Increasing Sensitivity of Tree Radial Growth to Precipitation

Geophysical Research Letters

RESEARCH LETTER
10.1029/2024GL110003

Increasing Sensitivity of Tree Radial Growth to Precipitation

Tiewei Li[1], Bin He[1], Deliang Chen[2], Hans W. Chen[3], Lanlan Guo[1], Wenping Yuan[4], Keyan Fang[5], Feng Shi[6], Lianyou Liu[1], Huan Zheng[1], Ling Huang[4], Xiuchen Wu[1], Xingming Hao[7], Xiang Zhao[1], and Weiguo Jiang[1]

[1]Faculty of Geographical Science, Beijing Normal University, Beijing, PR China, [2]Department of Earth Sciences, Regional Climate Group, University of Gothenburg, Gothenburg, Sweden, [3]Department of Space, Earth and Environment, Chalmers University of Technology, Gothenburg, Sweden, [4]College of Urban and Environmental Sciences, Peking University, Beijing, China, [5]Key Laboratory of Humid Subtropical Eco-Geographical Process (Ministry of Education), College of Geographical Sciences, Fujian Normal University, Fuzhou, China, [6]Key Laboratory of Cenozoic Geology and Environment, Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing, China, [7]Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Xinjiang, PR China

Abstract The sensitivity of tree growth to precipitation regulates their responses to drought, and is a crucial metric for predicting ecosystem dynamics and vulnerability. Sensitivity may be changing with continuing climate change, yet a comprehensive assessment of its change is still lacking. We utilized tree ring measurements from 3,044 sites, climate data and CO_2 concentrations obtained from monitoring stations, combined with dynamic global vegetation models to investigate spatiotemporal changes in the sensitivity over the past century. We observed an increasing sensitivity since around 1950. This increased sensitivity was particularly pronounced in arid biomes due to the combined effect of increased precipitation and elevated CO_2. While elevated CO_2 reduced the sensitivity of the humid regions, the intensified water pressure caused by decreased precipitation still increased the sensitivity. Our findings suggest an escalating vulnerability of tree growth to precipitation change, which may increase the risk of tree mortality under future intensified drought.

Plain Language Summary The sensitivity of tree growth to precipitation strongly regulates global vegetation dynamics and their responses to climate change, yet changes in sensitivity remain poorly understood. Here, we defined a sensitivity of tree radial growth to precipitation, and found that most tree species showed an increased sensitivity in the second half of the 20th century. This increased sensitivity in arid biomes could be attributed to increasing precipitation, while the increased sensitivity in humid biomes was caused by decreasing precipitation. Although elevated atmospheric CO_2 have generally increased sensitivity in arid biomes and decreased it in humid biomes, these contrasting influences were ultimately overshadowed by changes in precipitation, resulting in an overall increased sensitivity across both arid and humid biomes.

Key Points:

- The sensitivity of tree growth to precipitation is increasing since around 1950, both at the arid and humid biomes
- This increased sensitivity is particularly pronounced in arid biomes due to the combined effect of increased precipitation and elevated CO_2
- Although elevated CO_2 reduce the sensitivity in humid biomes, the decreased precipitation still lead to an increased sensitivity

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

B. He and L. Guo,
hebin@bnu.edu.cn;
guolanlan@bnu.edu.cn

Citation:

Li, T., He, B., Chen, D., Chen, H. W., Guo, L., Yuan, W., et al. (2024). Increasing sensitivity of tree radial growth to precipitation. *Geophysical Research Letters*, *51*, e2024GL110003. https://doi.org/10.1029/2024GL110003

Received 13 JUN 2024
Accepted 15 AUG 2024

1. Introduction

Trees play a critical role in regulating global carbon cycles by fixing approximately 15% of anthropogenic CO_2 emissions annually through photosynthesis and wood formation (Huang et al., 2020). Trees increasingly contribute to climate change mitigation efforts as countries strive to achieve their carbon reduction targets through carbon sequestration (Heilman et al., 2022). Precipitation regulates the water availability in soil and establishes an essential resource for cambial activity and wood production of trees (Żywiec et al., 2017). It has been identified as one of the primary environmental factors determining the radial growth of trees, especially in low- and mid-latitude regions (Zhang et al., 2022). For example, trees radial growth in tropical Mexico is predominantly influenced by interannual variations in precipitation (Biondi, 2001). With projected increases in climate variability, the interannual variation of precipitation may also increase, potentially posing strong impacts on trees growth (Berdugo et al., 2020). Therefore, quantifying accurately the sensitivity of tree growth to precipitation at a large spatiotemporal scale is essential for comprehending ecosystem processes and predicting dynamics of the global carbon cycle under climate change.

The sensitivity measures how tree radial growth changes with variations in precipitation and a positive sensitivity value indicates that increase in precipitation will promote tree growth and vice versa (Hu et al., 2018; Wilcox et al., 2016; Zeng et al., 2022). Spatially, it is generally believed that sensitivity are higher in arid biomes (Sala et al., 2012) and decreases with the increasing mean precipitation (Maurer et al., 2020). However, the temporal changes in the sensitivity are still under debate due to limited duration of satellite-derived vegetation indices.

Zeng et al. (2022) demonstrated a global declining trend in the sensitivity of vegetation productivity to precipitation over the past two decades attributed to the increase in precipitation. But a robust increase in the sensitivity of vegetation productivity to precipitation over many arid regions due to rising atmospheric CO_2 concentrations has also been reported (Zhang et al., 2022). These divergent perspectives highlight our limited understanding of the temporal changes in the precipitation sensitivity.

Here, we focus on examining the spatiotemporal changes of precipitation sensitivity from the perspective of the radial growth of trees based on tree ring chronologies. Tree ring chronologies provide information about radial growth of individual trees and are widely used to assess the response of tree growth to climate change (Anderegg et al., 2015; Gedalof & Berg, 2010; X. Li et al., 2020). Therefore, tree ring chronologies have great potential utility as robust and useful indicators for quantifying the changes of the sensitivity and to exploring the underlying mechanisms. We hypothesize that sensitivity may have changed significantly over the past century due to continued climate change. To test this hypothesis, we used 3,044 tree ring chronologies, combined with an ensemble of dynamic global vegetation models (DGVMs) simulations to evaluate the spatiotemporal patterns of change in sensitivity during 1901–2012 and investigate the possible factors driving its temporal dynamic.

2. Data and Methods

2.1. Climatic Metrics

The monthly precipitation, temperature, actual vapor pressure, potential evapotranspiration, and Palmer Drought Severity Index (PDSI) from 1901 to 2012 were obtained from the Climate Research Unit (CRU) data set provided by the University of East Anglia in the UK (CRU TS 4.07, 0.5° × 0.5°) (Harris et al., 2020; Karim et al., 2020; Pan et al., 2020; Zeng et al., 2022). The shortwave radiation data (SWR; 0.5° × 0.5°) were obtained from the Terrestrial Hydrology Research Group at Princeton University (Sheffield et al., 2006). The aridity index (AI) was calculated as the ratio between the precipitation and potential evapotranspiration (Figure S1 in Supporting Information S1) and was used identify arid regions (AI ≤ 0.65) and humid regions (AI > 0.65) (Jiao et al., 2021; Trabucco & Zomer, 2018). We also calculated the vapor pressure deficit based on the maximum temperature, minimum temperature, and actual vapor pressure:

$$e^0(T) = 0.6108 \exp\left[\frac{17.27T}{T + 237.3}\right] \tag{1}$$

$$e_s = \frac{e^0(T_{\max}) + e^0(T_{\min})}{2} \tag{2}$$

$$\mathrm{VPD} = e_s - e_a \tag{3}$$

where T is the air temperature (°C) and $e^0(T)$ is the saturated vapor pressure at temperature T (kPa); e_s is the saturated vapor pressure; $T_{\max}$ and $T_{\min}$ are daily mean maximum and minimum temperature; and e_a is the actual vapor pressure (Z. Li et al., 2014).

The atmospheric CO_2 concentration data were obtained from the Mauna Loa Observatory, provided by the Scripps Institution of Oceanography. We derived the monthly CO_2 growth rate as the first-order difference in CO_2 concentrations in two successive months. We then removed the mean seasonal cycle and applied a 12-month moving sum to convert the monthly values to an annual CGR (Humphrey et al., 2018).

2.2. Tree Ring Data

Tree ring width measurements provide information about tree radial growth and climatic signals (X. Li et al., 2020). The raw tree ring width measurements were obtained from the International Tree Ring Data Bank (ITRDB). We applied the regional curve standardization to remove the age-related trends from raw tree ring width measurements and preserve the effects of environmental signals at inter-annual timescales using the *dplR* package in R (Briffa & Melvin, 2011; Helama et al., 2017). Raw tree ring width series were aligned by cambial age (ring number from bark to pith), followed by mean tree ring width calculation for each series. A smoothing spline with a 50% frequency response cut-off at 10% maximum cambial age curve wavelength (the Regional Curve) was then fitted to mean tree ring width series. Tree-level standardized ring width index were calculated as ratios between

individual series and the smoothed the Regional Curve (Bosela et al., 2018). At each sites, multiple tree-level standardized tree ring index were processed into site-level standard chronologies using bi-weight robust mean method (Cook & Kairiukstis, 2013). Finally, a total of 3,485 site-level standard chronologies were selected based on availability of metadata, such as longitude, latitude, elevation and species code and 3,044 chronologies covering at least 70 years between 1901 and 2012 was used to analyze the sensitivity in order to ensure the robustness of the results (Figure S4 in Supporting Information S1). Among these sites, there were 292 tree species, with 65 tree species occurring in at least 10 sites. About 80% of the sites are gymnosperm species and about 20% of the sites are angiosperm species. Using the geographic coordinates of each tree ring site from the ITRDB metadata, we extracted the biomes in which each tree ring site occurred and grouped them into five major biomes (Figure S2 in Supporting Information S1): alpine and boreal, desert, Mediterranean, temperate forest, and tropical forest biomes (Olson et al., 2001).

2.3. Precipitation Sensitivity of Tree Growth and Its Temporal Dynamics

A multiple linear regression analysis of the standardized chronologies and the climate factors (average annual precipitation, temperature and shortwave radiation) from 1901 to 2012 was performed. Climate factors were standardized, and detrended by subtracting linear trends from original data (He et al., 2023; Tang et al., 2024). The slope of the regression was used as the sensitivity of the tree radial growth to precipitation (Maurer et al., 2020; Wang et al., 2018; Zeng et al., 2022). A positive sensitivity indicates that an increase in annual precipitation promoted tree growth, and vice versa. To account for multicollinearity among independent variables, we performed a ridge regression analysis to verify the results.

A 30-year moving window was used to quantify the temporal dynamics of sensitivity from 1901 to 2012. The independent and dependent variables within each 30-year window were also detrended and standardized according to the method mentioned above. 20-year, 25-year and 40-year moving windows were used to evaluate the robustness of the results of the 30-year moving window. The overall study period was divided into two sub-periods using the window "1950–1980" as a split: pre-1950 period and post-1950 period. And the sensitivity trend of the two sub-periods was calculated respectively.

2.4. Random Forest Model

To investigate the potential drivers of the temporal changes in sensitivity, we developed a Random Forest model and predicted the observed temporal change of sensitivity based on a set of environmental factors. Random forest model can deal with complex nonlinear relations and its prediction ability is believed to be more stable compared with linear regression model (Schwalm et al., 2017). Here, we considered factors that could potentially influence changes in sensitivity: CO_2 concentration, CO_2 growth rates, PDSI, precipitation, temperature, shortwave radiation, vapor pressure deficit and their coefficients of variation (CV). CV is an absolute value that measures the degree of dispersion of a variable and represent the inter-annual variability in these environmental factors (Chen et al., 2019). The formula is generally expressed as:

$$CV = SD/AVE \times 100\%$$

where SD is the standard deviation and AVE is the mean of the studied variable.

The mean annual climate value and the corresponding CV, CO_2 concentration and CO_2 growth rates within each 30-year moving window were calculated to obtain the change of these factors, which were used as explanatory variables. The temporal dynamics of sensitivity as response variables. The Random Forest model was developed by randomly splitting the observed temporal dynamics of sensitivity into two separate samples: 60% of the records were used for model calibration, and the remaining 40% were used to validate the model's performances in terms of the coefficient of determination (R^2), the mean squared error, and the percentage bias. The Random Forest model implemented here used 100 regression trees, whose depth and number of predictors sampled at each node were identified using Bayesian optimization (Forzieri et al., 2022). We then calculated the variable importance score, which reflect how important each covariate was in determining the change in sensitivity (Schwalm et al., 2017).

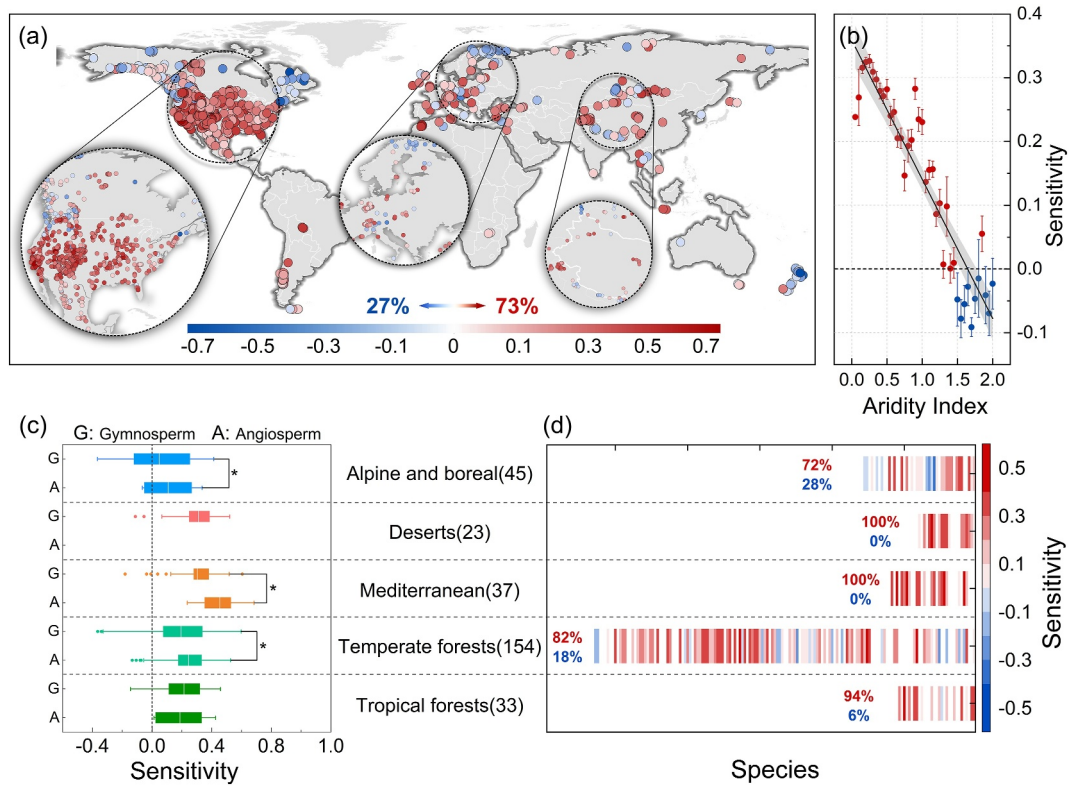

Figure 1. (a) Spatial pattern of the sensitivity for 1901–2012 calculated from a multiple linear regression between tree ring chronologies and precipitation, temperature, and shortwave radiation. (b) Variations in sensitivity along the gradient of the aridity index. (c) The average sensitivity of gymnosperms and angiosperms in each biome. The asterisk indicates a significant difference in the *t*-test. (d) The sensitivity of 210 tree species across five biomes. The numbers in parentheses indicate the number of species.

2.5. Analysis of Vegetation Models

In general, the radial growth of trees is reflected in the change in the carbon pool in the wood. Carbon has a long turnover time in wood, so comparing the sensitivity of this carbon pool to precipitation in these models with sensitivity calculated from tree ring should be useful (Anderegg et al., 2015). Here, we used simulated carbon content in sapwood and hardwood of DGVMs (Eight DGVMs simulate this variable) as a proxy for the trees radial growth to analyze how external driving factors affect the temporal changes of sensitivity (Zeng et al., 2022; Zhu et al., 2016). We selected three experimental scenarios to evaluate the relative contribution of three main driving factors, CO_2 fertilization effect, climate change and land cover change, to the change of sensitivity. S1 scenarios: varying CO_2 only; S2 scenarios: varying CO_2 and climate; S3 scenarios: varying CO_2, climate and land cover change. We only selected the model results that were consistent with the sensitivity observed by the tree ring and calculated the sensitivity in each 30-year moving window. The trend in sensitivity from S1 quantified the impact of the CO_2 fertilization effect; the differences between S2 and S1 and between S3 and S2 represent the changes in sensitivity attributable to changes in climatic factors and land cover changes, respectively (Table S2 in Supporting Information S1).

3. Results

3.1. Spatial Patterns of the Sensitivity of Tree Radial Growth to Precipitation

The sensitivity of tree radial growth to precipitation during 1901–2012 exhibited positive sensitivity at 73% of the sites. Only 27% of sites showed negative sensitivity, primarily in humid high latitude or altitude regions, such as Rocky, Alps, Tibetan Plateau and New Zealand (Figure 1a and Figures S5–S7 in Supporting Information S1). Moreover, the sensitivity declined along the AI gradient (Figure 1b), with trees in arid biomes generally showed higher sensitivity than trees in humid biomes (Figure S8 in Supporting Information S1). This suggests that in arid

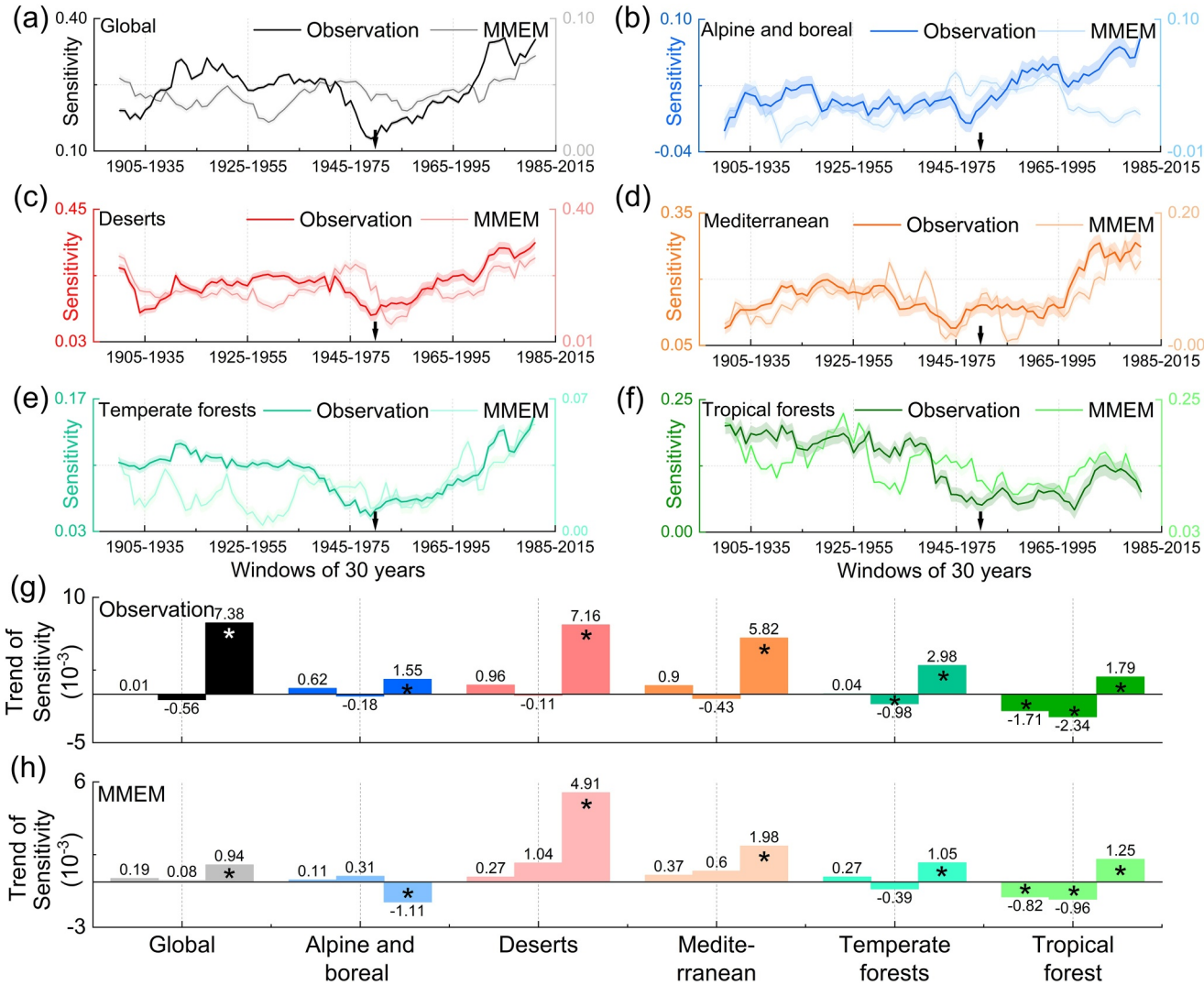

Figure 2. (a–f) Temporal changes in sensitivity determined using a 30-year moving window over 1901–2012. Dark lines represent changes in the average sensitivity calculated from tree rings, and light lines represent sensitivity calculated from the multi-model ensemble mean from six dynamic global vegetation models. The arrow in each subplot indicates the windows "1950–1980" as a split for the pre-1950 period and post-1950 period. (g–h) The mean trend in sensitivity for the entire study period, the pre-1950 period, and the post-1950 period. An asterisk (*) indicates a significant trend ($p < 0.001$).

regions, increased precipitation facilitates tree growth, whereas in humid regions, tree growth is not limited by precipitation and even excessive precipitation may impede tree growth due to excess waterlogging (W. Li et al., 2022). Additionally, we quantified the sensitivity at the tree species scale and found that gymnosperms exhibited lower sensitivity than angiosperm ($p < 0.05$) in Alpine and boreal, Mediterranean and Temperate forests biomes (Figure 1c). Approximately 85% of tree species showed positive sensitivity. All tree species growing in arid biomes showed positive sensitivity (23 species in the deserts biomes and 37 species in the Mediterranean biomes). Only 15% tree species showed negative sensitivity, mainly in humid biomes (Figure 1d). For example, *Larix laricina* in Alpine and boreal biomes, *Picea rubens Sarg* in Temperate forests biomes and *Picea smithiana Boiss* in Tropical forests biomes. Tree species code and corresponding sensitivity values are shown in the Table S1 in Supporting Information S1.

3.2. Temporal Changes in the Sensitivity of Tree Radial Growth to Precipitation

The global average sensitivity showed a significant increasing trend (trend= $(7.38 \pm 0.46) \times 10^{-3}$, $p < 0.05$) in the post-1950 period, indicating an overall increasing impact of precipitation on the radial growth of trees (Figure 2a). The sensitivity in the arid biomes showed a more pronounced increasing trend than in humid biomes (Figures 2c

and 2d). And the sensitivity in the post-1950 period of arid biomes is significantly larger than that in the pre-1950 period ($p < 0.05$), which implies an increasing impact of precipitation (Figure S9 in Supporting Information S1). The sensitivity of tropical forest biomes showed a smaller increasing trend compared to other biomes, and exhibited a significant decreasing trend throughout the study period (Figure 2f and Figure S9 in Supporting Information S1). At the tree species scale, both gymnosperms and angiosperms showed a significant increase trend (trend=$(7.54 \pm 0.55) \times 10^{-3}$ and $(6.95 \pm 0.77) \times 10^{-3}$, $p < 0.05$, respectively) in the post-1950 period (Figure S12 in Supporting Information S1). Amongst the 65 dominant tree species, approximately 40 species showed an increasing trend in sensitivity after 1950 (Figure S10 in Supporting Information S1). In addition, consistent results were obtained when accounting for the legacy effect of precipitation from the previous year (Figure S6 in Supporting Information S1), using ridge regression method (Figure S7 in Supporting Information S1) and the different moving window (Figure S14 in Supporting Information S1).

We examined whether DGVMs from the TRENDY project capture the observed trends in sensitivity by using simulated carbon content in sapwood and hardwood as a proxy for the radial growth of trees. Six of the eight models still captured the increasing trends in sensitivity during post-1950 period (Figure 2 and Table S2 in Supporting Information S1). For desert, Mediterranean, temperate forest, and tropical forest biomes, the trends in sensitivity based on the models were consistent with those based on the tree ring data. But for the alpine/boreal biomes, the sensitivity derived from the model data showed decreasing rather than increasing trends (Figures 1c and 1h). The mismatch between the models and observations may be attributable to the uncertainties in the DGVMs at high latitudes and in cold regions. For example, the carbon allocation between leaf and wood is insufficiently considered or omitted from most current model formulations (Byrne et al., 2022; X. Liu et al., 2020; Restrepo-Coupe et al., 2017).

3.3. Precipitation and CO_2 Concentration as the Major Contributor for the Change in Sensitivity

We employed Random Forest model to investigate the underlying factors contributing to the observed increase in sensitivity (Forzieri et al., 2022) and found that the changes in precipitation and rising CO_2 concentration were the two dominant drivers, affecting the observed temporal changes in sensitivity at 24% and 32% sites, respectively (Figure S15 in Supporting Information S1). Interestingly, the variation of precipitation had contrasting effect on the sensitivity in arid and humid biomes. The increase in sensitivity in humid alpine/boreal and temperate forest biomes was associated with decreasing precipitation (Figures 3c and 3e; Figures S16a and S16b in Supporting Information S1), while the increase in sensitivity in arid desert and Mediterranean biomes was caused by increasing precipitation (Figures 3i and 3k; Figures S16d and S16e in Supporting Information S1). For the tropical forest biomes, the negative relationship between precipitation and sensitivity is weak ($R^2 = 0.15$, $p < 0.001$). In the regions with less precipitation, sensitivity decreased significantly with the increasing precipitation, while when annual precipitation is high, the trend of sensitivity is not significant (Figure S18 in Supporting Information S1).

Rising CO_2 concentration also had an opposite effect on sensitivity in arid and humid biomes in the post-1950 period (Figure 3 and Tables S3 and S4 in Supporting Information S1). Specifically, rising CO_2 concentration mainly contributed positively to the increase in sensitivity in arid biomes (desert and Mediterranean biomes; Figures 3j and 3l), while negative contributions were primarily found in humid temperate forest biomes (Figure 3f). For tropical forests and alpine/boreal biomes, rising CO_2 concentration had negligible influence on the trend in sensitivity (Figures 3b and 3h).

4. Discussion

Based on tree ring measurements and climate data, our study shows an increasing sensitivity of tree growth to precipitation during the latter half of the 20th century. The sensitivity of arid biomes exhibited a more pronounced increasing trend, primarily attributed to the combined impact of precipitation and CO_2. In arid biomes, xerophytic trees have evolved strong hydrological controls and photosynthetic capacities to adapt to water deficit conditions (Carminati & Javaux, 2020). Even slight increments in the water availability tend to trigger dramatic changes in leaf formation in trees (Berdugo et al., 2020; W. Li et al., 2022). However, under greater evaporative demand in arid biomes, this excessive leaf formation essentially increases the transpiration per leaf area and the sap flow in sapwood (Duursma et al., 2019; Wei et al., 2022). Consequently, trees will be forced to absorb more water, creating a positive feedback that further enhances sensitivity.

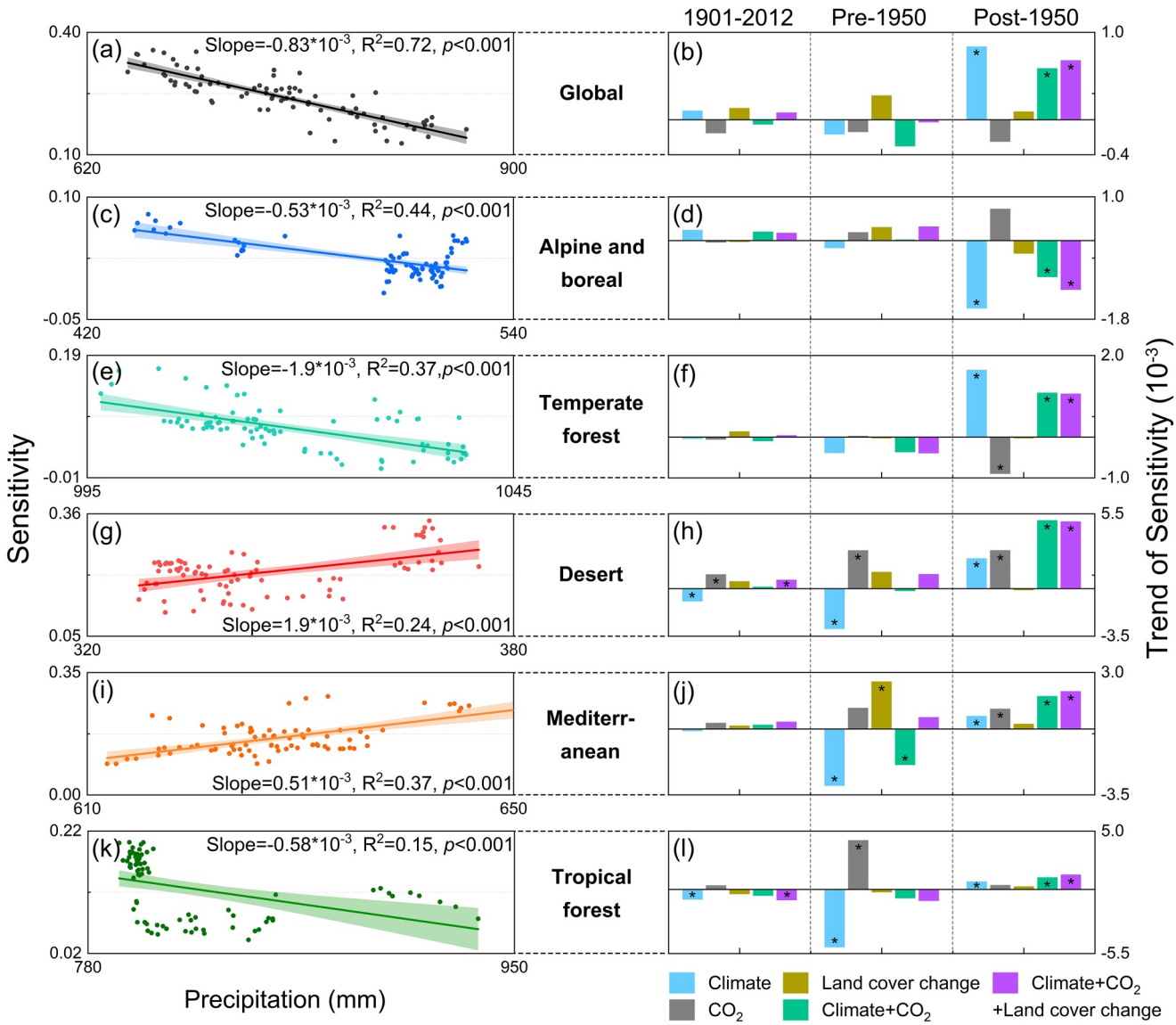

Figure 3. The left scatterplot shows the relationship between sensitivity and annual precipitation globally and in the five biomes, respectively. Shaded areas represent 95% CIs. The right histogram shows simulated trends of sensitivity driven by rising carbon dioxide (CO_2), climate change (climate), land use alone, or their combinations during the 1901–2012, pre-1950 and post-1950 period, respectively. The asterisk indicates a significant trend ($p < 0.05$). (a, b) Global; (c, d) Alpine and boreal biomes; (e, f) Temperate forest biomes; (g, h) Desert biomes; (h, i) Mediterranean biomes; (k, l) Tropical forest biomes.

Elevated CO_2 concentration is another important driver contributing to increased sensitivity in arid biomes. Elevated CO_2 increases the partial pressure of intercellular CO_2 and reduces transpiration by reducing stomatal conductance, which can lead to greater leaf-level photosynthesis and increase water-use efficiency (Keenan et al., 2013). Benefiting from this, trees further allocate excess carbon to other organs, which drives enhanced leaf or root formation, improving resource acquisition (Norby & Zak, 2011). However, for the arid desert and Mediterranean biomes, the strong increase in tree growth caused by CO_2 undoubtedly leads to an increase in water demand, and water loss through cuticular conductance and stomatal leakiness (Bazzaz, 1990; Donohue et al., 2017; Gedalof & Berg, 2010). The water-saving effect induced by elevated CO_2 is thus not sufficient to counteract the strong increasing water demand, leading to an increasing amount of water needed by the trees (Jiao et al., 2021; Zhang et al., 2022). Therefore, the elevated CO_2 concentration also contributed positively to the increase in sensitivity in arid biomes.

The decrease of precipitation in humid biomes results in increased sensitivity. Humid biomes typically possess sufficient water to maintain the normal growth of trees (Norby & Zak, 2011). However, subsequent exposure to reduced precipitation subsequently exacerbates water stress on trees (Wang et al., 2018; Zeng et al., 2022), compelling them to absorb more water to maintain steady water transport and avoid hydraulic failure-induced mortality (McDowell et al., 2008). Consequently, decreasing annual precipitation increases the dependence of tree growth on water conditions, thus increasing sensitivity (Donohue et al., 2017; Fatichi et al., 2016). For the tropical forest biomes that have experienced increasing annual precipitation, the overall alleviation of water stress due to increasing precipitation caused the decreasing trends in sensitivity. For example, Wang et al. (2018) reported that sensitivity is high in tropical vegetation in the dry season but is greatly reduced in the wet season when water stress is alleviated. However, the relationship between precipitation and sensitivity is segmented. This indicates that increasing precipitation reduced the dependence of tree growth on water conditions is only present in regions with lower precipitation. Conversely, tree growth is no longer limited by precipitation in regions with sufficient precipitation (Z. Liu et al., 2018). In addition, the decreasing trend in sensitivity is most likely also influenced by other factors, such as the strong negative influence of human activities (Abel et al., 2021).

Elevated CO_2 concentration mainly contributes negatively to changes in sensitivity in humid biomes. In temperate forest biomes, tree growth is mainly limited by light and nutrient availability, photosynthetic capacity, and carbon assimilation rate (Ainsworth & Rogers, 2007; Fatichi et al., 2014). The increase in water-use efficiency under elevated atmospheric CO_2 does not lead to a proportional increase in leaf and root formation (Norby & Zak, 2011; Zhang et al., 2022). Therefore, the CO_2-induced increase in water-use efficiency accompanied by an insignificant increase in tree growth reduces the total water consumption (Fatichi et al., 2016) and therefore sensitivity.

This increased sensitivity in both arid and biomes indicates that tree growth is more susceptible to precipitation changes. Despite precipitation is increasing in arid biomes, the increased leaf formation due to CO_2 fertilization effect may further increase water demand and reduce soil moisture and runoff (Mankin et al., 2017). The net effects lead to an increasing dependence of tree growth on precipitation. In the humid biomes, the CO_2 fertilizing effect reduces the sensitivity due to increase in water use efficiency, counter-intuitively, this cannot compensate for the impact of intensified water stress. The net effects still lead to an increased sensitivity. If the trend of increase in drought continues as the result of global warming (Lian et al., 2021), this increased sensitivity will force trees to face greater threats to survive in the future, affecting the ecosystem carbon exchange (He et al., 2023).

A possible limitation to keep in mind is that the sampling strategy of tree ring measurements usually focuses on trees in regions with strong climate change constraints, and the reduced formation of reliable tree rings in tropical forest biomes could be a source of uncertainty in terms of accurate assessments of spatiotemporal changes in sensitivity (X. Li et al., 2020; Zhao et al., 2019). Since meteorological observations were scarce in the early 20th century, there may be some uncertainty in the sensitivity calculated using CRU data sets. Therefore, we calculated the sensitivity using climate data during post-1950 and obtained the similar spatial pattern of sensitivity (Figure S17 in Supporting Information S1). Moreover, although earth system models are useful tools for assessing how ecosystems respond to inter-annual climate change, they must be evaluated using in-situ observational data. We have shown that the DGVMs reflect the observed temporal changes in sensitivity well, except in alpine/boreal biomes. Future modeling efforts must consider carbon reserve pools and the remobilization of non-structural carbohydrates in high-latitude and cold regions using carbon allocation schemes to refine the representation of stem wood carbon by explicitly simulating tree rings (Klesse et al., 2018; G. Li et al., 2014). This will likely increase the accuracy of the simulated sensitivity.

5. Conclusion

Our study answers the questions over whether the sensitivity of tree growth to precipitation has increased or decreased: A significant increase in sensitivity during the second half of the 20th century. Understanding and determining the changes in sensitivity in arid and humid biomes requires the combined consideration of changing precipitation and elevated CO_2 concentration. In arid biomes, an increase in water supply and the CO_2 fertilization effect both allow trees to accumulate carbon more rapidly, thus stimulating growth of trees. With higher evaporative water demands, the amount of water needed by trees and the water loss through leaf stomata also increase, so trees most likely can absorb additional water, which is reflected in the increase in sensitivity. However, in humid biomes, increasing CO_2 concentrations do not markedly stimulate tree growth, and the negative effects of

water stress due to declining precipitation eventually offset the CO_2 water-saving effect, similarly leading to increased sensitivity. The increasing sensitivity detected here may reflect increased ecosystem vulnerability to dryness. With the projected increases in the frequency and severity of droughts, increasing sensitivity is likely to counteract the CO_2 fertilization effect on tree growth, potentially reducing the strength of the terrestrial carbon sink.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data sets that support the findings of this study are publicly available. The input data sets were: The monthly precipitation, temperature (mean temperature, maximum temperature, minimum temperature), actual vapour pressure, potential evapotranspiration, and Palmer Drought Severity Index from 1901 to 2012 were obtained from the Climate Research Unit (CRU) data set provided by the University of East Anglia in the UK (CRU TS 4.07; https://crudata.uea.ac.uk/cru/data/hrg/). The shortwave radiation data were obtained from the Terrestrial Hydrology Research Group at Princeton University (https://hydrology.soton.ac.uk/). The atmospheric CO_2 concentration data were obtained from the Mauna Loa Observatory, provided by the Scripps Institution of Oceanography (Scripps CO_2 Program, https://scrippsco2.ucsd.edu/). The raw data on tree ring widths were obtained from the International Tree Ring Data Bank (https://www1.ncdc.noaa.gov/pub/data/paleo/treering/). DGVMs simulations from TRENDY were obtained from https://sites.exeter.ac.uk/trendy.

Acknowledgments
This work was supported by State Key Laboratory of Earth Surface Processes and Resource Ecology (Grant 2023-KF-02) and the National Natural Science Foundation of China (Grants 42361144877 and 42330502). We thank the reviewers for providing thoughtful and constructive comments on our manuscript.

References

Abel, C., Horion, S., Tagesson, T., De Keersmaecker, W., Seddon, A. W., Abdi, A. M., & Fensholt, R. (2021). The human–environment nexus and vegetation–rainfall sensitivity in tropical drylands. *Nature Sustainability*, *4*(1), 25–32. https://doi.org/10.1038/s41893-020-00597-z

Ainsworth, E. A., & Rogers, A. (2007). The response of photosynthesis and stomatal conductance to rising [CO_2]: Mechanisms and environmental interactions. *Plant, Cell & Environment*, *30*(3), 258–270. https://doi.org/10.1111/j.1365-3040.2007.01641.x

Anderegg, W. R., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., et al. (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, *349*(6247), 528–532. https://doi.org/10.1126/science.aab1833

Bazzaz, F. A. (1990). The response of natural ecosystems to the rising global CO_2 levels. *Annual Review of Ecology and Systematics*, *21*(1), 167–196. https://doi.org/10.1146/annurev.es.21.110190.001123

Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J. J., et al. (2020). Global ecosystem thresholds driven by aridity. *Science*, *367*(6479), 787–790. https://doi.org/10.1126/science.aay5958

Biondi, F. (2001). A 400-year tree-ring chronology from the tropical treeline of North America. *AMBIO: A Journal of the Human Environment*, *30*(3), 162–166. https://doi.org/10.1579/0044-7447-30.3.162

Bosela, M., Lukac, M., Castagneri, D., Sedmák, R., Biber, P., Carrer, M., et al. (2018). Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Science of the Total Environment*, *615*, 1460–1469. https://doi.org/10.1016/j.scitotenv.2017.09.092

Briffa, K. R., & Melvin, T. M. (2011). A closer look at regional curve standardization of tree-ring records: Justification of the need, a warning of some pitfalls, and suggested improvements in its application. *Dendroclimatology: Progress and prospects*, 113–145. https://doi.org/10.1007/978-1-4020-5725-0_5

Byrne, B., Liu, J., Yi, Y., Chatterjee, A., Basu, S., Cheng, R., et al. (2022). Multi-year observations reveal a larger than expected autumn respiration signal across northeast Eurasia. *Biogeosciences Discussions*, *19*(19), 1–28. https://doi.org/10.5194/bg-19-4779-2022

Carminati, A., & Javaux, M. (2020). Soil rather than xylem vulnerability controls stomatal response to drought. *Trends in Plant Science*, *25*(9), 868–880. https://doi.org/10.1016/j.tplants.2020.04.003

Chen, C., He, B., Yuan, W., Guo, L., & Zhang, Y. (2019). Increasing interannual variability of global vegetation greenness. *Environmental Research Letters*, *14*(12), 124005. https://doi.org/10.1088/1748-9326/ab4ffc

Cook, E. R., & Kairiukstis, L. A. (2013). *Methods of dendrochronology: Applications in the environmental sciences*. Springer Science & Business Media.

Donohue, R. J., Roderick, M. L., McVicar, T. R., & Yang, Y. (2017). A simple hypothesis of how leaf and canopy-level transpiration and assimilation respond to elevated CO_2 reveals distinct response patterns between disturbed and undisturbed vegetation. *Journal of Geophysical Research: Biogeosciences*, *122*(1), 168–184. https://doi.org/10.1002/2016jg003505

Duursma, R. A., Blackman, C. J., Lopéz, R., Martin-StPaul, N. K., Cochard, H., & Medlyn, B. E. (2019). On the minimum leaf conductance: Its role in models of plant water use, and ecological and environmental controls. *New Phytologist*, *221*(2), 693–705. https://doi.org/10.1111/nph.15395

Fatichi, S., Leuzinger, S., & Körner, C. (2014). Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. *New Phytologist*, *201*(4), 1086–1095. https://doi.org/10.1111/nph.12614

Fatichi, S., Leuzinger, S., Paschalis, A., Langley, J. A., Donnellan Barraclough, A., & Hovenden, M. J. (2016). Partitioning direct and indirect effects reveals the response of water-limited ecosystems to elevated CO_2. *Proceedings of the National Academy of Sciences*, *113*(45), 12757–12762. https://doi.org/10.1073/pnas.1605036113

Forzieri, G., Dakos, V., McDowell, N. G., Ramdane, A., & Cescatti, A. (2022). Emerging signals of declining forest resilience under climate change. *Nature*, *608*(7923), 534–539. https://doi.org/10.1038/s41586-022-04959-9

Gedalof, Z. E., & Berg, A. A. (2010). Tree ring evidence for limited direct CO_2 fertilization of forests over the 20th century. *Global Biogeochemical Cycles*, *24*(3), GB3027. https://doi.org/10.1029/2009gb003699

Harris, I., Osborn, T. J., Jones, P., & Lister, D. (2020). Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Scientific Data*, *7*, 109. https://doi.org/10.1038/s41597-020-0453-3

He, B., Xie, X., & Guo, L. (2023). A shift from temperature to water as the primary driver for interannual variability of the tropical carbon cycle. *Geophysical Research Letters*, *50*(15), e2023GL102812. https://doi.org/10.1029/2023gl102812

Heilman, K. A., Dietze, M. C., Arizpe, A. A., Aragon, J., Gray, A., Shaw, J. D., et al. (2022). Ecological forecasting of tree growth: Regional fusion of tree-ring and forest inventory data to quantify drivers and characterize uncertainty. *Global Change Biology*, *28*(7), 2442–2460. https://doi.org/10.1111/gcb.16038

Helama, S., Melvin, T. M., & Briffa, K. R. (2017). Regional curve standardization: State of the art. *The Holocene*, *27*(1), 172–177. https://doi.org/10.1177/0959683616652709

Hu, Z., Guo, Q., Li, S., Piao, S., Knapp, A. K., Ciais, P., et al. (2018). Shifts in the dynamics of productivity signal ecosystem state transitions at the biome-scale. *Ecology Letters*, *21*(10), 1457–1466. https://doi.org/10.1111/ele.13126

Huang, J.-G., Ma, Q., Rossi, S., Biondi, F., Deslauriers, A., Fonti, P., et al. (2020). Photoperiod and temperature as dominant environmental drivers triggering secondary growth resumption in Northern Hemisphere conifers. *Proceedings of the National Academy of Sciences*, *117*(34), 20645–20652. https://doi.org/10.1073/pnas.2007058117

Humphrey, V., Zscheischler, J., Ciais, P., Gudmundsson, L., Sitch, S., & Seneviratne, S. I. (2018). Sensitivity of atmospheric CO_2 growth rate to observed changes in terrestrial water storage. *Nature*, *560*(7720), 628–631. https://doi.org/10.1038/s41586-018-0424-4

Jiao, W., Wang, L., Smith, W. K., Chang, Q., Wang, H., & D'Odorico, P. (2021). Observed increasing water constraint on vegetation growth over the last three decades. *Nature Communications*, *12*(1), 1–9. https://doi.org/10.1038/s41467-021-24016-9

Karim, R., Tan, G., Ayugi, B., Babaousmail, H., & Liu, F. (2020). Evaluation of historical CMIP6 model simulations of seasonal mean temperature over Pakistan during 1970–2014. *Atmosphere*, *11*(9), 1005. https://doi.org/10.3390/atmos11091005

Keenan, T. F., Hollinger, D. Y., Bohrer, G., Dragoni, D., Munger, J. W., Schmid, H. P., & Richardson, A. D. (2013). Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature*, *499*(7458), 324–327. https://doi.org/10.1038/nature12291

Klesse, S., Babst, F., Lienert, S., Spahni, R., Joos, F., Bouriaud, O., et al. (2018). A combined tree ring and vegetation model assessment of European forest growth sensitivity to interannual climate variability. *Global Biogeochemical Cycles*, *32*(8), 1226–1240. https://doi.org/10.1029/2017gb005856

Li, G., Harrison, S., Prentice, I., & Falster, D. (2014). Simulation of tree-ring widths with a model for primary production, carbon allocation, and growth. *Biogeosciences*, *11*(23), 6711–6724. https://doi.org/10.5194/bg-11-6711-2014

Li, W., Migliavacca, M., Forkel, M., Denissen, J., Reichstein, M., Yang, H., et al. (2022). Widespread increasing vegetation sensitivity to soil moisture. *Nature Communications*, *13*(1), 1–9. https://doi.org/10.1038/s41467-022-31667-9

Li, X., Piao, S., Wang, K., Wang, X., Wang, T., Ciais, P., et al. (2020). Temporal trade-off between gymnosperm resistance and resilience increases forest sensitivity to extreme drought. *Nature Ecology & Evolution*, *4*(8), 1075–1083. https://doi.org/10.1038/s41559-020-1217-3

Li, Z., Qi, F., Wei, L., Tingting, W., Yan, G., Yamin, W., et al. (2014). Spatial and temporal trend of potential evapotranspiration and related driving forces in Southwestern China, during 1961–2009. *Quaternary International*, *336*, 127–144. https://doi.org/10.1016/j.quaint.2013.12.045

Lian, X., Piao, S., Chen, A., Huntingford, C., Fu, B., Li, L. Z., et al. (2021). Multifaceted characteristics of dryland aridity changes in a warming world. *Nature Reviews Earth & Environment*, *2*(4), 232–250. https://doi.org/10.1038/s43017-021-00144-0

Liu, X., He, B., Guo, L., Huang, L., & Chen, D. (2020). Similarities and differences in the mechanisms causing the European summer heatwaves in 2003, 2010, and 2018. *Earth's Future*, *8*(4), e2019EF001386. https://doi.org/10.1029/2019ef001386

Liu, Z., Ballantyne, A. P., Poulter, B., Anderegg, W. R., Li, W., Bastos, A., & Ciais, P. (2018). Precipitation thresholds regulate net carbon exchange at the continental scale. *Nature Communications*, *9*(1), 3596. https://doi.org/10.1038/s41467-018-05948-1

Mankin, J. S., Smerdon, J. E., Cook, B. I., Williams, A. P., & Seager, R. (2017). The curious case of projected twenty-first-century drying but greening in the American West. *Journal of Climate*, *30*(21), 8689–8710. https://doi.org/10.1175/jcli-d-17-0213.1

Maurer, G. E., Hallmark, A. J., Brown, R. F., Sala, O. E., & Collins, S. L. (2020). Sensitivity of primary production to precipitation across the United States. *Ecology Letters*, *23*(3), 527–536. https://doi.org/10.1111/ele.13455

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., et al. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Norby, R. J., & Zak, D. R. (2011). Ecological lessons from free-air CO_2 enrichment (FACE) experiments. *Annual Review of Ecology Evolution and Systematics*, *42*(1), 181–203. https://doi.org/10.1146/annurev-ecolsys-102209-144647

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V., Underwood, E. C., et al. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, *51*(11), 933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2

Pan, T., Zhang, L., Zhang, H., Ren, C., & Li, Y. (2020). Spatiotemporal patterns and variations of winter extreme precipitation over terrestrial northern hemisphere in the past century (1901–2017). *Physics and Chemistry of the Earth, Parts A/B/C*, *115*, 102828. https://doi.org/10.1016/j.pce.2019.102828

Restrepo-Coupe, N., Levine, N. M., Christoffersen, B. O., Albert, L. P., Wu, J., Costa, M. H., et al. (2017). Do dynamic global vegetation models capture the seasonality of carbon fluxes in the Amazon basin? A data-model intercomparison. *Global Change Biology*, *23*(1), 191–208. https://doi.org/10.1111/gcb.13442

Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbagy, E., & Peters, D. (2012). Legacies of precipitation fluctuations on primary production: Theory and data synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1606), 3135–3144. https://doi.org/10.1098/rstb.2011.0347

Schwalm, C. R., Anderegg, W. R. L., Michalak, A. M., Fisher, J. B., Biondi, F., Koch, G., et al. (2017). Global patterns of drought recovery. *Nature*, *548*(7666), 202–205. https://doi.org/10.1038/nature23021

Sheffield, J., Goteti, G., & Wood, E. F. (2006). Development of a 50-year high-resolution global dataset of meteorological forcings for land surface modeling. *Journal of Climate*, *19*(13), 3088–3111. https://doi.org/10.1175/jcli3790.1

Tang, J., Niu, B., Hu, Z., & Zhang, X. (2024). Increasing susceptibility and shortening response time of vegetation productivity to drought from 2001 to 2021. *Agricultural and Forest Meteorology*, *352*, 110025. https://doi.org/10.1016/j.agrformet.2024.110025

Trabucco, A., & Zomer, R. J. (2018). Global aridity index and potential evapotranspiration (ET0) climate database v2. *CGIAR Consortium Spatial Information*, *10*, m9.

Wang, X., Ciais, P., Wang, Y., & Zhu, D. (2018). Divergent response of seasonally dry tropical vegetation to climatic variations in dry and wet seasons. *Global Change Biology*, *24*(10), 4709–4717. https://doi.org/10.1111/gcb.14335

Wei, F., Wang, S., Fu, B., Wang, L., Zhang, W., Wang, L., et al. (2022). Divergent trends of ecosystem-scale photosynthetic efficiency between arid and humid lands across the globe. *Global Ecology and Biogeography*, *31*(9), 1824–1837. https://doi.org/10.1111/geb.13561

Wilcox, K. R., Blair, J. M., Smith, M. D., & Knapp, A. K. (2016). Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions? *Ecology*, *97*(3), 561–568. https://doi.org/10.1890/15-1437.1

Zeng, X., Hu, Z., Chen, A., Yuan, W., Hou, G., Han, D., et al. (2022). The global decline in the sensitivity of vegetation productivity to precipitation from 2001 to 2018. *Global Change Biology*, *28*(22), 6823–6833. https://doi.org/10.1111/gcb.16403

Zhang, Y., Gentine, P., Luo, X., Lian, X., Liu, Y., Zhou, S., et al. (2022). Increasing sensitivity of dryland vegetation greenness to precipitation due to rising atmospheric CO_2. *Nature Communications*, *13*(1), 1–9. https://doi.org/10.1038/s41467-022-32631-3

Zhao, S., Pederson, N., D'Orangeville, L., HilleRisLambers, J., Boose, E., Penone, C., et al. (2019). The International Tree-Ring Data Bank (ITRDB) revisited: Data availability and global ecological representativity. *Journal of Biogeography*, *46*(2), 355–368. https://doi.org/10.1111/jbi.13488

Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., et al. (2016). Greening of the Earth and its drivers. *Nature Climate Change*, *6*(8), 791–795. https://doi.org/10.1038/nclimate3004

Żywiec, M., Muter, E., Zielonka, T., Delibes, M., Calvo, G., & Fedriani, J. M. (2017). Long-term effect of temperature and precipitation on radial growth in a threatened thermo-Mediterranean tree population. *Trees*, *31*(2), 491–501. https://doi.org/10.1007/s00468-016-1472-8

References From the Supporting Information

Anav, A., Friedlingstein, P., Beer, C., Ciais, P., Harper, A., Jones, C., et al. (2015). Spatiotemporal patterns of terrestrial gross primary production: A review. *Reviews of Geophysics*, *53*(3), 785–818. https://doi.org/10.1002/2015rg000483

Friedlingstein, P., O'sullivan, M., Jones, M. W., Andrew, R. M., Gregor, L., Hauck, J., et al. (2022). Global carbon budget 2022. *Earth System Science Data*, *14*(11), 4811–4900. https://doi.org/10.5194/essd-14-4811-2022

Hurtt, G. C., Chini, L., Sahajpal, R., Frolking, S., Bodirsky, B. L., Calvin, K., et al. (2020). Harmonization of global land use change and management for the period 850–2100 (LUH2) for CMIP6. *Geoscientific Model Development*, *13*(11), 5425–5464. https://doi.org/10.5194/gmd-13-5425-2020

Klein Goldewijk, K., Beusen, A., Doelman, J., & Stehfest, E. (2017). Anthropogenic land use estimates for the Holocene–HYDE 3.2. *Earth System Science Data*, *9*(2), 927–953. https://doi.org/10.5194/essd-9-927-2017

MacBean, N., Scott, R. L., Biederman, J. A., Peylin, P., Kolb, T., Litvak, M. E., et al. (2021). Dynamic global vegetation models underestimate net CO_2 flux mean and inter-annual variability in dryland ecosystems. *Environmental Research Letters*, *16*(9), 094023. https://doi.org/10.1088/1748-9326/ac1a38

Zomer, R. J., Trabucco, A., Bossio, D. A., & Verchot, L. V. (2008). Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems & Environment*, *126*(1–2), 67–80. https://doi.org/10.1016/j.agee.2008.01.014