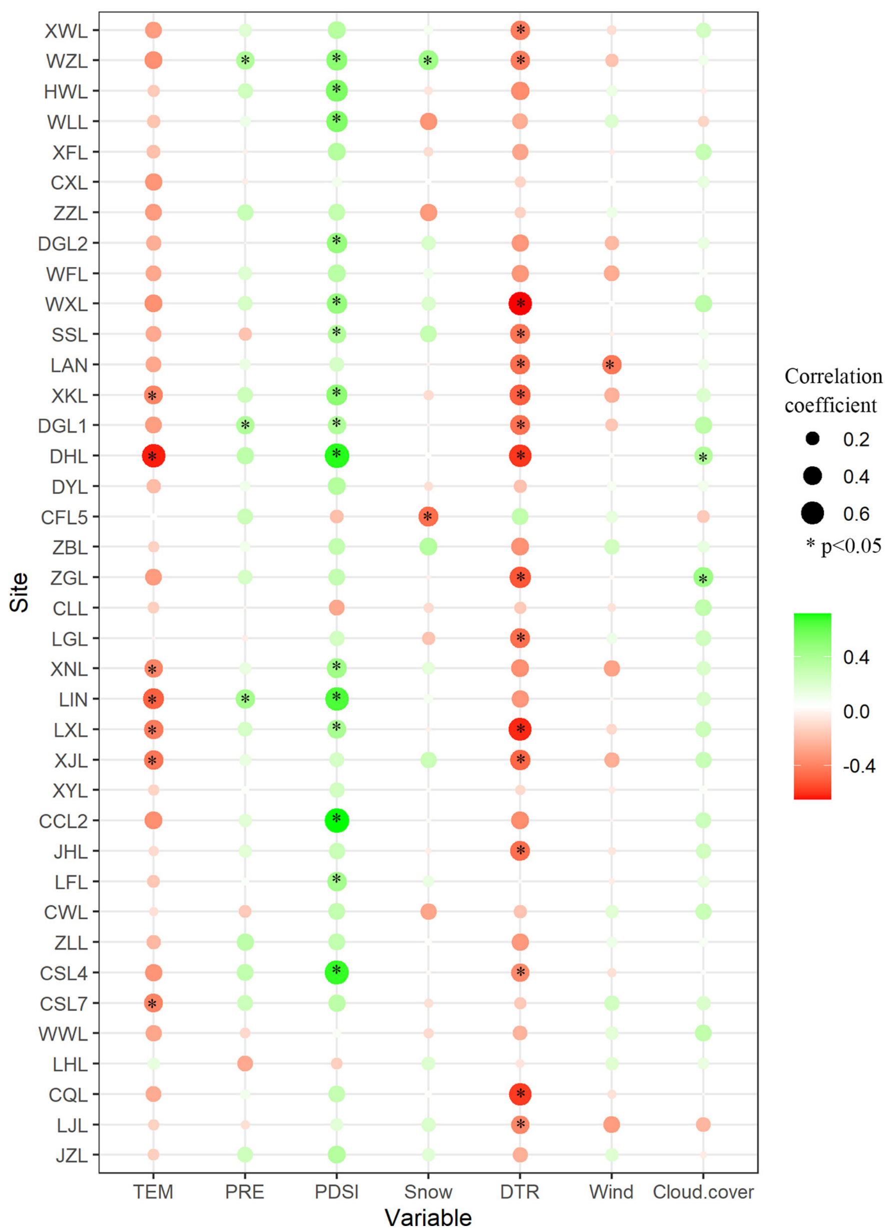

Fig. 2. Correlation between seasonal climate and site chronologies. Seasonal climate was averaged over June–August for TEM: temperature, PRE: precipitation, PDSI, Cloud cover, and May–July for DTR and wind. The sites are arranged from driest (top) to wettest (bottom.)

growth, though this relationship was significant only in 16 sites ($p < 0.05$). Tree growth was positively correlated with maximum wind speed in 18 sites while negative correlations between tree growth and maximum wind speed were observed in other 20 sites. Summer cloud cover had a positive influence on tree growth in 33 sites, but the relationship was only significant in two sites ($p < 0.05$). Hence, all of these seven climate factors can independently influence tree growth.

3.2. Interactions of climate factors and their relationship with tree growth

The results from the linear mixed model showed that the interactions of PDSI and DTR had a significant influence on tree growth (Table S2). Low DTR was beneficial to tree growth under low PDSI. Equally, strong interactions between the seven climate factors with tree growth were revealed by the SEM model (Fig. 3). Both precipitation and cloud cover had a positive influence on PDSI, implying that high precipitation and cloud cover reduce the drought effect. Temperature and DTR negatively influenced PDSI, suggesting that reduced DTR may alleviate drought stress. Cloud cover was negatively correlated with DTR but positively correlated with temperature and precipitation. Temperature, precipitation, and cloud cover did not significantly influence tree growth directly. Among all the climate variables, PDSI had the most significant influence on tree growth, but DTR also had detectable influence on tree growth ($p < 0.05$).

The commonality analysis revealed that the predictors PDSI, DTR, and temperature together explained 81.88 % of the variance in tree growth (Fig. 4, Table S3). The unique effects of PDSI, DTR and temperature on tree growth accounted for 46.00 %, 13.19 %, and 3.13 %, respectively. The common effect of DTR and PDSI explained another 11.42 % of the variance in tree growth. The combined contribution of PDSI and temperature explained 7.51 % of the variance in tree growth. Clearly, PDSI and DTR were the main factors to influence tree growth as per commonality analysis.

The unique effect of DTR and common effect of DTR and PDSI had stronger influence on tree growth under milder drought conditions (Fig. S2), whereas PDSI was highly correlated with tree growth during extreme drought conditions. In contrast, DTR by itself had no unique influence on tree growth during extreme drought. Therefore, we conclude that DTR mitigates the drought influence on tree growth only under milder drought conditions.

Cloud cover had lower unique effect to tree growth in drought conditions (PDSI > -3), whereas interactions of PDSI and cloud cover had weak effects on tree growth during extreme drought conditions. Cloud cover had high unique influences on tree growth, but weak interaction with PDSI to tree growth during extreme drought.

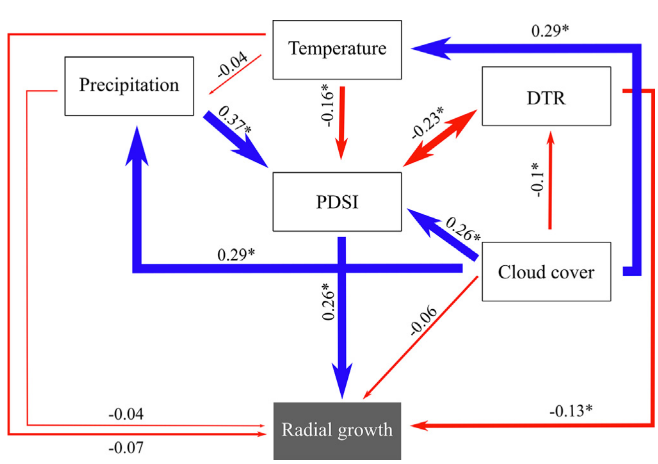

Fig. 3. SEM model linking environmental variables to radial growth. Positive relationships are marked as blue arrows, while negative ones are shown as red arrows. Path coefficients and line width indicate the relative strength of the relationship. Coefficients marked with stars illustrate significance ($p < 0.05$). $\chi 2 = 2.224$, p-value $= 0.329$, CFI $= 1$, RMSEA $= 0.01$.

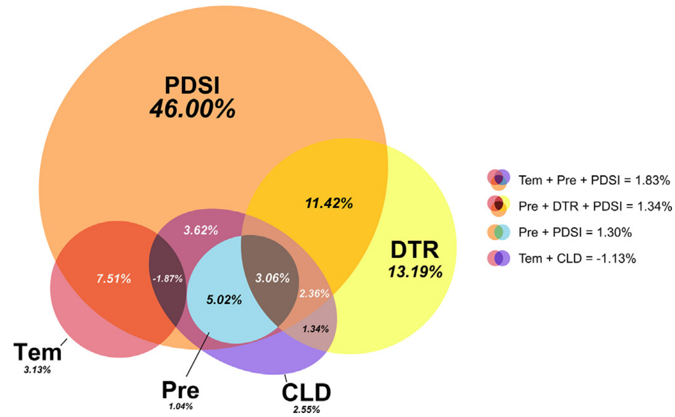

Fig. 4. Variance partition by commonality analysis of tree growth explained by predictors and their interactions (Tem: temperature, DTR: diurnal temperature range, Pre: precipitation, CLD: cloud cover). Only interactive relationships with explained variance larger than 1 % are displayed (see full table in Supplementary Table.S2). Values displayed indicated size of unique values (e.g. 46 % indicates the variance explained by PDSI alone). Note that some overlaps were not possible to represent graphically and are shown aside.

3.3. Influence of DTR and cloud cover on tree growth

DTR showed significant decreasing trends over time in 32 sites (slope $= -0.01$ °C/year, $p < 0.05$, Fig. S3). Tree growth benefitted more from decreasing DTR in those sites where tree growth was less affected by summer drought than in those where tree growth was highly restricted by summer drought (Fig. 5). On the other hand, increasing DTR benefited tree growth in sites where tree growth was highly restricted by summer droughts.

Trees grew faster under lower average DTR in the absence of severe droughts (PDSI > -1). Lower DTR seemed to be more beneficial to tree growth when PDSI was higher ($-3 <$ PDSI < -2, Fig. 6a), while the beneficial effect of higher cloud cover on tree growth was only found during severe droughts ($-4 <$ PDSI < -2, Fig. 6b). Tree growth increased by 6 %–12 % under high cloud cover conditions when compared with low could cover conditions during drought.

Tree growth was significantly correlated with PDSI ($p < 0.05$) under large DTR (DTR $>$ mean $+$ standard error of the mean), while PDSI had a week relationship with tree growth under small DTR (DTR $<$ mean-standard error of the mean, Fig. S4). The strong correlation between PDSI and tree growth faded with decreasing DTR. The influence of PDSI on tree growth was weaker when average cloud cover was high than when it was low.

4. Discussion

Tree growth is influenced by complex interactions including shifts in temperature and available moisture (Björklund et al., 2019; Peltier and Ogle, 2020; Wilmking et al., 2020; Zhang et al., 2019). While the relevance of interactions between temperature, precipitation and droughts on larch tree growth has been previously investigated (Zhang et al., 2021a), the effect of interactions between DTR, temperature, cloud cover, and droughts on larch growth remained unexplored. Here, we show a strong direct and indirect influence of DTR and cloud cover, as well as their interactions, on larch growth. Given the decreasing trends of DTR across most sites (Fig. S2), we suggest DTR could become increasingly important factors for tree growth in the future.

It should be noted that low DTR did not seem to benefit tree growth under extreme drought conditions (PDSI < -3) as tree growth remained highly restricted. Drought-induced water stress can cause the loss of hydraulic conductivity from vascular damage (Anderegg et al., 2015;

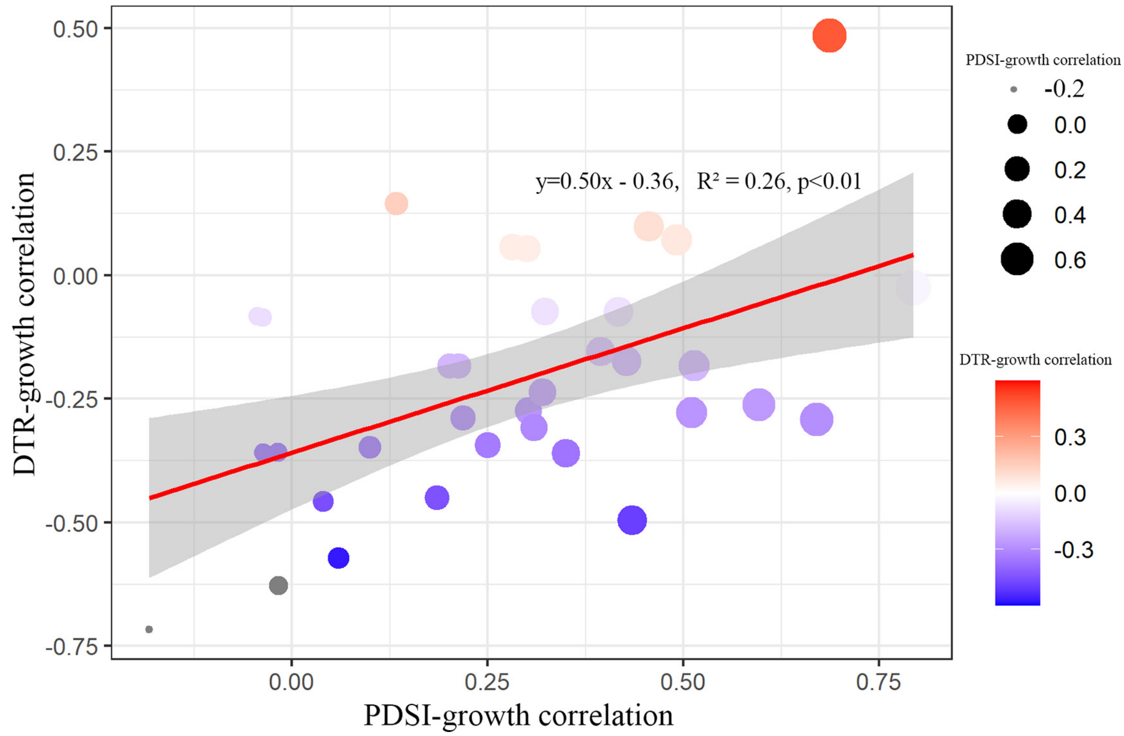

Fig. 5. Relationship between DTR-growth correlation and PDSI-growth correlation.

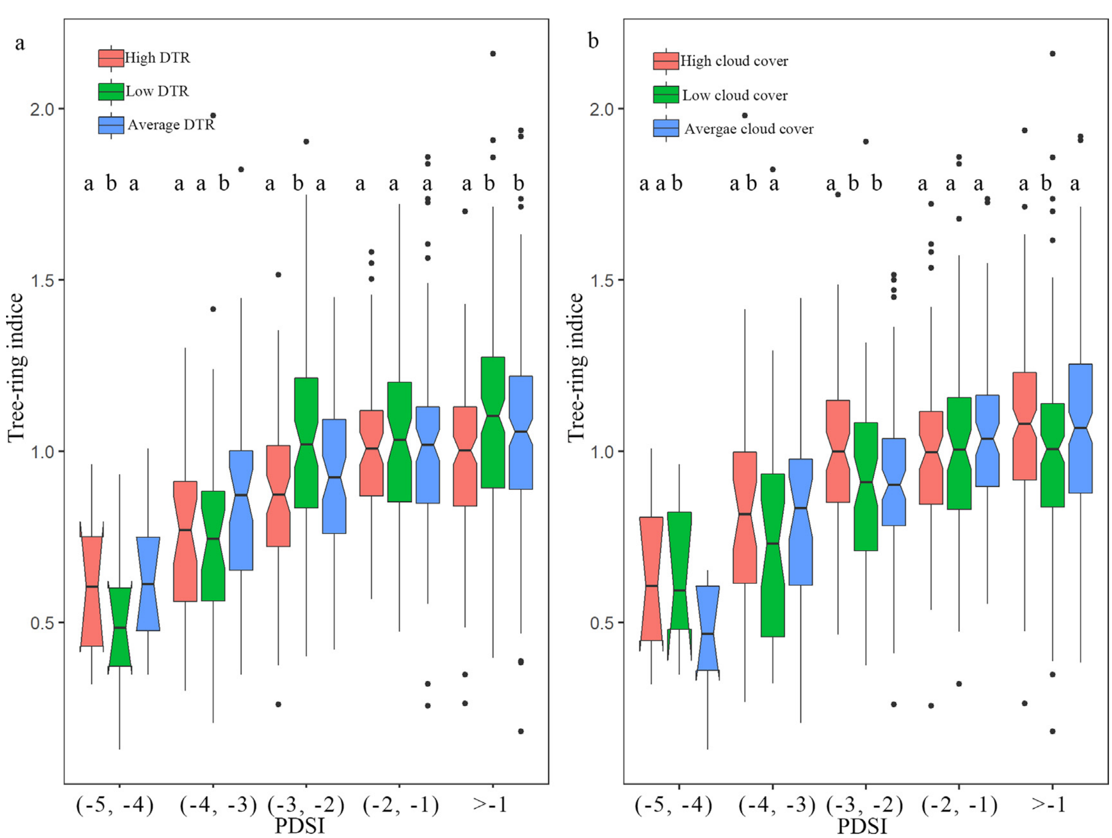

Fig. 6. Variation of tree growth with different DTR (a) and cloud cover (b) at the same drought level (e.g., PDSI bins). High/Average/Low were defined as the DTR/could cover higher, between, and lower than the mean ± one standard deviation. ANOVA with Dunnett's multiple comparisons test was used to compare the tree growth under different DTR/could cover for the same drought level.

Hammond et al., 2019). Severe xylem damage occurs when soil water deficit increased xylem water tension (Brodribb et al., 2020). Low growth by severe drought does not appear to be prevented by low DTR. On the other hand, as photosynthesis happens during the day and could be affected negatively by drought, leaf carbohydrates synthesis could also be restricted by water availability (Adams et al., 2013; O'Brien et al., 2014), leading to lack of carbohydrates for enhanced autotrophic respiration during warmer nights. Given the strong correlations of growth with drought in these ecosystems (also highlighted by the central role of PDSI in our models), warmer maximum temperatures are likely to become an increasingly limiting factor for tree growth in these ecosystems, via increase in vapor pressure deficient and heat stress during key growth periods.

Larch tree growth has been found to be primarily limited by drought throughout the study region (Zhang et al., 2021a). Increasing temperature and drought frequency had been hypothesized to lead to higher risk of tree growth reduction, in particular in the arid parts of our study region (Zhang et al., 2021a). However, decreasing DTR in the areas could alleviate these growth reductions in most of our sites (Fig. S5). Reduced DTR benefited tree growth under mild drought conditions, but not under extreme drought conditions (PDSI > -3). Over the study region, reduced DTR was mainly caused by faster increases of nighttime temperatures than daytime temperatures. Tree radial growth happens mostly at night, and is highly restricted by the level of air dryness (Zweifel et al., 2021). Under mild drought conditions, trees presumably synthesized enough carbohydrates for growth during daytime, while warmer nights allowed trees to maintain higher metabolic rates and thus trees have enough energy and resources to promote tree growth, as long as water status allows sufficient turgor. Higher leaf respiration in preceding warmer night has been argued to induce higher photosynthesis rates the following day (Griffin et al., 2002; Turnbull et al., 2002; Whitehead et al., 2004). There tends to be enough carbon gain (photosynthesis during the day) even during relatively cold days, while warmer nights increase carbon consumption (growth and respiration during the night), thus night-time warming enhances ecosystem carbon-use efficiency (Wang et al., 2020).

In contrast to the influences of DTR on tree growth, cloud cover benefited tree growth only during severe drought condition. High cloud cover can dampen daytime temperatures and decrease evapotranspiration (Cox et al., 2020). Since tree growth occurs mostly at night, high nighttime cloud cover is likely associated with high nighttime air moisture, which has been shown to be beneficial to tree growth (Zweifel et al., 2021). This could explain why high cloud cover can be beneficial to the growth of larch trees only under severe drought conditions ($-4 <$ PDSI < -3). However, high cloud cover also influences leaf photosynthesis during the daytime, consequently it is not surprising that we did not find a positive correlation between tree growth and cloud cover under normal conditions.

Many environmental variables are likely to change simultaneously in the context of climate change. These changes cause complex interactions between different climate factors, which will jointly affect tree growth. Drought events caused great growth reduction in our study region, however, there is no large area forest dieback to-date (Jiang et al., 2015; Zhang et al., 2021a). The changes in DTR seem to mitigate drought effects on larch growth and may be one reason why the larch trees manage to recover relatively well from chronic extreme droughts. Our findings highlight the importance of reduced DTR in predicting tree growth in the future.

5. Conclusion

Our study shows the importance of considering DTR as potential modifiers of the effect of drought on tree growth. We found that while drought had a strong influence on larch tree growth, DTR could mitigate drought stress under certain conditions. In the absence of severe droughts, low DTR seemed to reduce tree drought stress. By contrast, high cloud cover seemed to be beneficial to tree growth only during severe drought events. Our findings highlight that changing importance of reduced DTR to tree growth depending on drought conditions, and suggest that reduced DTR may help alleviate rising drought stress in many larch plantations across North China.

CRediT authorship contribution statement

Xiangliang Zhang: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft; **Xuanrui Huang** and **Xianliang Zhang**: Funding acquisition, Project administration; **Pengcheng Lv**, **Chen Xu**, and **Meiting Hou**: Resources, Data curation. **Tim Rademacher**, **Rubén D. Manzanedo**: Validation, Writing - Review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that no conflict of interests exists.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157808.

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