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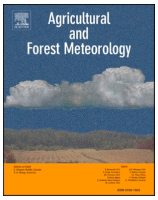

Dryness decreases average growth rate and increases drought sensitivity of Mongolia oak trees in North China

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ABSTRACT

Mongolian oak is a widely distributed tree species in broadleaf forests of North China, which are susceptible to increasing drought. Expansion of oak species ranges has been reported in Europe, America, and Asia with drought and heat stress, and thus, oak species are often deemed to be drought-resistant. As an expanding species in our study region, the Mongolian oak (*Quercus mongolica* Fisch. ex Ledeb) was used to investigate how tree growth rate and drought resistance change along a moisture gradient. In this study, we used a network of Mongolian oak tree-ring samples across a wide range of moisture gradients in North China to assess oak tree growth and its response to drought under different moisture conditions. Our results revealed that spatial variation in tree radial growth rate was highly related to the regions' moisture index, an index indicating moisture condition. Oak trees in drier portions grew slower than those in wetter portions and their growth was more sensitive to drought events. We used an ensemble of climate projections from general circulation models to predict future changes in the Ivanov moisture index, and then estimated the tree growth rate and drought-growth correlation for the period 2021–2100. Increased dryness is likely to reduce tree average growth rate markedly and increase the drought sensitivity of radial growth in the expanding dry portions of our study region, leading to substantial overall drought suppression of growth. Our results suggest that dryness will present an increasing challenge for the continuing expansion of Mongolia oak in already dry areas of North China, whereas oak trees will thrive better in high moisture conditions. The distribution of Mongolia oak trees will likely shift to regions with increased moisture availability, especially under the increasing drought.

1. Introduction

Forest dynamics have shown pervasive shifts in a changing world (McDowell et al., 2020). Increasing drought can cause high tree mortality under warm conditions (Adams et al., 2009; Allen et al., 2015). Doubling of tree mortality rates has been observed throughout most of the Americas and Europe in the past 40 years (Carnicer et al., 2011; McDowell et al., 2018; Senf et al., 2018). Large trees have a higher risk of mortality than smaller ones (Bennett et al., 2015; Ryan, 2015; Stovall et al., 2019). Hence, fast growth may expose trees to a high risk of size-related tree mortality (McDowell et al., 2018). Subsequently, tree radial growth rate and tree growth response to increasing drought determine whether tree species have high tree mortality in this changing world. As oak trees perform and adapt well to increasing drought, understanding the factors that control tree growth rates and trees' responses to drought in oak trees is crucial to understanding how oak trees adapt to warming-induced drought.

Increment in tree stem diameter reflects the radial growth rate of trees. Diameter growth performance varies with tree species and habitat characteristics (Kariuki et al., 2006; Nabeshimab et al., 2010). At regional scales, spatial variation in tree diameters is highly related to the climate condition of their growth sites (Yeh and Wensel, 2000). While fast-growing trees prefer moderate temperatures and humidity levels (Venter et al., 2017), slow-growing trees mainly grow in harsher environmental conditions. All else being equal, faster growth rates lead to larger trunk sizes. Hence, high variation in trunk size can be found

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within the same tree species that can grow in regions with different climate conditions. For example, the Dahurian larch grows normally in the warmer part of northeast China, but can persist with extremely slow growth in the colder part of northeast China resulting in substantial size variation between those populations (Zhang et al., 2019a). Size-related tree mortality indicated that the trunk size of the same tree species influences its responses to increasing droughts (Bennett et al., 2015; Mcdowell et al., 2020). Therefore, detection of how climate factors influence spatial variation in tree radial growth and size is crucial to predict how increasing drought will influences tree growth and survival in different regions.

Hot drought causes widespread forest decline worldwide (Allen et al., 2010). Water availability is one of the major factors to determine whether tree growth can cope with hot drought (McDowell and Allen, 2015; D'orangeville et al., 2016; Zhang et al., 2019b). Reduced growth and low growth resilience to drought can be an early signal of tree mortality (Liu et al., 2019; DeSoto et al., 2020), which can eventually impact the species distribution. As water shortages are predicted to increase in the future, water shortages are likely to become a major factor limiting species distribution (McDowell and Allen, 2015; Yuan et al., 2019).

Forests in warm and semi-arid regions may suffer the most in the decades ahead; however, there may also be notable changes in cooler and wetter regions (McDowell et al., 2020). Some pine species, such as the Scots pine, showed a shrinking distribution with drought caused by increased warming in North Europe (Reich and Oleksyn, 2008), and increasingly severe drought events caused a high risk of larch growth cessation in North China (Zhang et al., 2021a). Broadleaved species seem to be less affected by drought than needleleaved species (McDowell et al., 2016). The oak tree, a broadleaf species, is widely distributed worldwide (Plomion et al., 2018). Compared with the shrinkage in pine distribution, drought adapted Mediterranean oaks tend to expand their distributions (McIntyre et al., 2015; Al-Qaddi et al., 2016; Martín-Gómez et al., 2017; Martinez-Sancho et al., 2018; Etzold et al., 2019), although serious drought can cause a decline in tree growth of *Quercus rubra* in the driest regions of Europe (Čater, 2015; Natalini et al., 2016). Oaks species are assumed to be well positioned to fill the gaps left by other species in the face of drought. One study has predicted that the dense stands of spruce and fir in an evergreen forest of Australia will change to a mix of oaks and pines if warming continues (Albrich et al., 2020). Although oak trees are often assumed to expand their distribution, little is known about the actual growth performance of oak species in the regions where they may expand to.

The Mongolian oak (*Quercus mongolica* Fisch. ex Ledeb) is an oak species that is widely distributed in North China (Lyu et al., 2017; Su et al., 2020), where it is a dominant tree species in broadleaf and needleleaf mixed forests. The distribution of Mongolian oak forests covers the large latitude range of 34°N to 55°N from its southern sub-arid edge to the northern semi-humid edge. The wide geographic distribution and vast climatic variation in its distribution makes Mongolian oak an ideal species to study how drought determines the growth rate, growth response to drought and its response to varying degrees of dryness.

Like the expansion of oak species in the Mediterranean regions (Martín-Gómez et al., 2017; Etzold et al., 2019), Mongolian oak is also projected to expand its distribution in northeast China with continued warming (He et al., 2005). To better understand Mongolian oak's drought response, we investigated whether the basal area growth rate and growth trend of Mongolian oak trees varied with climate factors across most of its distribution. Accordingly, we aimed to detect the spatial variation of basal area growth rate, and investigate the spatial variations in trees' response to drought across a regional moisture gradient spanning most of the species distribution.

2. Materials and methods

2.1. Study region

Mongolian oak forests are mainly distributed in North China (Fig. 1). The Mongolian oak is the dominant tree species in these regions, accompanied by some broadleaf tree species such as *Betula platyphylla* Suk, *Fraxinus mandshurica* Rupr., *Phellodendron amurense* Rupr., and some needleleaf tree species such as *Pinus koraiensis* Sieb, and *Larix gmelinii*. Ten sites, in regions ranging from semi-arid to sub-humid zones, were selected as the sample sites to collect tree-ring cores (Fig. 1). The region has a monsoon climate, as the summer is hot and humid, while winter is cold and dry. Mean temperatures in January can be as low as -25°C∼-28°C, while July mean temperature can reach 18°C∼20°C. The lowest minimum temperature recorded in our study region was lower than -40°C. Annual total precipitation is low (c. 450 mm) with more than 80% falling between June and September.

2.2. Sampling network and width measurement

Cores were collected from natural Mongolian oak forests in ten sites in North China (Table S1). We randomly sampled at least 20 individual trees per site. In each location, two samples were collected from each randomly selected tree at breast height (1.3 m) using an increment borer. In total, we collected 456 cores from 233 trees (Table S1). Tree cores were dried and stabilized, and sanded until ring boundaries and wood structure were clearly visible by following standard dendrochronological methods (Cook & Kairiukstis, 1990).

The cores were visually cross-dated, and then measured to the nearest 0.01 mm using the LINTAB6 measuring system. Crossdating quality was assessed using COFECHA software (Holmes, 1983). Tree-ring width measurements were transformed to basal area increment (BAI) to characterize tree radial growth. BAI indicates accurate tree vigor and growth over time, and is a good indicator of growth trend (Duchesne et al., 2002). BAI was calculated from tree ring growth according to the formula:

$$\mathrm{BAI} = \pi\left(\mathrm{R}_t^2 - \mathrm{R}_{t-1}^2\right)$$

where R is the radius of the tree and t is the year of tree-ring formation.

The age of the sampled Mongolian oak trees was approximately 30–50 years, which is close to the average age in those forests. We excluded trees that were older than 65 years and younger than 20 years to limit the influence of age on tree radial growth. The growth rate of stem diameter was calculated as the total BAI divided by the age of each tree. The mean basal area growth rate was calculated as the average of the basal area growth rate for all trees in one sample site.

Each measurement series was standardized in ARSTAN using the Friedman method (alpha = 5) to remove non-climatic trends such as geometrical or disturbance signals that could obscure climatic responses (Cook & Holmes 1986). A prewhitening method was used to remove the autoregression of tree-ring series in ARSTAN. The resulting growth index chronology was calculated using the biweight robust mean. For further chronology statistics, such as the expressed population signal (Wigley et al., 1984), see Table S1.

We also compiled published tree-ring chronologies of the Mongolian oak in our study. The tree-ring width chronologies from literature were digitized using GetData Graph Digitizer (https://getdata-graph-digitizer.com/download.php) from Lyu et al. (2017) and Han et al. (2019). These chronologies were sampled from eight additional sites that did not overlap with our sample sites (Fig. 1 and Table S1).

2.3. Climate data

Climatic data from 18 weather stations, distributed throughout the region from which we obtained chronologies, were used (Zhang et al.,

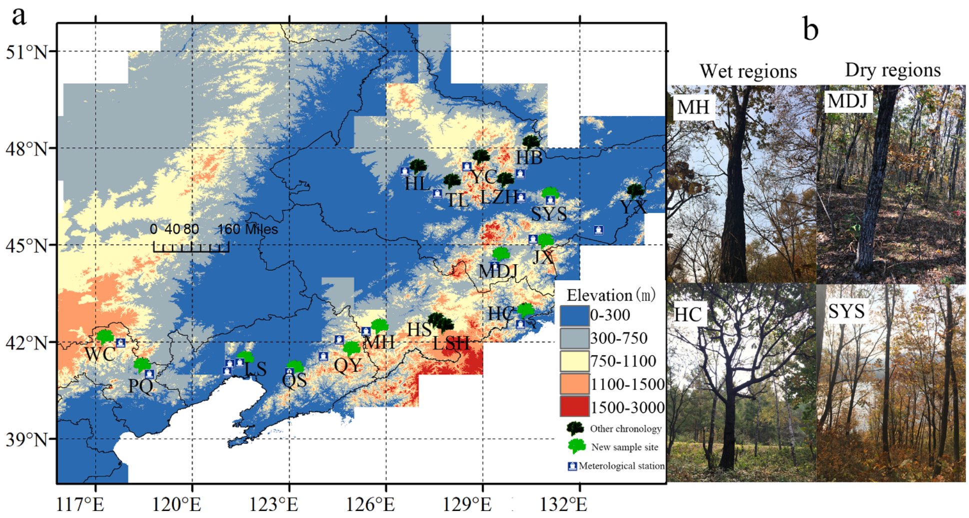

Fig. 1. Location of sample site and meteorological stations (a), and images of oak trees in different moisture conditions (b). The site IDs and other basic information for each site are listed in Table. S1.

2021b). Monthly mean temperature, total precipitation, and relative humidity for 18 stations were obtained from the Chinese Meteorological Data Sharing Service System (http://cdc.cma.gov.cn/). The climate records from these weather stations stretched from 1957 to 2019.

To quantify the response of drought to tree growth, adequate drought indices for the study region are needed. Various drought indices have been proposed. The moisture index of Ivanov (1948), self-calibrating Palmer Drought Severity Index (PDSI), and vapor pressure deficit (VPD) were used in this study to investigate which was the best one to link tree growth rate and drought.

The moisture index of Ivanov (henceforth referred to as K value) was calculated to reflect the moisture conditions in every sample site, as follows (Ivanov, 1948).

$$K = \frac{P}{E_0} = \frac{P}{\sum_{m=1}^{12} 0.0018 * (25 + T_m)^2 * (100 - RH_m)}$$

where K is moisture index of Ivanov, P is total annual precipitation (mm), T_m is monthly temperature (°C), and RH_m is monthly relative humidity (%).

The PDSI is a drought index used to estimate relative dryness based on temperature and precipitation data (Dai et al., 2004). PDSI is calculated based on a supply-and-demand model of soil moisture and generally reflects the soil moisture condition. PDSI data were retrieved for every sample site from the website (https://crudata.uea.ac.uk/cru/data/drought/). VPD was calculated based on monthly maximum temperature, minimum temperature, and relative humidity.

The future projections of general circulation models (GCMs) can be used to predict tree growth (Zhang et al., 2017). We calculated K values based on climate projections for the period 2021-2100. Climate data under different scenarios were obtained using GCM simulations from the Coupled Model Intercomparison Project 5 website (https://pcmdi.llnl.gov/mips/cmip5/). The multi-model mean method has been shown to produce more accurate results compared to the single simulations (Zhang et al., 2016; Zhang et al., 2018). Therefore, we interpolated the simulations of 28 GCMs to 2.5° × 2.5° for the study region to calculate the multi-model mean monthly mean temperatures, monthly total precipitation and monthly relative humidity. There are four Representative Concentration Pathways (RCPs), however, only RCP 2.6 was used in this study, as it simulated moderate warming, thus presents a conservative estimate.

2.4. Methods

The linear regressions between mean basal area growth rate and moisture condition (K, VPD, and PDSI) were estimated using the ordinary least square method to quantify the influence of site moisture condition on the radial growth rate across regions.

The correlation between each site chronology and climate (monthly mean temperature, monthly total precipitation, monthly relative humidity, and monthly PDSI) from the nearest climate station were calculated to identify growth-climate correlations. Growth–PDSI correlation was calculated to detect the influence of drought on tree radial growth, as PDSI had better relationship with tree radial growth than K value and VPD. The correlation between moisture conditions and the growth–PDSI correlation during growing season (June–August) across sites was calculated to investigate the potential interactive effects of moisture conditions on growth–drought dependencies.

K values were calculated based on projected monthly temperature, precipitation, and relative humidity for the period 1957–2100; however, a bias existed between the projected K values and observed K values when two series were compared. Therefore, we adjusted the mean value and standard deviation of the projected K values according to the observed K values. Future projections of tree radial growth and drought-growth correlation were calculated for the period 2021–2100 based on their relationship with the K value in the period 1957–2017.

3. Results

3.1. Spatial variations of basal area growth rate with moisture conditions

Mean annual temperatures in the southern stations were much higher than those in the northern stations, and annual total precipitation was higher in the eastern part of the study region than in the western part of the study region (Fig. s1). K values ranged from 0.5 to 1.2, indicating a moisture gradient from semi-arid in the southwest to sub-humid region in the north east of the study region (Fig. 2), and but K values did not change significantly in the past 60 years (i.e. 1957–2017, $p > 0.05$, Fig. s2).

Tree basal area growth rate is highly related to moisture condition (Fig. 2). We found a high positive correlation between tree basal area growth rate and the K value ($r = 0.84$, $p < 0.001$). High tree basal area growth rate was found at sites with high K values, whereas low tree basal area growth rate was found at sites with low K values. Compared to the results from K value, VPD had weaker but significant correlation with tree basal area growth rate ($R^2 = 0.41$; Fig. S3). PDSI did not have a

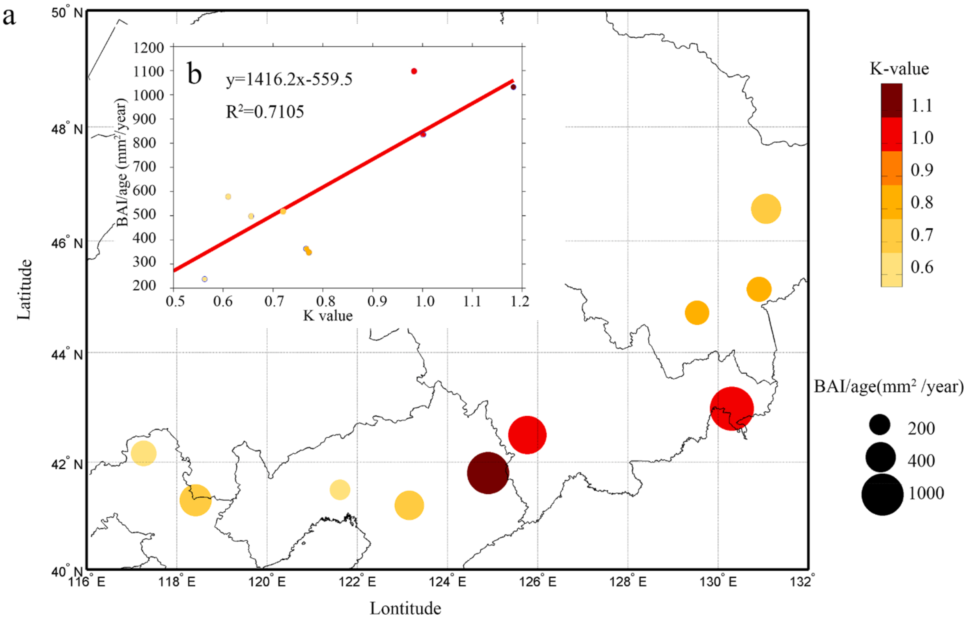

Fig. 2. Higher BAI increment was found in higher K value regions (a), and linear relationship between BAI and K value (b). The dot size represents the BAI, while the dot color indicates the K value. The BAI increment was calculated as the total BAI divided by the age to reflect the basal area growth rate. The trees that younger than 20 years and older than 65 years were excluded to minimize the influences of age on tree basal area growth.

significant correlation with tree basal area growth rate ($p > 0.05$, Fig. S3).

3.2. *Climate-growth relationship*

A significant correlation between site chronologies and monthly mean temperature was mostly found in June, July, and August (Fig. 3). There were significant negative correlation coefficients between June mean temperature and site chronologies in seven of ten sites ($p < 0.05$). Summer (June-August) mean temperature was negatively correlated with tree radial growth in six of ten sites ($p < 0.05$). Monthly precipitation had no significant correlation with site chronologies in most months ($p > 0.05$, Fig. 3). Negative correlation coefficients were mostly found between pre-growing season precipitation and site chronologies, whereas positive correlation coefficients were found during the growing season. Total summer precipitation had a significant positive correlation with site chronologies in six sites ($p < 0.05$). No significant correlation was found between mean relative humidity and site chronologies in months except June and July. June-July mean relative humidity had a significant positive correlation with site chronologies in nine sites ($p < 0.05$, Fig. 3). There was a significant positive correlation between summer mean PDSI and basal area growth in ten sites ($p < 0.05$, Fig. 3). Winter PDSI showed a negative correlation with basal area growth in six sites, although the correlation was not statistically significant ($p > 0.05$, Fig. 3).

3.3. *Relationship between moisture conditions and trees' response to drought*

There was a spatial pattern of the influence of summer PDSI on tree growth (Fig. 3). Increasing PDSI had a significant positive influence on tree growth in ten sites, but showed the opposite relationship/was less

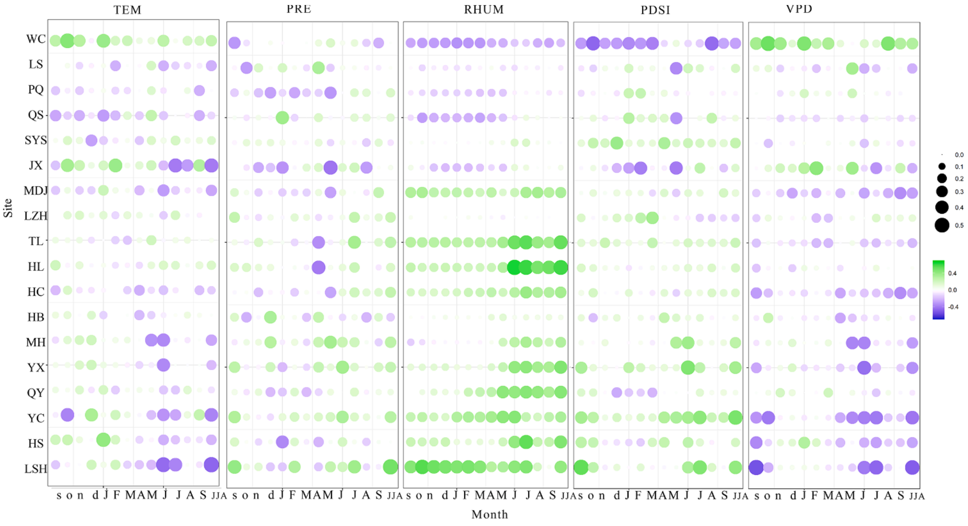

Fig. 3. Correlation coefficients between site chronologies and climate variables (PDSI, PRE (precipitation), RHUM (relative humidity), TEM (temperature), and VPD) during the period 1957-2017. The sites were arranged from the driest at the top to wettest at the bottom.

influential in the other eight sites. Tree growth response to increasing drought was significantly correlated with their K values (Fig. 4a). Trees growing in low K value regions had a significant positive correlation with summer PDSI, however, no significant correlation was found between site chronologies and summer PDSI in high K value regions (Fig. 4a). Tree growth on sites with K values lower than 0.7 were likely to be more affected by summer drought. The relationship between summer drought and tree growth was significantly correlated with VPD ($R^2 = 0.65$); however, the relationship was not as strong as their correlation with K values (R^2=0.71, Fig. s4).

Tree growth was negatively correlated with pre-growing season PDSI in high K value regions; however, a positive correlation was found between site chronologies and pre-growing season PDSI in low K value regions (Fig. 4b).

3.4. *Future project of tree basal area growth and trees' response to drought*

Simulated K values could reflect the observed changes in K values after bias-correction (Fig. S5a). A decline in K value was observed in all sites during 2021–2050, but it increased slightly during 2051–2100 when projected multi-model means of 28 GCMs for RCP 2.6 (Fig. S5b). The K value will decline when increasing precipitation does not compensate for evaporation. Tree growth rate was projected to decrease and drought sensitivity to increase in regions where the K value declined (Fig. 5). The reduction in tree basal area growth rate was less than 50% in all sites during 1957–2017; however, tree growth will reduce by more than 40% in six sites during 2051–2100. Tree basal area growth rate is projected to reduce by at least 80% in six sites (SYS, JX, MJD, HC, LZH, and YX) and will only reduce by less than 30% in three sites during 2021–2050 (Fig. 5a), indicating a pervasive decline in projected tree growth.

The positive drought-growth correlation will increase in all sites during the periods 2021–2050 and 2051–2100. The correlation coefficients will be higher than 0.4 in 10 sites for 2021–2050, and a decrease in correlation coefficients will be only observed in one site during this period. Tree growth is projected to have high correlation coefficients with summer drought in six sites during 2051–2100 (Fig. 5b).

4. Discussion

Our findings revealed that Mongolian oak trees tend to grow faster in wetter regions, where their radial growth is less affected by drought. Radial growth of trees may depend on tree species, climate, tree age, and other tree-related factors (Rentch et al., 2002; Nabeshima et al., 2010; Gómez-Aparicio et al., 2011). In this study, Mongolian oak trees from a similar age group were used to remove the influence of tree age, tree species, and other tree-related factors, in order to detect how climate conditions influence spatial variation in the basal area growth rate of oak trees. Mongolian oak trees are widely distributed in northern China, and they occur in both relatively wet and dry areas. The trunk sizes of Mongolian oak trees vary significantly with moisture gradients (e.g., Su et al., 2020). Thinner and shorter oak trees are mainly found in drier areas in the western part of northeast China, whereas thicker and taller oak trees are mainly found in wetter areas in the eastern part of northeast China. Our results suggest that the spatial differences in the basal area growth, thus size, of oak trees were mainly driven by the moisture gradient across their distribution. Relatively wetter climates appear more suitable for nursing bigger oak trees compared to drier regions.

The influence of climate factors on tree growth varied with moisture conditions. The negative influence of June temperature and the positive influence of June precipitation on tree growth were mainly found in drier sites; this is consistent with findings of other studies conducted in these drier sites (e.g., Liu et al., 2013; Lyu et al., 2017). The influence of drought on tree growth was largest between June to August in drier sites, and supports previous findings from independent studies that growing season drought had a negative influence on the growth of Mongolian oak (Lyu et al., 2017). The peak growing season of Mongolian oak mainly coincides with this June to August window, as it is a deciduous broadleaf tree species. The negative influence of growing season drought on tree growth in dry regions suggests that increasing drought would result in tree growth declines in these sites under projected increases in drought and warming.

Rapid warming has already resulted in an increase in drought in major parts of North China (Greve et al., 2014; Zhang et al., 2019b; Zhang et al., 2021). Drought suppression of growth was strongly related to the aridity of the studied sites. The negative influence of summer drought on tree growth was significant in the driest region; however, tree growth was not much reduced by drought in the wetter regions. Our results suggested that generally slow-growing oak trees grew even slower in the drier sites. Although small trees are less vulnerable to increasing drought (Bennett et al., 2015), slow-growing trees reduced their radial growth in response to drought at the drier end of our study region. However, the size-associated trade-off between drought resistance and growth decline clearly warrants additional research.

The combine effects of high precipitation and high PDSI (both proxies for available soil moisture) in the pre-growing season had a negative influence on tree growth in wetter regions. High precipitation is often associated with low minimum temperature, which has negative influence on oak growth in the pre-growing season (Lyu et al., 2017). Additionally, oak trees prefer well-draining loamy soils (Pike et al., 2006). Thick snowpacks in the wet region of northeast China maybe however supply high soil moisture levels in the pre-growing season. This high soil water content in pre-growing season affects the rate of rooting activity, leading to a negative influence on tree growth. In support of this idea, the negative influence of high PDSI diminished with increasing dryness in the study region.

Interactions between precipitation and evapotranspiration influence tree basal area growth rate and trees' responses to drought. Our results

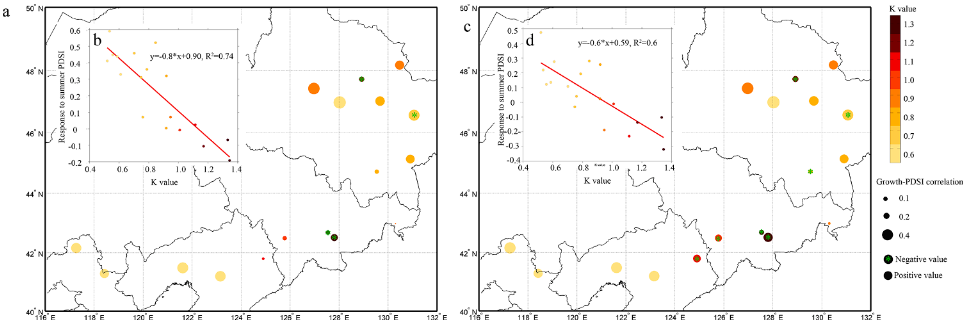

Fig. 4. Relatinoship between the summer (a, b) and pre-growing season (c, d) PDSI -growth correlation of *Quercus Mongolica* tree growth and K value. The dot size represents the size of correlation coefficient.

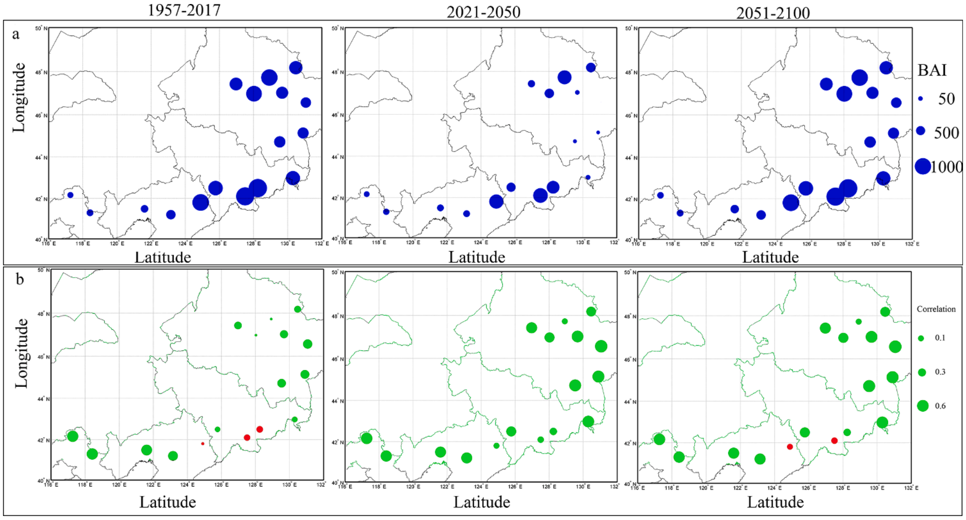

Fig. 5. Spatial variations of BAI increment and summer drought-growth correaltion for the past 60 years and future 80 years. Spatial variations of BAI increment (mm^2/year) during the periods 1957-2017, 2021-2050, and 2051-2100 (a), and spatial variations of PDSI –growth correlation during the periods 1957-2017, 2021-2050, and 2051-2100 (b). The green dots represents positive correlation, and red dots represent negative correlation.

suggest that the growth of Mongolian oak was more restricted by the balance between evapotranspiration and precipitation. Generally, oak trees have high transpiration rates as they have large leaves (Oliveira et al., 1992), and can transpire 45%–80% of total annual precipitation during the growing season (Ffolliott et al., 2003). The drought index, PDSI, reflects the soil water availability, whereas VPD reflects the atmospheric demand for water. Subsequently, neither PDSI, nor VPD constitutes a holistic image of drought; hence, they did not correlate as well with oak tree growth rate and suppression of growth during drought as K values. VPD may not show a better relationship because it does not capture the soil water supply. The K value captures the competing effects of water supply and atmospheric demand for water and arguably reflects the hydrological conditions in the study region better. The importance of the K value to Mongolian oak tree growth suggests that water status (driven by both supply and demand) greatly influences tree growth.

Generally, expansion in the distribution of oak trees with simultaneous contractions in the range of pine species were assumed to indicate that the oak tree species are able to endure increasing drought, while pines were not (McIntyre et al., 2015; Al-Qaddi et al., 2016; Martín-Gómez et al., 2017; Etzold et al., 2019). Although oak trees can certainly grow in dry regions, our results suggest that oak trees grow more rapidly in wetter parts of their distribution, where they are less impacted by drought. Smaller trees are likely to grow even more slowly in drier regions in the future, if the spatial relationship between drought and growth is valid over time. Reduced radial growth has been argued to be an indicator of tree mortality likelihood (Dobbertin et al., 2005; Camarero et al., 2015). Hence, the survival of smaller oak trees in dry regions may be more challenging then commonly assumed when faced with increasing drought.

We estimate that oak trees growing in dry regions may become highly limited by summer drought in about 30 years. The Mongolian oak trees that grow in drier regions are likely to suffer increasingly from drought growth suppression in the future. Although Mongolian oak trees are deemed to be a drought-resistant species, they are already vulnerable to summer drought in dry regions. Any natural and managed expansion of Mongolian oak forests is more likely to be successful towards wetter regions in northern China.

Declaration of Competing Interest

The authors declare that no conflict of interests exists.

Acknowledgement

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108611.

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