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## RESEARCH LETTER

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## Land Models Likely Underestimate the Impact of Future Atmospheric Dryness on European Tree Growth

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### Key Points:

- The land absorbs one third of human CO<sub>2</sub> emissions, making it critical to understand how tree growth will respond to climate change
- Drier air reduces photosynthesis and the processes of cell division and expansion, but this second effect is not represented in land models
- We show that a widely used land model underestimates the impact of drying air on tree growth, with implications for carbon storage forecasts

### Supporting Information:

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

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**Abstract** Understanding how the land carbon sink will be altered by climate change is critical for projecting future atmospheric CO<sub>2</sub> concentrations under different emission pathways in Earth System Models (ESMs). Most land models assume that woody growth, the main driver of land carbon storage, is driven by photosynthetic carbon supply. In reality, growth is often constrained by physiological processes limiting cell division independent of carbon availability, like reduced turgor pressure. Rising vapor pressure deficit (VPD) under climate change reduces turgor pressure and suppresses actual growth more strongly than photosynthesis, suggesting ESMs may overestimate future terrestrial carbon uptake. We compare simulations of the Community Land Model (CLM) to a statistical model built on dendrometer observations, showing that CLM underestimates decreases to growth under elevated VPD by a factor of 2–3. This highlights the need for land models to represent physiological constraints on tree growth to improve projections of future terrestrial carbon uptake.

**Plain Language Summary** The land surface absorbs about a third of human carbon dioxide emissions. Climate change is expected to impact tree growth, and global numerical models are used to make predictions of how that will impact the land's ability to store carbon in the future. As the air becomes drier under climate change, it causes trees to close their stomata, reducing photosynthesis. However, dry air can also directly slow tree growth by limiting cell division and expansion. This process is not included in global numerical models, yet it can be more sensitive to the drying of air than photosynthesis. We show that a widely used global land model underestimates how much drying air in the future may reduce tree growth, which could have important implications for projections of carbon storage and future climate change.

## 1. Introduction

Many anthropogenic activities release large quantities of planet-warming carbon dioxide (CO<sub>2</sub>) into the Earth's atmosphere. Of these CO<sub>2</sub> emissions, about 25% is absorbed by the ocean, and about 27% is absorbed by the land, with the remainder staying in the atmosphere, causing warming (Friedlingstein et al., 2025). Climatic changes from warming, land use changes, and other anthropogenic activities are expected to have a large impact on the ocean and land's ability to take up CO<sub>2</sub> in the future (IPCC, 2019; IPCC, 2021). Land models exhibit substantial spread in projections of the future land carbon sink, which has been identified as a major source of uncertainty in future projections of climate change (IPCC, 2021). Due to the lack of representation of relevant processes, past coupled model intercomparison project (CMIP) phases, up to CMIP6, have directly prescribed changes in CO<sub>2</sub> concentrations within Earth system models in their historical and future scenario (ScenarioMIP) simulations, excluding explicit climate change impacts on the carbon cycle (Eyring et al., 2016). In the next CMIP phase (CMIP7), however, atmospheric CO<sub>2</sub> concentrations are expected to no longer be prescribed. Instead, Earth system models will be driven by CO<sub>2</sub> emissions and permitted to compute concentrations internally via fully coupled carbon cycle feedbacks (Sanderson et al., 2024). This change makes the uncertainty in projected future land carbon storage from land models even more critical than in previous CMIP phases.

Vegetative assimilation of carbon through growth is the largest source of uncertainty in future projections of the global carbon cycle (Friedlingstein, 2015). Projections of future terrestrial carbon storage are often done by global land models. These models assume that new growth depends on how much carbon a plant produces through photosynthesis, a dependence known as source limitation (Capon et al., 2022). However, increasing evidence indicates that tree growth is not just governed by carbon supply, but also by how much of that supply can be used to form new tissues, a concept known as sink limitation (Capon et al., 2022; Körner, 2015). The carbon might be

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there, but the ability of plants to use it might not. Radial growth is often regulated directly by cambial physiology rather than the amount of carbon assimilated through photosynthesis. Empirically, carbon remaining after photosynthesis and autotrophic respiration is not always allocated to long-lived woody biomass. When physiological constraints limit the formation of new tissue, this carbon could be respired back to the atmosphere, or released into the soil through the roots, where it may again be respired or transformed through microbial processes into more persistent forms of soil carbon (Jiang et al., 2020). In contrast, land models assume that carbon available after photosynthesis and autotrophic respiration (net primary production) is directly available for allocation to plant growth, with no representation of physiological constraints on growth.

Turgor pressure, the internal water pressure essential for cell expansion and division, strongly influences cambial activity and radial growth, often independently of photosynthetic carbon supply, and can impose a physiological constraint on carbon allocation to growth (Hsiao et al., 1976; Peters et al., 2020; Zweifel et al., 2006, 2021a). Land models have been criticized for excluding key sink driven processes that regulate wood growth, such as turgor pressure, potentially reducing their reliability in projecting future climate change impacts on carbon storage (Eckes-Shephard et al., 2022; Friend et al., 2019). As drought stress intensifies, photosynthesis and growth are expected to become more decoupled in many places, reflecting a transition toward sink limitation, where growth is constrained by the plant's ability to use carbon rather than to produce it (Müller & Stitt, 2011). This shift suggests that current land model formulations may underestimate the impacts of climate change on future carbon storage.

Growing evidence suggests that vapor pressure deficit (VPD), defined as the difference between the maximum water vapor the air can hold at a given temperature and the actual water vapor content, is a key driver of plant water status and thereby contributes to sink limitation of growth in many tree species (Cabon et al., 2022). Climate change is projected to increase VPD globally (Hermann et al., 2024; Yuan et al., 2019). Elevated VPD subjects plants to greater evaporative demand, causing a decline in turgor pressure as plants lose water. Plants often respond by reducing stomatal conductance, which mitigates water loss but also limits photosynthesis. While land models are designed to capture this response, recent evidence suggests they may not fully represent the diurnal sensitivity of photosynthesis to VPD (Fu et al., 2022; Zhang et al., 2023). Furthermore, in many species under many conditions, actual cambial growth is often more sensitive to reduction in turgor than photosynthesis, to the point that carbon supply is no longer limiting (Peters et al., 2020). This decoupling of growth from photosynthesis highlights the importance of accounting for sink-limited processes in land models when estimating future terrestrial carbon storage potential. However, the consequences of omitting sink limitation in land models, particularly under elevated VPD, have not yet been quantified for future projections of tree growth and carbon storage.

Here we simulate tree radial growth using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) incorporated into the Community Land Model Version 5 (CLM5) (Fisher et al., 2015; Lawrence et al., 2019). We compare these photosynthesis-driven (source-limited) land model simulations with a statistical model based on dendrometer-derived radial growth that explicitly accounts for physiological constraints on new growth (sink limitation) (Etzold et al., 2022a). We force the land model and statistical model with elevated VPD scenarios to show that the photosynthesis-driven land model does not represent future decreases to tree radial growth due to elevated VPD that are seen in the observation-based regression model. We then use a constant CO<sub>2</sub> climate change scenario to show that the absence of sink limitation processes in the land model has implications for future projections of terrestrial carbon storage potential. We postulate that representing physiological constraints on tree growth in land models could alter projections of the CO<sub>2</sub> fertilization effect, terrestrial carbon uptake, and associated climate impacts simulated by Earth system models.

## 2. Methods

### 2.1. CLM5-FATES Simulations

CLM5-FATES was spun up for approximately 300 years repeating forcing for the years 1978–1987 until relevant variables (gross primary production, leaf area index, tree height, tree area, basal area) reached equilibrium, in accordance with CLM5 documentation. Global gross primary production and leaf area index interannual variability were below 0.02 PgC/yr and 0.02 m<sup>2</sup>/m<sup>2</sup>/yr, respectively, with global values showing no trend. A 300 years spin-up has been identified as satisfactory in several previous studies using CLM5-FATES (Koven et al., 2020; Shi et al., 2024; Shuman et al., 2024). More details on spin up criteria can be found in the CLM5 documentation and

source code (Lawrence et al., 2019). A historical simulation was run from 1988 to 2014, and then future Shared Socioeconomic Pathway 2, Representative Concentration Pathway 4.5 (SSP2-4.5) is followed from 2015 to 2069. Historical (1978–2014) and future (2015–2069) atmospheric forcing was generated by the Community Earth System Model version 2, Whole Atmosphere Community Climate Model version 6 (CESM2-WACCM6) (Danabasoglu et al., 2020; Gettelman et al., 2019). CLM5-FATES was run at 1.25° by 0.9° longitude-latitude resolution with 3-hourly timesteps. Constant CO<sub>2</sub> was used throughout the historical and future simulations to make a proper comparison to the dendrometer-based regression analysis, which lacked CO<sub>2</sub> measurements. CLM5-FATES was run in fixed biogeography, no competition mode to isolate climate impacts.

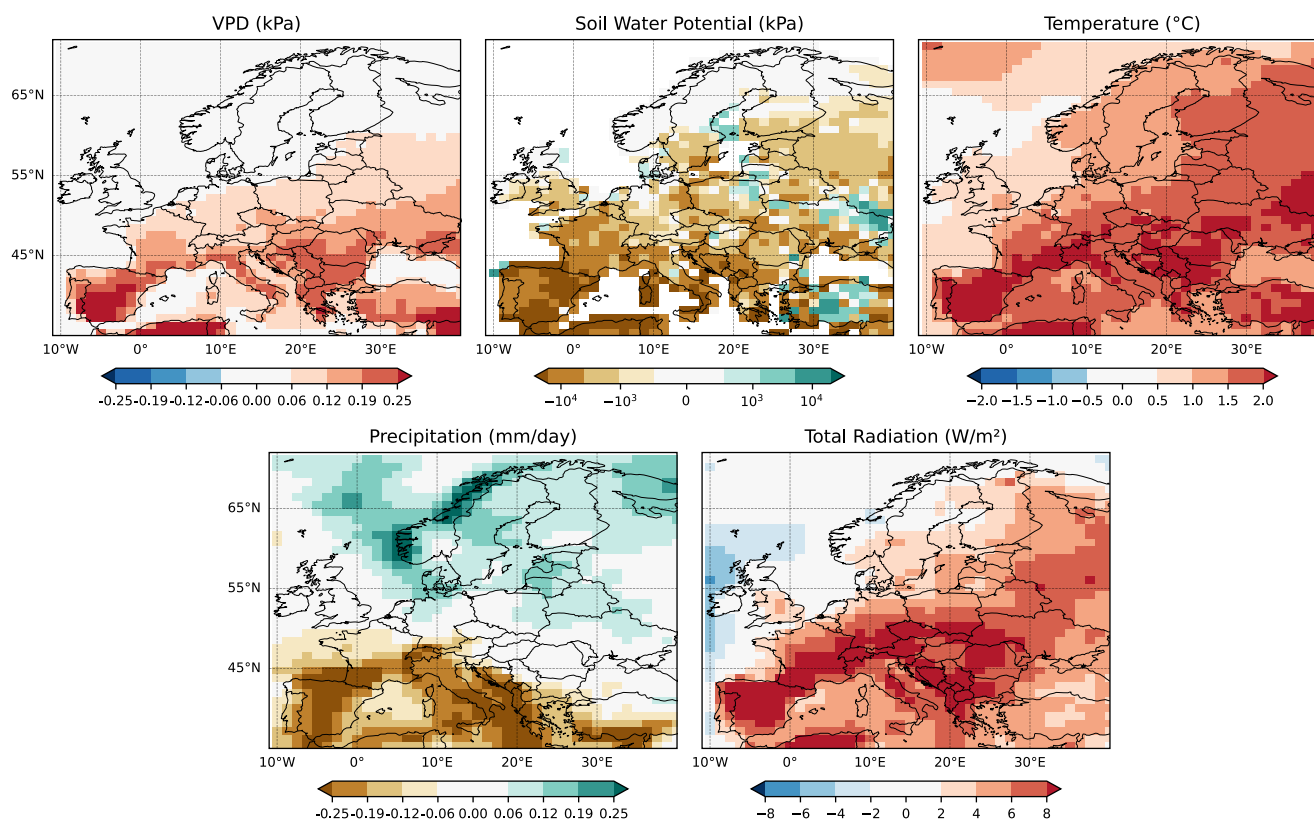
## 2.2. Radial Growth Observations and Statistical Model

To understand how radial growth is impacted by climate, we use dendrometer observations and weather measurements from Etzold et al. (2022a). This data set comprises daily measurements of radial growth over the course of eight years from 160 individual temperate trees from 47 sites in Switzerland, alongside daily measurements of VPD, soil water potential, temperature, precipitation, radiation, and daylength (Etzold et al., 2022a). This data set is comprised of the primary tree species found across temperate and boreal Europe, with observations from a wide variety of elevation, temperature, and soil moisture conditions (Etzold et al., 2022a). Daily temporal resolution allows results to capture impacts of extreme events, lag effects, and seasonal dynamics. Soil water potential is preferred over soil moisture because it directly quantifies how difficult it is for plants to extract water, making it a more mechanistically relevant measure of plant water stress than just the amount of water present in the soil.

We use these measurements to fit a generalized linear model (GLM) with a binomial logit link to daily tree growth occurrence (growth vs. no growth), where the response variable is a binary indicator coded as 1 if daily radial growth is positive and 0 otherwise, using the Python module statsmodels for seven species during the growing season. Growth probability is modeled as a nonlinear function of vapor pressure deficit and soil water potential using natural cubic splines (4 and 3 degrees of freedom, respectively), with temperature, radiation, precipitation, and daylength included as linear predictors. Due to the use of splines, the GLM was fit on predictors left in raw units, which allows the splines to be fit across the natural range of the observed data. Standard errors are clustered by station to account for repeated measurements. Collinearity among predictors was assessed using variance inflation factors (VIF), and any predictor with a VIF exceeding 5 was removed from the model. Daily growth probabilities are summed over the growing season to get the number of growth days, then growth days are multiplied by observed average growth per day for each species (Etzold et al., 2022a). This creates a statistical model that can predict future radial growth from climate model output. Future forcings were obtained from CESM2-WACCM6 (see Section 2.1 for details), and the statistical model was run daily at each grid cell to spatially predict future radial growth for each species.

## 3. Results

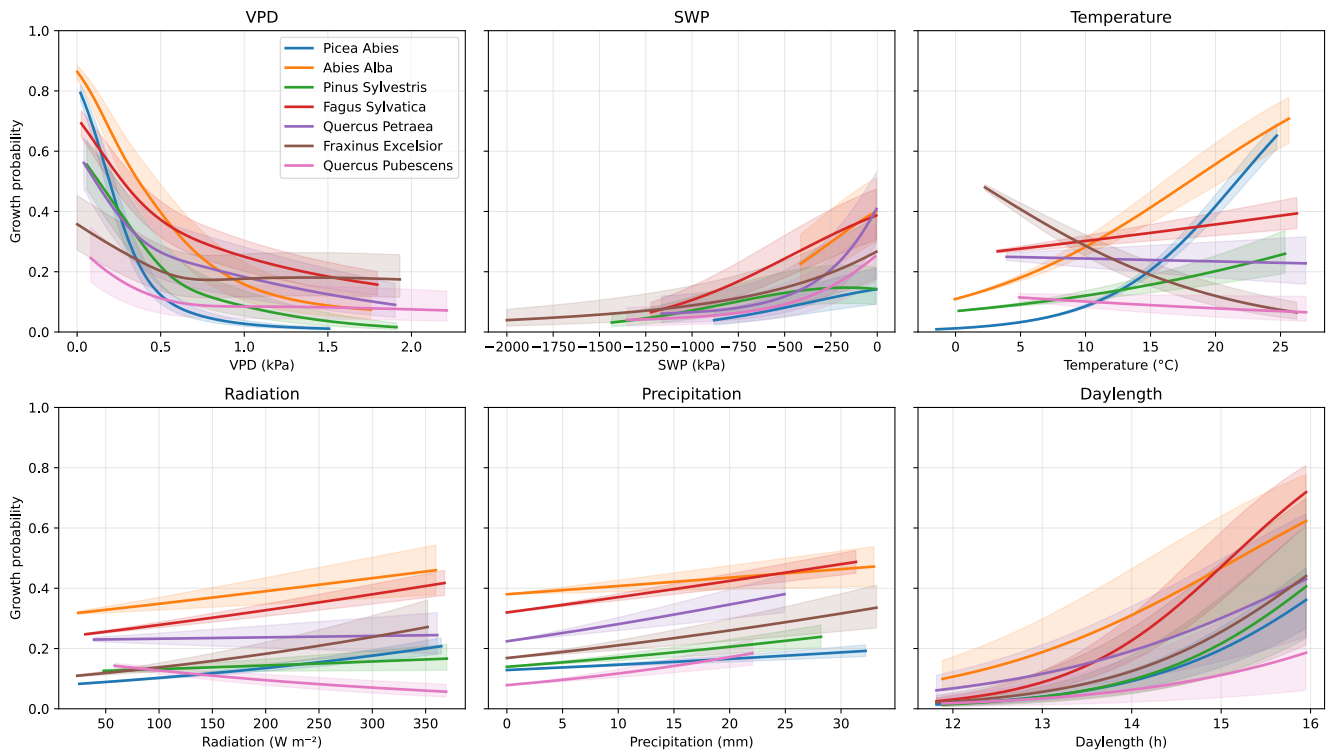
Under the middle of the road emissions scenario SSP2-4.5, as simulated by CESM2-WACCM6, future climate change causes regional changes to precipitation and radiation, and increases to temperature of about 2°C in southern parts of Europe during the period 2050–2069 relative to the historical period (Figure 1). Soil water potential decreases in many parts of Europe and VPD increases across Europe, with the largest increases in southern Europe of about 30% relative to a historical period (Figure 1). These same climate variables were measured alongside the dendrometer observations to build a relationship between observed growth and changes to these variables. Figure 2 shows the relationship between growth probability and these climate variables for the seven European tree species. Radiation and precipitation had minimal effects on growth probability across species, whereas daylength exerted a strong influence (Figure 2). Higher temperatures tended to benefit *Picea abies* and *Abies alba*, while the remaining species were minimally affected by temperature. Lower soil water potential (less water available for roots) reduced the probability of growth across species, with the most sensitive being *Quercus petraea*, *Fagus sylvatica*, and *Fraxinus excelsior* (Figure 2). The most important climate variable for predicting growth probability across species was VPD (Table S1 in Supporting Information S1). The probability of growth for all seven species dropped markedly with daily average VPD values above 0.25 kPa in the observations (Figure 2). Because VPD exerts the strongest control on growth in the dendrometer observations, it is essential to evaluate how VPD influences radial growth in CLM5-FATES, to determine whether the model's lack of explicit sink limitation leads to a reduced sensitivity to elevated VPD.



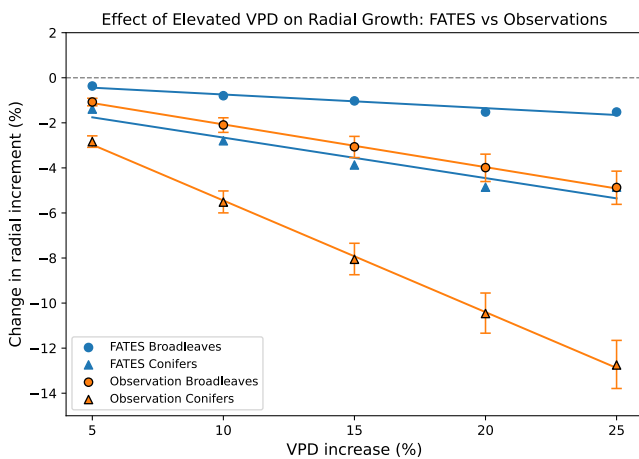
**Figure 1.** The relative change to VPD, soil water potential, temperature, precipitation, and total radiation under SSP2-4.5 (2050–2069) minus the historical period (1990–2009) as simulated by CESM2-WACCM6.

Figure 3 shows the response of both the dendrometer based statistical model and CLM5-FATES to varying levels of just elevated VPD, holding all else constant, for both broadleaved and coniferous trees. For a VPD increase of 25% relative to the baseline period, radial growth for broadleaved trees in CLM5-FATES is only reduced by about 2%, and coniferous radial growth is only reduced by about 4% (Figure 3). In the dendrometer derived statistical model, elevated VPD of 25% reduces radial growth by about 4% and 13% averaged across Europe for broadleaf and coniferous trees, respectively (Figure 3). In the land model, which lacks representation of sink limited growth, future impacts to radial growth from elevated VPD tend to be underestimated by a factor of 2 for broadleaf trees, and a factor of 3 for coniferous trees relative to what dendrometer observations would suggest (Figure 3).

To assess how future climate may impact radial growth in both the CLM5-FATES and the statistical model, each is forced with the same climate model output from CESM2-WACCM6, which simulated the medium emissions scenario SSP2-4.5. Figure S1 in Supporting Information S1 shows the average impact to radial growth for broadleaved and coniferous trees in Europe under this scenario with constant CO<sub>2</sub> for each model. Under SSP2-4.5, CLM5-FATES underestimates the impact of climate change on broadleaf radial growth in Europe compared to the statistical model by a factor of about 2. This underestimation is likely driven by the model's weaker sensitivity to elevated VPD, as shown in Figure 3. Even though conifers are more sensitive to elevated VPD (Figure 3), CLM5-FATES predicts similar reductions to radial growth under the constant CO<sub>2</sub> SSP2-4.5 scenario relative to the regression (Figure S1 in Supporting Information S1). This is likely because conifers have a positive impact from warming in the regression that is not captured by CLM5-FATES (Figure 2). This means that CLM5-FATES is still underestimating the impact of elevated VPD on radial growth for conifers (Figure 3), and if sink limited growth was included, the reductions to radial growth for conifers in CLM5-FATES seen in Figure S1 in Supporting Information S1 would be even larger. This underestimation of future impacts to radial growth means that land models that lack sink limitation, such as CLM5, are likely underestimating the negative impact of climate change on the land's ability to store carbon in the future.



**Figure 2.** The effect of daily average VPD, soil water potential, temperature, radiation, precipitation, and daylength on the probability of growth for *Picea abies*, *Abies alba*, *Pinus sylvestris*, *Fagus sylvatica*, *Quercus petraea*, *Fraxinus excelsior*, and *Quercus pubescens* as estimated from a GLM with observations from Etzold et al., 2022b. Upper and lower bounds are derived by refitting the GLM with predictor coefficients perturbed by  $\pm 1.96$  standard errors.

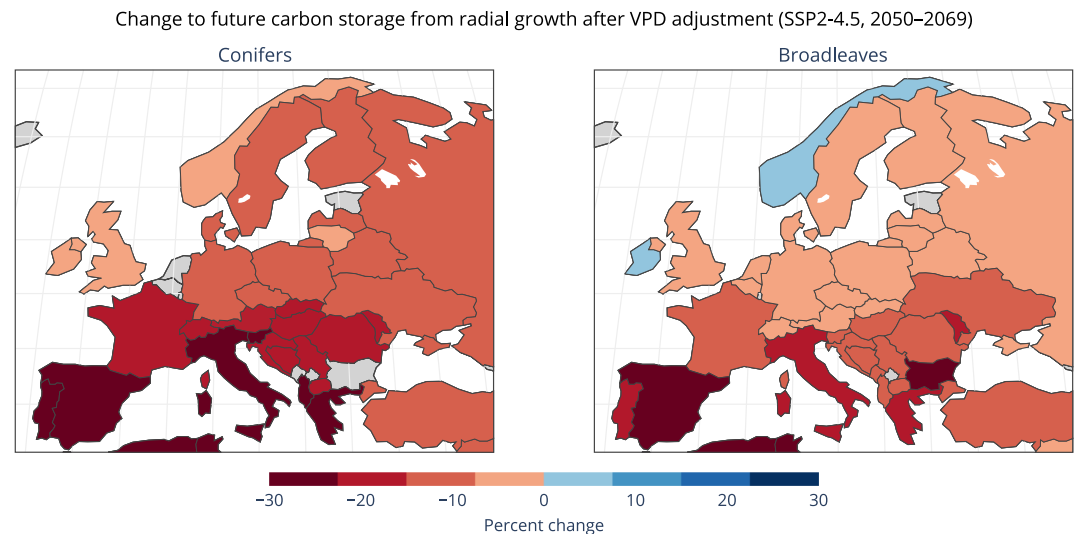


**Figure 3.** The effect of incremental elevated VPD (kPa) on radial growth (mm/yr) in CLM5-FATES (blue) and the statistical model (orange) for broadleaves and conifers in Europe. Elevated VPD scenarios are relative to a historical period (1989–1993). In the statistical model conifers are represented by the average impact to *Picea abies*, *Abies alba*, and *Pinus sylvestris*, and broadleaves are represented by the average impact to *Fagus sylvatica*, *Quercus petraea*, *Fraxinus excelsior*, and *Quercus pubescens*. In CLM5-FATES conifers are represented by the needleleaf extratropical tree plant functional types and broadleaves are represented by the broadleaf extratropical tree plant functional types. Error bars for the statistical model represent the 95% confidence interval of predicted values.

Figure 4 shows the impact to national future volumetric carbon storage under SSP2-4.5 after CLM5-FATES output is adjusted to match decreases to radial growth that are seen in the statistical model under a SSP2-4.5 “VPD-only” scenario. Figure S4 in Supporting Information S1 shows the results of the statistical model when forced with a VPD-only scenario, used to adjust CLM5-FATES output. Radial growth output of CLM5-FATES is adjusted at each grid cell to match the relative reductions to radial growth that are seen in the statistical model VPD-only scenario (Figure S4 in Supporting Information S1), which assumes that VPD has little impact on photosynthesis in CLM5-FATES. After the adjustment, which attempts to account for VPD driven sink-limited growth, CLM5-FATES estimates of national volumetric carbon storage are reduced by as much as 30% (Figure 4). Reduced radial growth for both broadleaf and coniferous trees is concentrated in southern Europe, as that is where VPD increases the most under SSP2-4.5 (Figure 1). This suggests that land models used to project future carbon storage, which lack representation of sink-limited growth, may be underestimating the impacts of elevated VPD on the ability for the land to store carbon as wood.

#### 4. Discussion

This study is an important step toward quantifying how a source (photosynthesis)-driven land model simulates the response of radial growth to elevated VPD and assessing how missing sink limitation affects projections of future tree growth and carbon storage. This study is limited by its use of forcing from only a single ensemble member. A more comprehensive analysis using forcings from multiple climate models, and simulating radial growth across multiple land models, is needed to evaluate whether missing



**Figure 4.** The impact of VPD-driven, sink-limited reductions in radial growth on volumetric carbon storage is quantified by adjusting CLM5-FATES SSP2-4.5 outputs using scaling factors derived from the statistical model. The statistical model is forced with an SSP2-4.5 VPD-only scenario, and reductions in radial growth are defined relative to a 2005–2014 baseline. For each grid cell and time step over 2015–2069, the fractional reduction in growth (relative to the baseline) is applied as a multiplicative factor to the corresponding CLM5-FATES radial growth. Results are reported as relative changes in carbon storage compared to the unadjusted CLM5-FATES SSP2-4.5 simulation. Species-level responses from the statistical model are aggregated to plant functional types by averaging across species: conifers are represented by the mean response of *Picea abies*, *Abies alba*, and *Pinus sylvestris*, and broadleaves by the mean response of *Fagus sylvatica*, *Quercus petraea*, *Fraxinus excelsior*, and *Quercus pubescens*. Gray values indicate areas outside of the modeled plant functional type distribution.

sink-limited growth representation substantially affects carbon storage projections across all models. Our analysis focuses on extratropical trees located in Europe, as most openly available dendrometer data comes from Switzerland, but future work could be extended to other extratropical regions. Although the dendrometer data are derived from observations in Switzerland, they are among the primary species found across temperate and boreal Europe, spanning a broad range of elevations as well as mean annual temperature and precipitation conditions (Etzold et al., 2022a; Zweifel et al., 2021b). However, this limits the ability for which these observations can be extrapolated for all of Europe. Some species (*Fraxinus excelsior*, *Quercus pubescens*, and *Quercus petraea*) are represented by relatively small sample sizes (Table S1 in Supporting Information S1) and limited climate ranges, which reduces the extent to which their growth relationships can be generalized across Europe (Etzold et al., 2022a). These 3 species also had the lowest sensitivity to VPD, meaning decreases to projections of carbon storage are amplified when focusing on other species with more robust data (Figures S2 and S3 and Table S2 in Supporting Information S1). The statistical model assumes that growth occurring on a given growth day remains unchanged in the future, which may further lead to an underestimation of future reductions in radial growth. Furthermore, similar analysis with dendrometer data from tropical species would enable us to understand if sink-limited growth representation is needed for all plant functional types. Combined, these analyses could enable a first order quantification of the global land sink overestimation in current ESM projections.

The dendrometer data used here did not test for the effects of elevated CO<sub>2</sub>, so we were limited to focusing on constant CO<sub>2</sub> scenarios for our analysis. Differences in baseline atmospheric CO<sub>2</sub> concentrations between the CLM5-FATES simulations and the dendrometer observations could influence our comparisons. However, we expect this effect to be small because our analysis focuses on future-versus-baseline climate impacts using constant CO<sub>2</sub> concentrations across all experiments. Differences in baseline nitrogen fertilization rates could also contribute to discrepancies between the model and observations. We expect this influence to be small because the future-versus-baseline scenarios we compare use the same fertilizer inputs. While a 300-year spin-up for CLM5-FATES is sufficient to equilibrate tree growth, it may not fully equilibrate soil conditions, particularly at higher latitudes. However, we assume this has a minimal impact on simulated radial growth, and that future climate forcing is the dominant driver of our results. Using CLM5-FATES in fixed biogeography, no competition mode allows the isolation of climate-driven impacts, but neglects the effect of vegetation redistribution and competition,

which could be important for long-term responses of tree growth to climate. This first attempt at accounting for sink limitation in CLM5-FATES output is necessarily simplified due to observational constraints. Specifically, we assume that VPD does not influence photosynthesis or tree height in CLM5-FATES, as there were no measurements of either alongside the dendrometer observations. Due to these assumptions, the results are best viewed as first-order estimates rather than definitive predictions. Incorporating sink-limited growth processes into land model code, such that wood formation is downregulated under low turgor pressure, is still needed as it may modify the strong CO<sub>2</sub> fertilization effect commonly observed in land model simulations.

## 5. Conclusions

Global Earth system models are used to project the severity of climate change and its associated impacts. One of the largest sources of uncertainty in Earth system model estimates is how the land surface will respond to future climate change. We show that a commonly used land surface model underestimates the negative impacts of future climate change on tree growth because it is 2–3 times less sensitive to increasing VPD than an observation-based statistical model derived from dendrometer measurements. Under SSP2-4.5 with constant CO<sub>2</sub>, the statistical model estimates that tree radial growth in Europe will decline by about 13% for broadleaves and 9% for conifers by mid-century. Under the same climate change scenario, the land model shows weaker sensitivity to VPD, but still projects similar impacts for conifers because the regression model includes a positive temperature effect that benefits their growth. In contrast, broadleaf tree radial growth declines by only about 7% in the land model, reflecting its lower sensitivity to VPD. If the land model output is adjusted to match the VPD-driven growth reductions under SSP2-4.5 inferred from the statistical model, projected national tree carbon storage across Europe decreases by up to 30%, with the largest decreases in southern Europe where VPD is projected to increase the most. Additional research is needed to evaluate other land models and determine whether this underestimation is a systemic issue. Land models likely need to be updated to include representation of physiological constraints on tree growth to better estimate future climate impacts on terrestrial carbon uptake. If physiological constraints limit carbon allocation to woody growth even when photosynthesis remains high, then land models may overestimate the magnitude of the CO<sub>2</sub> fertilization effect under future climate scenarios, which requires further exploration.

## Conflict of Interest

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

## Availability Statement

The dendrometer data used in this study is available at <https://dryad.org> (Etzold et al., 2022b). CLM5-FATES output is available at <https://zenodo.org> (Clark, 2026a). Code and figure generation scripts are available at <https://zenodo.org> (Clark, 2026b).

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