



The frequency and severity of past droughts shape the drought sensitivity of juniper trees on the Tibetan plateau

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ARTICLE INFO

Keywords:

Resistance
Resilience
Dendroecology
Tree rings
Juniper
Drought

ABSTRACT

The resistance of forests to extreme climatic events such as drought shapes their sensitivity to future extreme events in space and time. To a large extent, the ability of trees to learn from prior droughts explains how trees adjust their sensitivity to water deficit. We use tree-ring width data collected from 1565 juniper trees (*Juniperus przewalskii* and *Juniperus tibetica*) across 57 sites on the Tibetan Plateau to model tree resistance to water deficit and to map drought sensitivity across the species' distribution. We test the effect of both the frequency and severity of drought on the drought memory of trees. We find that trees at mid-latitudes and in the northwestern part of the juniper distribution range exhibit higher drought sensitivity. Water deficit is the main factor controlling tree resistance and thus affects spatial sensitivity to drought. At wetter sites, higher drought frequency enhances tree adaptability through ecological memory, thereby promoting tree resistance and decreasing tree sensitivity to extreme drought events. At drier sites, higher drought frequency causes junipers' growth decline that is not beneficial for tolerance to extreme drought events. Regional drought conditions and the frequency of pre-droughts affect tree resistance and sensitivity to extreme drought events. This explains the spatial pattern of drought risk for juniper forests on the Tibetan Plateau, and helps us to better understand the vulnerability of this high-elevation forest ecosystem. Such information is important for maintaining forest health and informing the sustainable development of the Tibetan Plateau under a changing climate.

1. Introduction

Increasing frequency and severity of extreme drought events due to global warming have already caused massive forest decline and dieback around the world (Breshears et al., 2005, Allen et al., 2015, Brienen et al., 2015, Choat et al., 2018, Crockett and Westerling, 2018) and the contribution of droughts to forest decline is stronger than some warming induced secondary disaster such as insect outbreaks (Chen et al., 2018). This alarming situation has resulted in an increasing number of studies focused on the ability of trees to withstand extreme drought events (Cavin and Jump, 2017, Gazol et al., 2018, DeSoto et al., 2020), based on their resistance and resilience to these events (Holling, 1973). However, resilience is a complex framework, and a unified theoretical definition of processes in resilience is lacking because several essential questions remain unanswered. Among them, two key questions were identified by Willis et al. (2018): (i) Where are the most resilient ecosystems and (ii) what attributes make ecosystems to have high

resilience? Indeed, identifying the spatial variability in forest resilience is crucial to answer these questions and ecologically fragile hotspots lie at the heart of the forest management (Allen et al., 2016, Schwalm et al., 2017). With extreme drought events expected to increase in both frequency and severity, these questions become more challenging as one considers the effects of ecological memory on extreme droughts (Blonder et al., 2017, Camarero et al., 2018). These memory effects, based on stored information from recurrent non-lethal abiotic stimuli, would alter the tree sensitivity to disturbance in the form of physiological adaptations or stresses that can shape ecological resilience to future disturbance (Peltier and Ogle, 2019, Galviz et al., 2020).

Our understanding of trees resilience to drought can be assessed through both temporal and spatial gradients. Tree-ring width is a common indicator of climate responses at tree level as this metric integrates most physiological processes related to resource acquisition and use. This is an effective indicator of ecological resilience because ring widths provide record of radial growth of trees in the past disturbances (Zhang

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and Fang, 2020). Based on ring-width sequences, the main components of tree resilience can be quantified (Lloret et al., 2011). This quantification has been recently applied to study resilience on large spatial scales, which shows differences across biomes and species (Gazol et al., 2017, Vitasse et al., 2019). Despite this, spatial patterns have not yet been explained, which limits the scalability of current understanding of forest disturbance regimes in responses to climate change.

The Tibetan Plateau (TP), the highest plateau in the world, is known as “the third pole” and “the water tower of Asia” because it modulates atmospheric circulation and provides water to the surrounding regions. In the last five decades, temperature on the TP has increased at approximately three times the global mean warming rate (Qiu, 2008). Significant warming and changes in regional water conditions are currently threatening forest sustainability on the TP. Forest declines due to the increasing frequency of extreme drought have been already observed at the Qinghai-Tibet border (Mou et al., 2019), which attracted our attention on forest health under the currently warming condition. Junipers are drought-resistant tree species known on the plateau. Previous studies about juniper resilience to drought on the TP showed that drought resistance and recovery varied over time and space (Fang and Zhang, 2019). Although the temporal changes were well understood in regards to climatic fluctuations, the reason for the spatial variation in drought sensitivity was relatively poorly investigated. The goal of this study is to map the spatial pattern of tree’s sensitivity to drought on the TP and to identify the impact of antecedent drought conditions on the spatial pattern. We hypothesize that tree sensitivity to drought depends on the frequency and severity of the droughts that the tree has experienced in the past, leading to physiological adjustments. Ecological drought memory should then be related to previous background climatic conditions and therefore result in a specific spatial variability of drought vulnerability on the TP.

To test this hypothesis, we used tree-ring width series from a large network of 1565 juniper trees from 57 forest sites encompassing wide geographical and climatic gradients across the TP. We identified the spatial distribution of tree sensitivity to drought since the year 1950, and explore the sensitivity response to pre-drought conditions. Specifically, we aim to answer the following three questions: (1) What is the spatial pattern of juniper’s sensitivity to drought on the TP? (2) Is this spatial pattern linked to past drought frequency and severity? (3) How does ecological memory affect tree’s sensitivity to drought?

2. Material and methods

2.1. Study sites and tree-ring sampling

The study sites are distributed over the eastern and southeastern parts of the TP. *Juniperus przewalskii* and *Juniperus tibetica* are the two main species, and occur mostly in pure forests or forests with relatively simple structures between 2800 and 4900 m a.s.l. The study area is minimally affected by interspecific interactions and human influences, but is strongly affected by the south Asian monsoon and the westerly wind belt (Gao et al., 2019a,b). The southeastern part of the area receives as much as 2158 mm of precipitation annually, whereas the northern part receives as little as 78 mm. The main precipitation season occurs from May to September. Due to the high elevation, temperatures remain very low throughout the year. Annual mean temperatures across the study sites range from -4.4 °C to 7.5 °C; January is the coldest month and July is the warmest with regional mean temperatures -11.2 °C and 9.3 °C, respectively.

We collected 1769 cores from 1719 trees at 57 sites on the TP (Supplementary Table 1). Ring-width data of 1317 trees at 44 sites were already reported in previous studies (Zhang et al., 2015, Fang et al., 2018, Fang and Zhang, 2019, Lyu et al., 2019, Mu et al., 2021). These tree-ring samples were processed following classical dendrochronological methods (Fritts, 1976). We measured tree-ring widths at a resolution of 0.01 mm using a LINTAB 6 system (Rinntech, Germany). Tree-ring

width were then cross-dated using standard dendrochronological techniques (Schweingruber, 1988) and the quality of the cross-dated series was checked using the COFECHA program (Holmes, 1983). We removed the low frequency trend of each tree-ring sequence by applying a smoothing spline of 50% frequency cut off at half the length of the series (Cook et al., 1990). We then developed standard chronologies for each of the 57 sites using the R package “dplR” (Bunn, 2008) and the biweight robust mean of the detrended tree-ring indices.

2.2. Climate data and drought background indices

Monthly temperature, precipitation, and Palmer Drought Severity Index (PDSI) data were obtained from the CRU gridded dataset (Climatic Research Unit: <http://climexp.knmi.nl>) at a geographical resolution of 0.5° . Data from the nearest grid point were used for each sampling site.

Monthly potential evapotranspiration based on local elevation and mean monthly temperature was computed using Thornthwaite’s approach (Thornthwaite, 1948) with the R package “SPEI” (Vicente-Serrano et al., 2010). Then, the monthly climatic water balance was computed as the difference between the monthly total precipitation and potential evapotranspiration.

Drought frequency (DrF) was determined using the PDSI from May to June. We counted the number of severe droughts ($PDSI < -2$) and extreme droughts ($PDSI < -3$) from the year 1950 to 2015 as drought background frequency. Local drought severity (DrS) was quantified according to the mean May-June water balance from the year 1950 to 2015 at each site, where positive and negative mean values indicate wetter and drier sites, respectively.

2.3. Indices of tree resistance and sensitivity

The valid ring widths of 1565 juniper trees were used to calculate the indices of resistance and sensitivity. Resistance of each individual tree to potential drought events was calculated following the methodology provided in Lloret et al. (2011) and using a pre-period of four years before studied year, as follows:

$$\text{Resistance} = \text{Ring width}_t / \text{Ring width}_{t-4},$$

where Ring width_t is the ring width in the corresponding year t and Ring width_{t-4} is the averaged ring width for the four years preceding the year t . We calculated the resistance of each individual tree in each year during the available period and then averaged per site. Site-averaged resistance indices in years with site ring-width standard chronology values higher than one were removed to reduce the impact of similar trends after growth release.

We examined the correlation between site-averaged tree resistance to drought and water balance from May to June as a proxy for tree sensitivity to drought events (SI). Correlation was determined using Pearson’s correlation since the year 1950.

2.4. Statistical analyses and spatial interpolation

An exponential function and a binomial distribution function were, respectively, used to simulate the changing resistance indices with water balance and the variation of SI along latitude. The statistically significant test was based on Fisher’s test. Spatial interpolation of SI was carried out by the Thiessen polygon method in ArcGIS 10.6 software.

To detect the relationship between SI and drought memory (DrF and DrS), linear regression analysis was conducted between SI of each site and either DrF or DrS of previous droughts. All statistical analyses were performed in R software (version 4.0.0).

3. Results

3.1. Impact of May–June drought on tree resistance

We built tree-ring width chronologies for juniper trees at 57 sites across the TP. The mean length of the ring-width chronologies was 590 years. Extreme values across the ring-width indices were consistent over the last two centuries (Supp Fig. 1).

Tree-ring width chronologies at 52 sites correlated positively with PDSI from May to June and these correlations were significant for 37 sites ($P < 0.05$) (Supp Fig. 2).

Across all study years and chronologies, tree resistance indices decrease rapidly with declining climatic water balance from May to June when water deficit happens (water balance is below zero) (Supp Fig. 3).

3.2. Spatial pattern of tree sensitivity to drought on the Tibetan Plateau

We found higher tree sensitivity (SI) to drought in the northwestern and center region of the juniper forest distribution. There is a significant binomial distribution for SI across latitudes with a max SI between 32 and 36°N (Fig. 2).

3.3. Impact of past drought severity and frequency on tree sensitivity

SI is related to a tree's memory of previous-year drought severity and frequency. The mean DrS was found to be negative for 22 out of 57 sampling sites. We found a significant negative linear relationship ($P < 0.01$) between SI and DrS , i.e. trees were less resistant to drought in sites where drought severity was higher in the past (Fig. 3).

At wetter sites ($DrS > 0$), there is a significant negative linear relationship between SI and DrF . Higher drought frequency could result in lower sensitivity to drought (Fig. 4a). Interestingly, at drier sites ($DrS < 0$), the relationship between SI and DrF is reversed. In other words, higher drought frequency at drier sites led to higher drought sensitivity (Fig. 4b).

4. Discussion

Tree sensitivity to drought, characterized as the correlation relationship between tree resistance and water deficit over long periods, shows a clear spatial pattern across the TP and could be the result of a legacy effect of anterior droughts. On one hand, forests in high drought-severity areas were found to be more sensitive to drought and may therefore decline in response to future extreme drought events. On the other hand, drought frequency affected tree sensitivity differently in wet and dry regions. That is, in more humid regions, populations that experienced more frequent droughts coped better with additional droughts, but in drier regions, frequent droughts caused adverse effects.

4.1. Spatial sensitivity of juniper to drought

We evaluated drought sensitivity for each of the 57 populations of juniper trees based on the correlation coefficients between resistance indices and water balance from May to June. The spatial pattern of tree's sensitivity to drought is roughly consistent with the regional water conditions and reveals ecologically vulnerable areas where juniper forests may suffer more under future droughts.

Junipers are long-lived trees that exhibit high resistance and adaptability to extreme climates and environments (Shao et al., 2009, Fang et al., 2020). Growth of juniper trees has been reported significantly positively correlated with moisture conditions during the growing seasons on the TP, even along the Northern Hemisphere's highest tree line (Zhang et al., 2015, Yin et al., 2016, He et al., 2018, Lyu et al., 2019). The composition and diversity of juniper forests over the TP is highly influenced by local moisture conditions. Juniper trees form almost pure forests in the northwest dry region of the TP, which may

display less resistance to stresses; and form mixed forests with higher functional diversity in the wet regions, which may display higher resistance. This assumption aligns with those of other studies showing that forest resistance decreases with decreasing forest diversity (Pimm, 1984; Gazol and Camarero, 2016). Resistance to extreme drought events has been shown to be higher in diverse forests because of interspecific and intraspecific interactions that alleviate the effects of drought (Jucker et al., 2014, Jactel et al., 2017). An equilibrium among plants can effectively improve the utilization of resources; thus, forests with more functional diversity usually show higher resistance and lower sensitivity to extreme climatic events (Gazol and Camarero, 2016, Versace et al., 2020). Similar examples can be found in the literature. For instance, Pretzsch et al. (2013) reported that *Fagus sylvatica* in Germany is more resistant to extreme drought events in mixed beech-oak stands than in pure stands. Lebourgeois et al. (2013) found higher resistance to summer drought in *Abies alba* growing in mixed stands than in pure stands in the Vosges Mountains, western Europe.

Along a latitudinal gradient, we found drought sensitivity to be highest in the mid-latitudes rather than at the latitudinal edges of the forest distribution and trees in the border zone of Yushu and Changdu prefectures showed highest sensitivity to drought (Fig. 1). This persistent pattern reveals variation in the ecological risk of forest health and suggests a regulatory role of local attributes for forest vulnerability. But further research needs to be conducted to explain the pattern. A similar latitudinal pattern was reported regarding the drought sensitivity and resistance of *Fagus sylvatica* in Europe (Cavin and Jump, 2017). In their study, Cavin and Jump showed that *F. sylvatica* exhibits the highest drought sensitivity in the core of the species distribution. They suggested that local environmental conditions and the responses of individual trees to extremes could be responsible for the spatial pattern. Moreover, plasticity in junipers' xylogenesis pattern could enhance their adaptation to variable climatic conditions (Camarero et al., 2010), which may also shape their drought sensitivity patterns. Despite the different climatic responses of tree growth, our results support the view that drought sensitivity is driven by local water availability and climatic conditions.

Given the spatial pattern of tree resistance to drought, we recommend paying close attention to the health of juniper trees in forests of dry-condition in the northwest TP and forests with relatively simple structure.

4.2. Effect of ecological drought memory on tree sensitivity

Juniper trees show higher sensitivity to drought in drier regions, which is consistent with earlier studies that show a higher risk of extreme drought events at sites with generally drier conditions (Jump et al., 2006, Camarero et al., 2018, Camarero et al., 2020, Piraino, 2020, Sánchez-Salguero and Camarero, 2020). Similarly, Camarero et al. (2011) found that *Abies alba* declined more severely throughout the western Spanish Pyrenees, a region subject to higher water deficit during the late growing season, than in the eastern Pyrenees. Long-term drought stress and water deficit were considered key factors controlling declines in tree growth. Gazol et al. (2015) further analyzed the growth response of *A. alba* across Europe and confirmed a forest decline in southwestern populations, the growth of which is strongly limited by precipitation. Gazol et al. (2018, 2020) found more resistance in wet regions dominated by hardwood species and more resilience in dry regions dominated by conifers. On the TP, moisture conditions decrease from southeast to northwest as a result of topography and climate. A similar spatial pattern was found regarding the sensitivity of juniper to water deficit: junipers in northwestern TP are more sensitive to water deficit. The Himalayas, which are mostly influenced by the South Asian monsoon, have more abundant precipitation, and trees there exhibit lower sensitivity to drought.

The frequency of past droughts has been shown to have different impacts on populations with different local moisture conditions. We

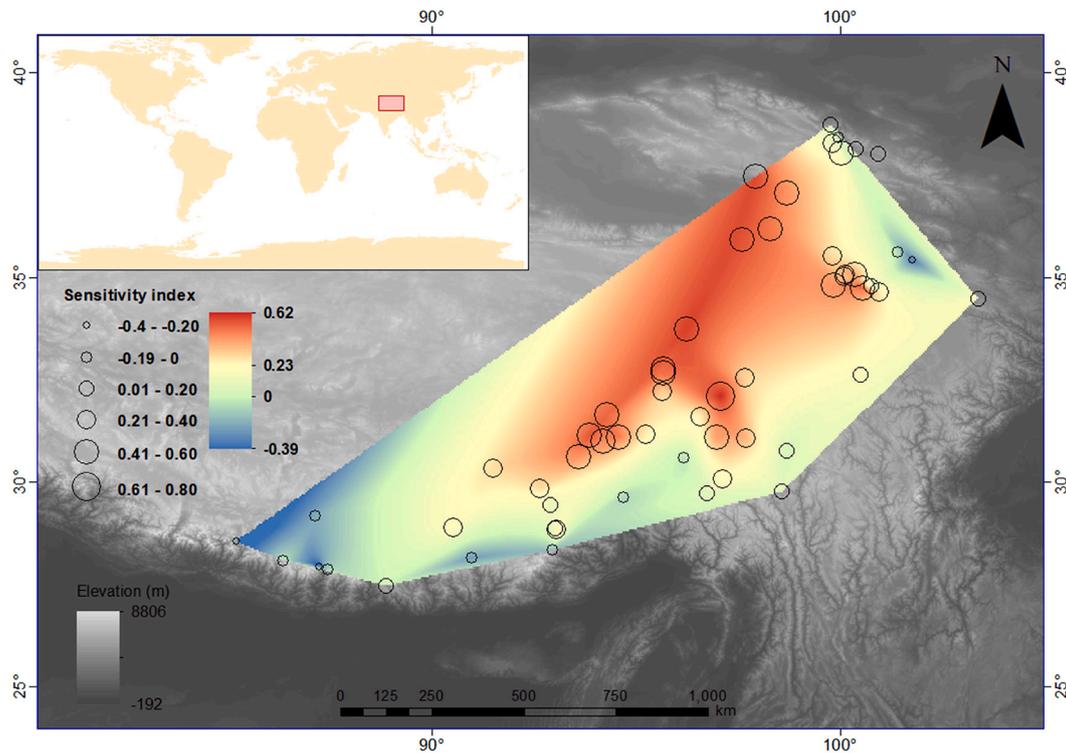


Fig. 1. Spatial variability of the ring-width sensitivity (*SI*) of juniper to water deficit on the Tibetan Plateau. The black circles indicate the *SI* at each sampling site and the size of the circles represent the degree of *SI*. The coloured spatial interpolation surface represents the spatial interpolation of *SI* and is computed using the Natural Neighbor spatial interpolation method in ArcGIS software. The red colour indicates the highest sensitivity of growth to drought and the blue colour the lowest one. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

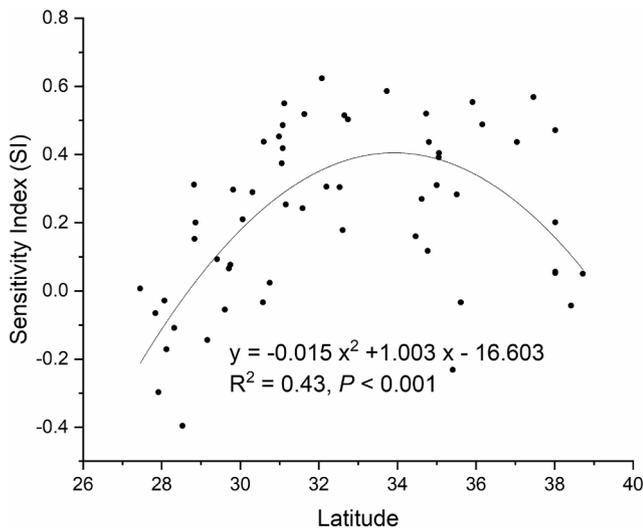


Fig. 2. Juniper sensitivity indices (*SI*) to water deficit for each site across latitude. Each point represents the *SI* value at a site corresponding to a certain latitude. The curve shows the binomial regression of tree sensitivity indices.

found that, in more humid regions of the TP, frequent droughts increase tree’s drought tolerance, thus promote forest resistance. Ecological drought memory improves the ability of trees to adapt to future drought stress, in line with some other studies elsewhere in the world. Ciemer et al. (2019) found higher forest resilience in regions of the Amazon with higher rainfall variability. Frequent alternation between drought and rainfall would exert a ‘training effect’ on trees, resulting in increased resistance and lower drought sensitivity. This ‘training effect’ would change the morphological and physiological traits in juniper trees,

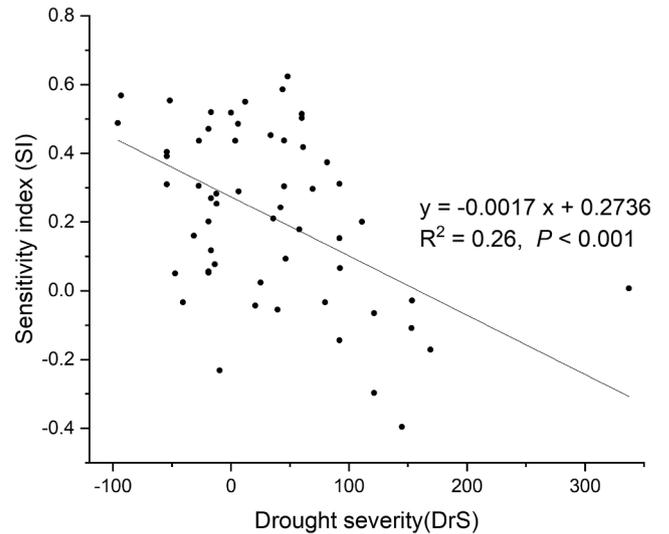


Fig. 3. Juniper sensitivity indices (*SI*) in relation to drought severity (*DrS*) represented by mean May-June water balance from the year 1950 to 2015. The straight line represents a linear regression.

which in turn have important impact on tree’s responsiveness to climatic change (Zweifel et al., 2020). In a long-term field experiment, Backhaus et al. (2014) showed that plant resistance to extreme drought stress increased when plants were exposed to frequent mild drought events. One possible mechanistic explanation is that plants change structures and accumulate signaling proteins during drought stress. As a result, they develop higher resistance to subsequent recurrent drought events (Bruce et al., 2007, Ramírez-Valiente and Cavender-Bares, 2017, Hilker and Schmölling, 2019). Therefore, tree experience of drought within a

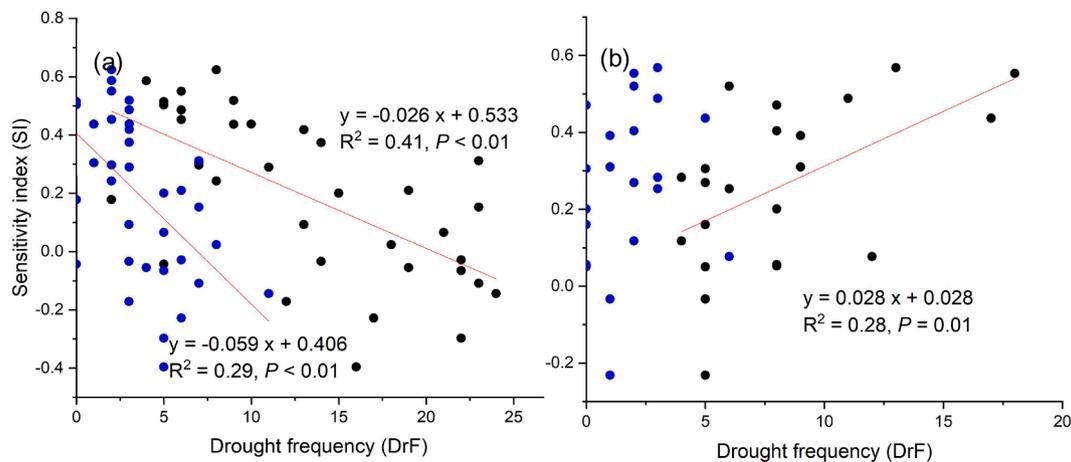


Fig. 4. Juniper sensitivity indices (*SI*) to water deficit at wetter sites (a) and drier sites (b) is subject to different drought frequencies (*DrF*). The dots represent sensitivity indices in “severe-drought” (black dots) and “drought” (blue dots) years, which are defined as years in which the mean PDSI in May and June is below -3 and -2, respectively. Red lines represent linear regression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

certain range produces stress memory, which appears to reduce sensitivity to extreme drought events.

However, contrary to results obtained in wetter regions, we found that frequent drought leads to higher tree sensitivity and does not result in increased forest resistance in drier regions. Trees located in drier regions have already suffered from long-term drought; more frequent droughts would cause physiological damage, especially for juniper, an anisohydric species that can maintain stomatal conductance during conditions of water deficit (Wei et al., 2019, Fang et al., 2020). Continuous water deficit in long-term drought conditions would further increase the tension in the xylem possibly leading to embolisms and hydraulic failure (Hartmann, 2011). In this case, trees would run slowly out of reserves, which reduces their ability to survive another drought.

4.3. Forest sustainability on the Tibetan Plateau under global warming

Increasing temperature and precipitation have been reported over the TP during the last century (Li et al., 2010, Deji et al., 2017). Local meteorological stations also recorded significantly increasing temperature over the TP and increasing precipitation in central TP and decreasing precipitation in the southern Himalayas from 1979 to 2018. Current global warming was predicted to have increasing impacts on forest ecosystems on the TP.

In most regions, increased precipitation would reduce the sensitivity of juniper to extreme drought events. It is therefore likely that juniper forests on the TP will benefit from increasing precipitation and alleviation of drought stress. Indeed, increasing resilience was reported in recent decades on the TP (Fang and Zhang, 2019), which may promote forest health and lead to a greening trend (Zhu et al., 2016, Lamsal et al., 2017).

On the southern TP, tree resistance could benefit from more water supply induced by climate change. Glaciers on the TP have experienced serious mass loss over the last five decades, especially on the southeastern TP (Gao et al., 2019a,b, Yao et al., 2019). Thousands of moraine-dammed glacial lakes have formed since the 1980s (Veh et al., 2019). It is possible that trees at high-elevation sites benefit from the surplus of soil moisture. But changes in the moisture balance as glaciers retreat also introduce considerable uncertainty with regard to forest resilience to drought.

Forest sensitivity to drought is highly dependent on hydrological dynamics. Therefore, we emphasize the important of effective hydrological monitoring and management on the high-elevational TP, which will help us evaluate and predict forest health under global warming.

5. Conclusion

Our study reveals a spatial pattern in the sensitivity of juniper forests to drought across the TP. This pattern is strongly influenced by the frequency and severity of past droughts, which therefore implies the effect of ecological memory on the current growth response. On the one hand, trees at drier sites, where past drought frequency and severity were higher, are more sensitive to drought. On the other hand, at more humid sites, frequent droughts increased tree’s tolerance to drought. Forest at wetter sites would grow better given their higher resistance to drought, while an inverse case would occur at drier sites. This may result in a shift in ecosystem over broad spatial scale on the TP. This study may allow for a better prediction of forest health risk over the TP and provide directions for spatially targeted forest management according to different moisture conditions in a changing climate.

Data accessibility statement

The information of tree-ring data is available in the Supporting Information for this article. All metrological data used for this study can be accessed via <http://climexp.knmi.nl>.

CRediT authorship contribution statement

Ouya Fang: Data curation, Formal analysis, Writing - original draft. **Qi-Bin Zhang:** Project administration, Conceptualization, Resources, Funding acquisition. **Yann Vitasse:** Methodology, Software, Validation. **Roman Zweifel:** Visualization. **Paolo Cherubini:** Supervision, Methodology, Validation, Writing - original draft.

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.

Acknowledgements

This work was supported by the Second Tibetan Plateau Scientific Expedition and Research Program, China (STEP) [NO. 2019QZKK0301] and by the National Natural Science Foundation of China, China project [No. 31870460 and 31700412]. We thank members of Qi-Bin Zhang’s team for assistance in tree-ring sampling and we thank Hengfeng Jia for assist in programming.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.118968>.

References

- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, art129. <https://doi.org/10.1890/ES15-00203.1>.
- Allen, C.R., Angeler, D.G., Cumming, G.S., Folke, C., Twidwell, D., Uden, D.R., 2016. Quantifying spatial resilience. *J. Appl. Ecol.* 53, 625–635. <https://doi.org/10.1111/1365-2664.12634>.
- Backhaus, S., Kreyling, J., Grant, K., Beierkuhnlein, C., Walter, J., Jentsch, A., 2014. Recurrent mild drought events increase resistance toward extreme drought stress. *Ecosystems* 17, 1068–1081. <https://doi.org/10.1007/s10021-014-9781-5>.
- Blonder, B., Moulton, D.E., Blois, J., Enquist, B.J., Graae, B.J., Macias-Fauria, M., Svenning, J.C., 2017. Predictability in community dynamics. *Ecol. Lett.* 20, 293–306. <https://doi.org/10.1111/ele.12736>.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *PNAS* 102, 15144–15148. <https://doi.org/10.1073/pnas.0505734102>.
- Brienen, R.J., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., Zagt, R.J., 2015. Long-term decline of the Amazon carbon sink. *Nature* 519, 344–348. <https://doi.org/10.5521/ForestPlots.net/2014.4>.
- Bruce, T.J., Matthes, M.C., Napier, J.A., Pickett, J.A., 2007. Stressful “memories” of plants: evidence and possible mechanisms. *Plant Sci.* 173, 603–608. <https://doi.org/10.1016/j.plantsci.2007.09.002>.
- Bunn, A.G., 2008. A dendrochronology program library in R (dplR). *Dendrochronologia* 26, 115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>.
- Camarero, J.J., Olano, J.M., Parras, A., 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytologist* 185, 471–480.
- Camarero, J.J., Bigler, C., Linares, J.C., Gil-Pelegrín, E., 2011. Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *Forest Ecol. Manage.* 262, 759–769. <https://doi.org/10.1016/j.foreco.2011.05.009>.
- Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Cantero, A., Sánchez-Salguero, R., Sánchez-Miranda, A., Ibáñez, R., 2018. Forest growth responses to drought at short- and long-term scales in Spain: squeezing the stress memory from tree rings. *Frontiers Ecol. Evol.* 6, art 9. <https://doi.org/10.3389/fevo.2018.00009>.
- Camarero, J.J., Gazol, A., Sánchez-Salguero, R., Sangüesa-Barreda, G., Díaz-Delgado, R., Casals, R., 2020. Dieback and mortality of junipers caused by drought: dissimilar growth and wood isotope patterns preceding shrub death. *Agric. For. Meteorol.* 291, 108078.
- Cavin, L., Jump, A.S., 2017. Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Glob. Change Biol.* 23, 362–379. <https://doi.org/10.1111/gcb.13366>.
- Cook, E.R., Briffa, K., Shiyatov, S., Mazepa, V., 1990. In: Cook, E.R., Kairiukstis, L.A. (Eds.), *Tree-ring standardization and growth-trend estimation. Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic, pp. 104–123.
- Chen, L., Huang, J.G., Dawson, A., Zhai, L.H., Stadt, K., Comeau, P., Whitehouse, C., 2018. Contributions of insects and droughts to growth decline of trembling aspen mixed boreal forest of western Canada. *Glob. Change Biol.* 24, 655–667. <https://doi.org/10.1111/gcb.13855>.
- Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., Lopez, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. *Nature* 558, 531–539. <https://doi.org/10.1038/s41586-018-0240-x>.
- Cierner, C., Boers, N., Hirota, M., Kurths, J., Muller-Hansen, F., Oliveira, R.S., Winkelmann, R., 2019. Higher resilience to climatic disturbances in tropical vegetation exposed to more variable rainfall. *Nat. Geosci.* 12, 174–179. <https://doi.org/10.1038/s41561-019-0312-z>.
- Crockett, J.L., Westerling, A.L., 2018. Greater temperature and precipitation extremes intensify Western US droughts, wildfire severity, and Sierra Nevada tree mortality. *J. Clim.* 31, 341–354. <https://doi.org/10.1175/JCLI-D-17-0254.1>.
- Deji, Y., Yao, T.D., Yang, X.X., Xu, B.Q., Zhao, H.B., Li, J.L., ... Li, Q.L., 2017. Warming and wetting climate during last century revealed by an ice core in northwest Tibetan Plateau. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 487, 270–277. doi: 10.1016/j.palaeo.2017.09.009.
- DeSoto, L., Caillere, M., Sterck, F., Jansen, S., Kramer, K., Robert, E.M.R., Martínez-Vilalta, J., 2020. Low growth resilience to drought is related to future mortality risk in trees. *Nat. Commun.* 11, art4545. <https://doi.org/10.1038/s41467-020-14300-5>.
- Fang, O.Y., Alfaro, R.I., Zhang, Q.-B., 2018. Tree rings reveal a major episode of forest mortality in the late 18th century on the Tibetan Plateau. *Global Planet. Change* 163, 44–50. <https://doi.org/10.1016/j.gloplacha.2018.02.004>.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, London, New York and San Francisco.
- Fang, O.Y., Qiu, H.Y., Zhang, Q.-B., 2020. Species-specific drought resilience in juniper and fir forests in the central Himalayas, 106615 *Ecol. Ind.* 117. <https://doi.org/10.1016/j.ecolind.2020.106615>.
- Fang, O.Y., Zhang, Q.-B., 2019. Tree resilience to drought increases in the Tibetan Plateau. *Glob. Change Biol.* 25, 245–253. <https://doi.org/10.1111/gcb.14470>.
- Galviz, Y.C.F., Ribeiro, R.V., Souza, G.M., 2020. Yes, plants do have memory. *Theor. Exp. Plant Physiol.* 32, 195–202. <https://doi.org/10.1007/s40626-020-00181-y>.
- Gao, J., Yao, T.D., Cai, R., Zhang, T.H., He, Z.Q., Niu, X.W., Xu, B.Q., Wu, G.J., 2019a. Observation of the atmospheric water vapor stable isotopes in three dimensions over the Tibetan Plateau. *Chin. Sci. Bull.* 64, 2822–2829. <https://doi.org/10.1360/TB-2019-0125>.
- Gao, J., Yao, T.D., Masson-Delmotte, V., Steen-Larsen, H.C., Wang, W.C., 2019b. Collapsing glaciers threaten Asia’s water supplies. *Nature* 565, 19–21. <https://doi.org/10.1038/d41586-018-07838-4>.
- Gazol, A., Camarero, J.J., Gutiérrez, E., Poppo, I., Andreu-Hayles, L., Motta, R., Carrer, M., 2015. Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *J. Biogeogr.* 42, 1150–1162. <https://doi.org/10.1111/jbi.12512>.
- Gazol, A., Camarero, J.J., 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. *J. Ecol.* 104, 1063–1075. <https://doi.org/10.1111/1365-2745.12575>.
- Gazol, A., Camarero, J.J., Anderegg, W.R.L., Vicente-Serrano, S.M., 2017. Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Glob. Ecol. Biogeogr.* 26, 166–176. <https://doi.org/10.1111/gcb.12526>.
- Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sanchez-Salguero, R., Gutierrez, E., de Luis, M., Galvan, J.D., 2018. Forest resilience to drought varies across biomes. *Glob. Change Biol.* 24, 2143–2158. <https://doi.org/10.1111/gcb.14082>.
- Gazol, A., Camarero, J.J., Sánchez-Salguero, R., Vicente-Serrano, S.M., Serramalquer, X., Galván, J.D., 2020. Drought legacies are short, prevail in dry conifer forests and depend on growth variability. *J. Ecol.* 108, 2473–2484. <https://doi.org/10.1111/1365-2745.13435>.
- Hartmann, H., 2011. Will a 385 million year-struggle for light become a struggle for water and for carbon? – How trees may cope with more frequent climate change-type drought events. *Glob. Change Biol.* 17, 642–655. <https://doi.org/10.1111/j.1365-2486.2010.02248.x>.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* 43, 69–78.
- He, M.H., Bräuning, A., Griebinger, J., Hochreuther, P., Wernicke, J., 2018. May–June drought reconstruction over the past 821 years on the south-central Tibetan Plateau derived from tree-ring width series. *Dendrochronologia* 47, 48–57. <https://doi.org/10.1016/j.dendro.2017.12.006>.
- Hilker, M., Schmölling, T., 2019. Stress priming, memory, and signalling in plants. *Plant, Cell Environ.* 42, 753–761. <https://doi.org/10.1111/pce.13526>.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23. <https://doi.org/10.1146/annurev.ec.04.110173.000245>.
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Brockerhoff, E.G., 2017. Tree diversity drives forest stand resistance to natural disturbances. *Curr. Forestry Rep.* 3, 223–243. <https://doi.org/10.1007/s40725-017-0064-1>.
- Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. *Ecol. Lett.* 17, 1560–1569. <https://doi.org/10.1111/ele.12382>.
- Jump, A.S., Hunt, J.M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Change Biol.* 12, 2163–2174. <https://doi.org/10.1111/j.1365-2486.2006.01250.x>.
- Lamsal, P., Kumar, L., Shabani, F., Atreya, K., 2017. The greening of the Himalayas and Tibetan Plateau under climate change. *Global Planet. Change* 159, 77–92. <https://doi.org/10.1016/j.gloplacha.2017.09.010>.
- Lebourgeois, F., Gomez, N., Pinto, P., Mérian, P., 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol. Manage.* 303, 61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>.
- Li, L., Yang, S., Wang, Z.Y., Zhu, X.D., Tang, H.Y., 2010. Evidence of warming and wetting climate over the Qinghai-Tibet Plateau. *Acta. Antarct. Alp. Res.* 42, 449–457. <https://doi.org/10.1657/1938-4246-42.4.449>.
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>.
- Lyu, L.X., Zhang, Q.-B., Pellatt, M.G., Büntgen, U., Li, M.-H., Cherubini, P., 2019. Drought limitation on tree growth at the Northern Hemisphere’s highest tree line. *Dendrochronologia* 53, 40–47. <https://doi.org/10.1016/j.dendro.2018.11.006>.
- Mou, Y.-M., Fang, O.Y., Cheng, X.H., Qiu, H.Y., 2019. Recent tree growth decline unprecedented over the last four centuries in a Tibetan juniper forest. *J. For. Res.* 30, 1429–1436. <https://doi.org/10.1007/s11676-018-0856-6>.
- Mu, Y.-M., Zhang, Q.-B., Fang, O.Y., Lyu, L.X., Cherubini, P., 2021. Pervasive tree-growth reduction in Tibetan juniper forests, 118642 *For. Ecol. Manage.* 480. <https://doi.org/10.1016/j.foreco.2020.118642>.
- Peltier, D.M.P., Ogle, K., 2019. Legacies of La Niña: North American monsoon can rescue trees from winter drought. *Glob. Change Biol.* 25, 121–133. <https://doi.org/10.1111/gcb.14487>.
- Pimm, S.L., 1984. The complexity and stability of ecosystems. *Nature* 307, 321–326. <https://doi.org/10.1038/307321a0>.
- Piraino, S., 2020. Assessing *Pinus pinea* L. resilience to three consecutive droughts in central-western Italian Peninsula. *iForest – Biogeosci. Forestry* 13, 246–250. <https://doi.org/10.3832/ifor3320-013>.
- Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol.* 15, 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>.
- Qiu, J., 2008. China: the third pole. *Nature* 454, 393–396. <https://doi.org/10.1038/454393a>.
- Ramírez-Valiente, J.A., Cavender-Bares, J., 2017. Evolutionary trade-offs between drought resistance mechanisms across a precipitation gradient in a seasonally dry tropical oak (*Quercus oleoides*). *Tree Physiol.* 37, 889–901. <https://doi.org/10.1093/treephys/tpx064>.

- Schweingruber, F.H., 1988. *Tree Rings: Basics and Applications of Dendrochronology*. Kluwer Academic.
- Schwalm, C.R., Anderegg, W.R.L., Michalak, A.M., Fisher, J.B., Biondi, F., Koch, G., Tian, H., 2017. Global patterns of drought recovery. *Nature* 548, 202–205. <https://doi.org/10.1038/nature23021>.
- Shao, X.M., Wang, S.Z., Zhu, H.F., Xu, Y., Liang, E.Y., Yin, Z.-Y., Xu, X.G., Xiao, Y.M., 2009. A 3585-year ring-width dating chronology of Qilian juniper from the northeastern Qinghai-Tibetan Plateau. *IAWA J.* 30, 379–394. <https://doi.org/10.1163/22941932-90000226>.
- Sánchez-Salguero, R., Camarero, J.J., 2020. Greater sensitivity to hotter droughts underlies juniper dieback and mortality in Mediterranean shrublands, 137599 *Sci. Total Environ.* 721. <https://doi.org/10.1016/j.scitotenv.2020.137599>.
- Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38, 55–94. <https://doi.org/10.2307/210739>.
- Veh, G., Korup, O., von Specht, S., Roessner, S., Walz, A., 2019. Unchanged frequency of moraine-dammed glacial lake outburst floods in the Himalaya. *Nat. Clim. Change* 9, 379–383. <https://doi.org/10.1038/s41558-019-0437-5>.
- Versace, S., Gianelle, D., Garfi, V., Battipaglia, G., Lombardi, F., Marchetti, M., Tognetti, R., 2020. Interannual radial growth sensitivity to climatic variations and extreme events in mixed-species and pure forest stands of silver fir and European beech in the Italian Peninsula. *Eur. J. Forest Res.* 139, 627–645. <https://doi.org/10.1007/s10342-020-01274-8>.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscale drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Clim.* 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>.
- Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Wohlgemuth, T., 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. *Glob. Change Biol.* 25, 3781–3792. <https://doi.org/10.1111/gcb.14803>.
- Wei, L., Xu, C.G., Jansen, S., Zhou, H., Christoffersen, B.O., Pockman, W.T., McDowell, N. G., 2019. A heuristic classification of woody plants based on contrasting shade and drought strategies. *Tree Physiol.* 39, 767–781. <https://doi.org/10.1093/treephys/tpy146>.
- Willis, K.J., Jeffers, E.S., Tovar, C., 2018. What makes a terrestrial ecosystem resilient? *Science* 359, 988–989. <https://doi.org/10.1126/science.aar5439>.
- Yao, T.D., Yu, W.S., Wu, G.J., Xu, B.Q., Yang, W., Zhao, H.B., Li, Z.Q., 2019. Glacier anomalies and relevant disaster risks on the Tibetan Plateau and surroundings. *Chin. Sci. Bull.* 64, 2770–2782. <https://doi.org/10.1360/TB-2019-0246>.
- Yin, Z.-Y., Zhu, H.F., Huang, L., Shao, X.M., 2016. Reconstruction of biological drought conditions during the past 2847 years in an alpine environment of the northeastern Tibetan Plateau, China, and possible linkages to solar forcing. *Global Planet. Change* 143, 214–227. <https://doi.org/10.1016/j.gloplacha.2016.04.010>.
- Zhang, Q.-B., Evans, M.N., Lyu, L.X., 2015. Moisture dipole over the Tibetan Plateau during the past five and a half centuries. *Nat. Commun.* 6, 8062. <https://doi.org/10.1038/ncomms9062>.
- Zhang, Q.-B., Fang, O.Y., 2020. Tree rings circle an abrupt shift in climate. *Science* 370, 1037–1038.
- Zhu, Z.C., Piao, S.L., Myneni, R.B., Huang, M.T., Zeng, Z.Z., Canadell, J.G., Zeng, N., 2016. Greening of the Earth and its drivers. *Nat. Clim. Change* 6, 791–795. <https://doi.org/10.1038/nclimate3004>.
- Zweifel, R., Etzold, S., Sterck, F., Gessler, A., Anfodillo, T., Mencuccini, M., Rigling, A., 2020. Determinants of legacy effects in pine trees – implications from an irrigation-stop experiment. *New Phytol.* 227, 1081–1096. <https://doi.org/10.1111/nph.16582>.