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Soil nitrogen drives inverse acclimation of xylem growth cessation to rising temperature in Northern Hemisphere conifers

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Controlled experiments suggest that the seasonal build-up of nitrogen (N) limitation constrains the responses of forest autumn phenology to elevated temperatures. Therefore, rising soil N is expected to increase the delaying effects of elevated temperature on the end of the season, i.e., leaf senescence. However, the interactive effects of temperature, soil N, and aridity on xylem autumn phenology remain unknown. We conducted a wide spatial analysis from 75 conifer sites in the Northern Hemisphere and found that rising soil N increases the delaying effects of elevated temperature on the end of xylem cell wall thickening but reduced the delaying effects on the cessation of cell enlargement, especially in humid regions. The contrasting effects of elevated soil N on cell enlargement versus cell wall thickening could affect xylem cell anatomy, thereby induce changes in wood density, and induce a decoupling of stem size growth from photosynthate production. These analyses extend previous findings on forest autumn phenology by systematically investigating the spatial variation in the interactive effects of temperature and soil N on xylem autumn phenology at the cellular scale.

soil moisture | stem growth | autumn phenology | wood formation | xylogenesis

Forests offset approximately 20% of anthropogenic CO_2 emissions and play a crucial role in the global carbon cycle and the climate system (1). The carbon allocated to woody growth has a long residence time, ranging from several decades to centuries, as woody biomass (2). Elevated temperatures can increase the stem carbon sink by extending the xylem growing season, and it has been reported that a delayed cessation of xylem growth contributes to xylem growth in a manner similar to an advanced onset time (3). Extensive reports exist on the advanced onset of xylem spring phenology in the Northern Hemisphere (4, 5). By contrast, autumn phenology responses to elevated temperatures remain unclear, introducing substantial uncertainty regarding the actual global potential for carbon sequestration in forest ecosystems (3).

One of the largest uncertainties arises from the fact that advanced tree growth in spring requires higher water and nutrient inputs, which can lead to water and nutrient limitations in the autumn (6–8). Therefore, compared to spring phenology, autumn phenology responses to elevated temperature are more likely constrained by water or nutrient limitation (9, 10). Nitrogen (N) is essential for tree growth and photosynthesis (11), and a growing body of evidence shows that N limitation can advance the cessation of primary growth (12–15). To date, despite natural forests typically being considered as sites with moderate to low soil N concentrations, the delayed end of the growing season following elevated soil N has only been reported in controlled experiments, mainly based on leaf phenology (12–15). However, it remains unknown whether rising soil N could lead to delayed xylem autumn phenology in natural forests.

Higher soil N could decrease the hydraulic safety margin of trees by causing structural overshoot, which promotes hydraulic failure and increases forest vulnerability to water limitations (16). Unlike controlled experiments conducted in chambers with guaranteed water supply, natural forests are subjected to seasonal water shortages or drought periods, even in humid regions. To examine the interactive effects of temperature, soil N, and the aridity index on the cessation of xylem growth, we conducted a spatial analysis using

Significance

Theory and experiments suggest that rising soil nitrogen (N) could delay the cessation of the growing season based on leaf phenology data, but no intercontinental analyses on xylem phenology have been carried out. Using data on xylem phenology from conifers across the Northern Hemisphere, we found that rising soil N delays the end of xylem cell wall thickening but advances the cessation of cell enlargement. While xylem cell enlargement is responsible for stem size growth, cell wall thickening accounts for 90% of woody biomass production. The contrasting effects of soil N on these two xylem differentiation processes would affect xylem cell anatomy and consequently influence water transport and wood density in conifers.

The authors declare no competing interest.

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a wide and unique dataset of xylem phenology collected at weekly resolution, including data from 20 conifer species across 75 sites in the Northern Hemisphere (*SI Appendix*, Fig. S1 and Dataset S1).

Results

How Soil N Concentrations Regulate the Responses of Xylem Autumn Phenology to Rising Temperature. Temperature, precipitation, soil moisture, and photoperiod during the growing season are important drivers of the cessation of xylem autumn phenology in forest trees (17). By constructing Bayesian mixed-effect models (BMMs), we explored the effects of site aridity index (AI), soil N concentration, mean daily values of temperature (Tmean), photoperiod (photoperiod), soil moisture in the root zone ($Moisture_{root}$), and total precipitation during the growing season, and the interaction among AI, soil N, and Tmean on the cessation dates of xylem cell enlargement (Ee_DOY) and cell wall thickening (We_DOY) (Fig. 1 *A* and *C* and *SI Appendix*, Table S1 and S2). The growing season was defined as period from the onset of xylem cell enlargement (Es_DOY) to the cessation of cell wall thickening (We_DOY). Multiple collinearities among these predictors were also checked, which show no significant collinearity among these predictors (*SI Appendix*, Table S3).

We found that elevated soil N significantly advanced the cessation of xylem cell enlargement but delayed cell wall thickening. By contrast, AI exerted nonsignificant effects on both the cessation of cell enlargement and wall thickening. Rising Tmean delayed both processes (Fig. 1 *A* and *C*). Significant interactions were observed among AI, soil N, and Tmean, so we focused on the significant three-way interactions between these variables for Ee_DOY and We_DOY (Fig. 1 *B* and *D*).

In general, rising Tmean delayed the cessation of xylem cell enlargement, but the delaying effects were reduced with rising soil N, meaning they were weaker in sites with more fertile soils (Fig. 1 *B* and *D* and *SI Appendix*, Figs. S2 and S3). Furthermore, these reductions were exacerbated by higher site-mean soil moisture. Similarly, rising Tmean delayed cell wall thickening, but high soil N amplified the delaying effects of rising Tmean on We_DOY (Fig. 1 *B* and *D*). At the biome level, elevated soil N significantly reduced the delaying effects of rising Tmean on Ee_DOY in temperate forests but not in boreal forests (*SI Appendix*, Fig. S4 and Table S1). Similarly, elevated soil N significantly increased the delaying effects of rising Tmean on We_DOY in temperate forests but not in boreal forests (*SI Appendix*, Fig. S5 and Table S2).

How Elevated Soil N Advanced Xylem Cell Enlargement. Xylem cell enlargement is a process that requires a continuous supply of water (18, 19), which is absorbed from the soil by the roots and transported via the xylem throughout the tree, driven largely by transpiration (20, 21). An advanced onset of forest growth could deplete soil moisture, leading to water shortages that are carried over into the mid-to-late growing season (6, 22, 23).

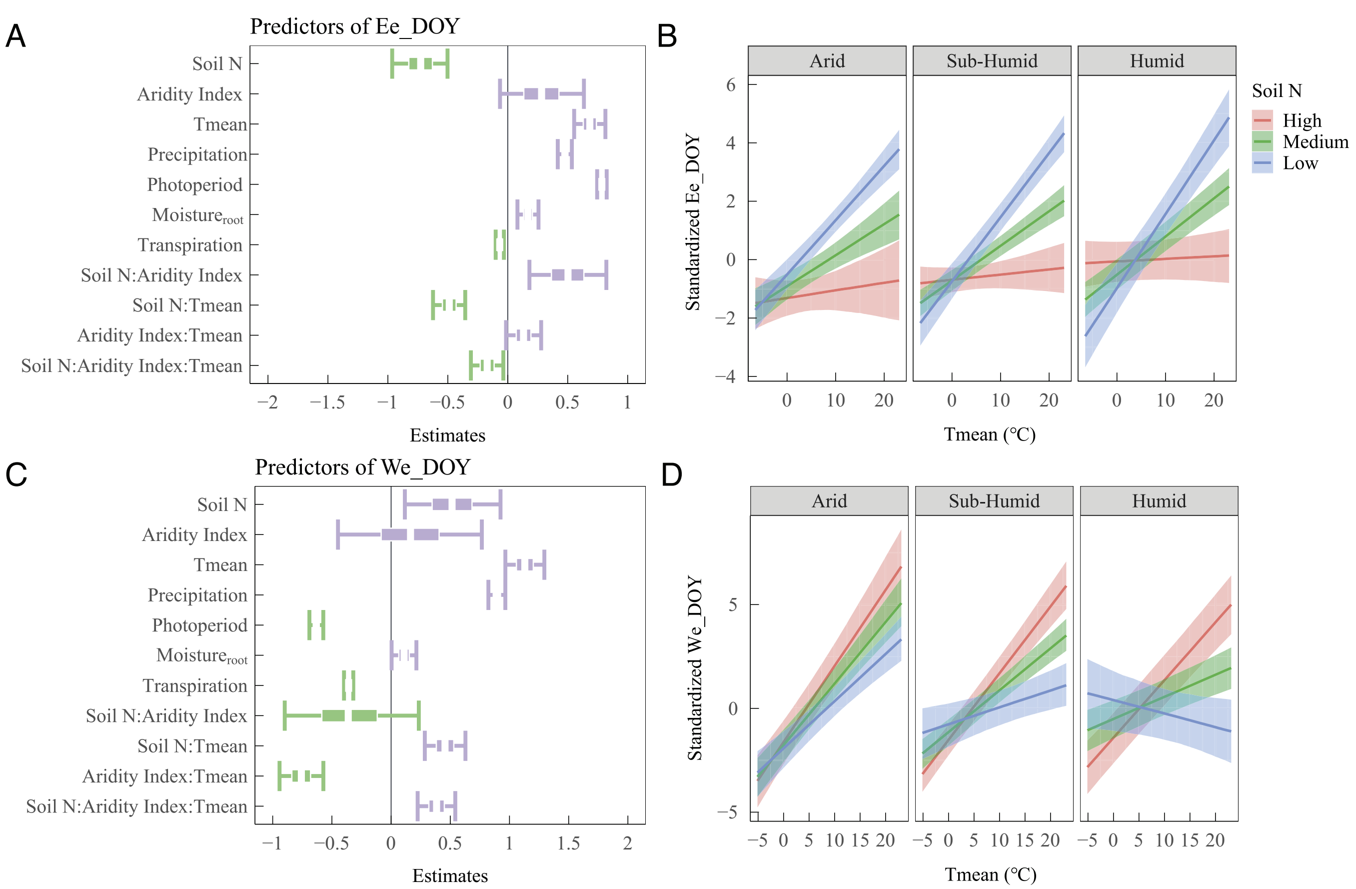

Fig. 1. Summary of the direction and strength of the effects of all predictors using Bayesian linear mixed-effect models on Ee_DOY (*A*) and the three-way interaction effects of Tmean, soil nitrogen (N), and aridity index (AI) (*B*) on Ee_DOY; Summary of the direction and strength of the effects on We_DOY (*C*) and the three-way interaction effects (*D*) on We_DOY. Significant effects are indicated when there is no overlap between the 95% error bars and zero. The purple and green colors denote positive and negative effects, respectively. Lines and ribbons represent the posterior mean and the 95% CI. Ee_DOY: cessation dates of cell radial enlargement; We DOY: cessation dates of cell wall thickening; Tmean: mean daily temperature during the growing season; Precipitation: total precipitation during the growing season; Photoperiod: mean daily photoperiod during the growing season; $Moisture_{root}$: mean daily soil moisture in the root zone during the growing season; Transpiration: mean daily transpiration during the growing season. The growing season is defined as the period from the onset dates of radial cell enlargement to the cessation dates of cell wall thickening. The soil N data used here are obtained from field-measured sources.

We therefore constructed SEM to reveal whether elevated soil N advanced the cessation of xylem cell enlargement through modulating the onset dates of xylem cell enlargement (Es_DOY), transpiration, $Moisture_{root}$, and total xylem cells (Fig. 2 and *SI Appendix*, Table S4). We observed total xylem cells were positively related with the cessation dates of xylem cell enlargement (Ee_DOY). Elevated soil N could decrease total xylem cells via delaying the Es_DOY and increasing transpiration rate, or increase total xylem cells via increased cell production rate, but the total effect on xylem cells is nonsignificant (Figs. 2 and 3*C* and *SI Appendix*, Tables S4 and S5). We also found that elevated soil N accelerated transpiration rate, which had a two-way relationship with $Moisture_{root}$, and this covariation between transpiration rate and $Moisture_{root}$ could also advance the Ee_DOY. However, elevated soil N primarily advanced Ee_DOY directly, suggesting the involvement of other mechanisms (Fig. 2 and *SI Appendix*, Tables S4 and S5).

Effects of Soil N on Es_DOY, $Moisture_{root}$, and Xylem Cells. To better visualize the partial effects of soil N on Es_DOY, $Moisture_{root}$, and xylem cells within the final SEM, we present partial residual plots. Rising soil N significantly delayed the onset dates of xylem cell enlargement (Es_DOY) (Fig. 3*A*) and increased mean daily transpiration rate during the growing season (Fig. 3*B*), but had no significant effect on the total number of xylem cells produced (Fig. 3*C*).

Discussion

Here, based on a spatial analysis from 75 conifer sites across the Northern Hemisphere, we examined the interactive effects of temperature, soil N, and site aridity (AI) on the cessation of xylem growth at the cellular scale. We found significant but contrasting interactive effects on xylem cell enlargement and cell wall thickening, particularly in humid regions. These contrasting effects support and extend previous findings that stem size growth is decoupled from photosynthate production at xylem cell scale (24, 25). This decoupling could also influence xylem cell anatomy, i.e., inducing smaller xylem cell size but thicker cell walls, consequently affecting water transport and tree ring density differently across sites.

Elevated Soil N Constrains the Effects of Rising Temperature on the Cessation of Xylem Cell Enlargement. Warmer temperatures can promote the conversion of starch to sugar, thereby inducing cell division in the vascular cambium zone (26), which is expected to delay the cessation of wood formation (27). In general, we observed a trend toward delayed cessation of xylem autumn phenology with elevated temperatures (Fig. 1 *A*–*D* and *SI Appendix*, Figs. S2 and S3). Existing evidence suggests that the responses of autumn xylem phenology to rising temperature are more likely constrained by soil water and/or nutrient limitations, which are necessary to maintain photosynthesis rates during the growing season, compared with spring xylem phenology (9, 10). Consequently, increased availability of water and/or nutrients has been shown to delay the end of the growing season in forest trees (13). Therefore, we expected that rising soil N could increase the delaying effects of rising temperature on xylem growth cessation. Our results supported this for the cessation of xylem cell wall thickening (Fig. 1 *A* and *B*) but not for xylem cell enlargement (Fig. 1 *C* and *D*). Intriguingly, we observed that rising soil N reduced the delaying effects of rising temperature on the cessation of xylem cell enlargement, and this reduction was amplified by increased water availability; that is, the strongest reduction occurred in more humid sites, where the delaying effects even reversed (Fig. 1*D*). Xylem cell enlargement is responsible for stem size growth, while cell wall thickening contributes to 90% of woody biomass production (28), which mainly depends on the supply of recently fixed carbohydrates (29, 30). Our results indicate that elevated soil N may induce a decoupling of stem size growth from photosynthate production, as has been reported in other studies (24, 25). Furthermore, the contrasting effects of elevated soil N on xylem cell enlargement versus cell wall thickening could affect xylem cell anatomy by inducing changes

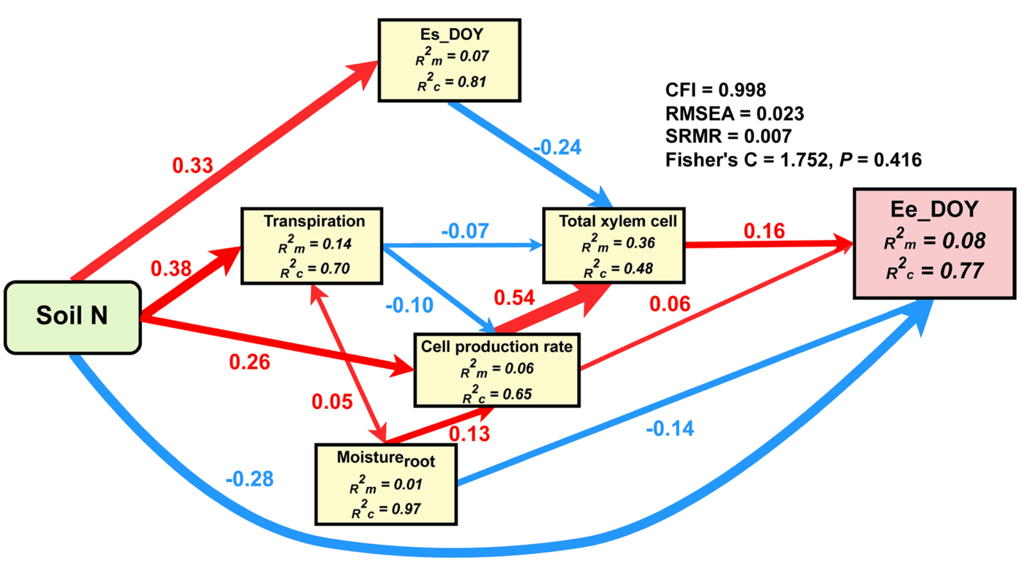

Fig. 2. Direct and indirect effects of soil nitrogen (N) on the cessation dates of xylem cell enlargement (Ee_DOY) through its influence on Es_DOY, transpiration, $Moisture_{root}$, and total xylem cells. The arrows indicate the direction and strength of the effects; solid red and blue arrows represent significant positive and negative standardized path coefficients ($P < 0.05$), respectively. Es_DOY: onset dates of xylem cell enlargement; Transpiration: mean daily transpiration during the growing season; $Moisture_{root}$: mean daily soil moisture in the root zone during the growing season. The growing season is defined as the period from the onset of radial cell enlargement to the cessation of cell wall thickening. The soil N concentrations data used here are obtained from field-measured sources. We computed the conditional R^2 (R^2c) and the marginal R^2 (R^2m) for every dependent variable: the former indicates the total variance explained by both the fixed and random effects, whereas the latter reflects only the variance explained by the fixed effects. The reported values for R^2m and R^2c are provided alongside each response variable. Notes: red and blue single-headed arrows indicate tested positive and negative causal relationships, respectively; two-way headed arrows indicate bidirectional covariances. Global goodness-of-fit: measures of overall model fit including Fisher's C. statistics, comparative fit index (CFI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR) are shown in the *Upper Right*.

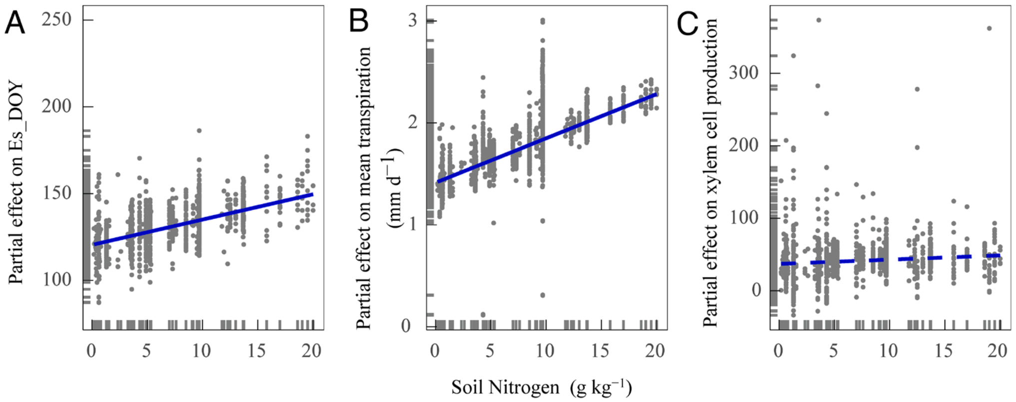

Fig. 3. The effect of field-measured soil nitrogen concentration on (*A*) the onset dates of cell enlargement (Es DOY), (*B*) mean daily transpiration during the growing season, and (*C*) the xylem cell production.

in cell size and cell wall thickness, ultimately affecting the carbon uptake and storage as woody tissues by conifer forests (31). When considered at the biome level, such changes in xylem cell anatomy were observed only in temperate forests but not in boreal forests (*SI Appendix*, Figs. S4 and S5).

How Elevated Soil N Reduces the Delaying Effects of Rising Temperature on Xylem Cell Enlargement. We examined two existing mechanisms in the literature that could constrain the delaying effects of elevated temperature on xylem cell enlargement. The first is amplified water stress induced by the advanced onset of the growing season (6–8). An advanced spring onset could accelerate water limitation later in the season through the seasonal build-up of water stress (6, 32, 33), leading to an advanced cessation of tree growth. A growing body of evidence on xylem growth indicates that an advanced onset could also lead to an advanced cessation (17, 34). For example, previous studies conducted in semiarid forests revealed that the advanced onset of xylem cell enlargement was accompanied by its earlier cessation (34). However, we rule out this possibility, as rising soil N led to a delayed onset of wood formation (Figs. 2 and 3*A*). The second mechanism is the saturation of a tree's annual carbon sink. The underlying hypothesis here is that the strength of the carbon sink governs the timing of autumn phenology (35–39). We observed that xylem cell wall thickening was delayed under rising soil N concentrations. This suggests that the hypothesis of saturation of a tree's annual carbon sink does not apply in our study (37, 38).

We observed higher amounts of xylem cells could significantly delay the cessation dates of xylem cell enlargement (Fig. 2 and *SI Appendix*, Tables S4 and S5), since more xylem cells require more time to complete the enlargement process (40). However, elevated soil N exerted nonsignificant effect on the total xylem cells (Fig. 3*C*). This is because rising soil N, on one hand, decreased total xylem cells via delaying the onset dates of cell enlargement and increasing transpiration rate. On the other hand, rising soil N increased total xylem cells via increased cell production rate (Fig. 2 and *SI Appendix*, Tables S4 and S5). Hence, elevated soil N could not affect the cessation dates of cell enlargement via regulating total xylem cells.

Then, what are the possible mechanisms driving the earlier termination of xylem cell enlargement under elevated soil N? High soil N could enhance stomatal conductance, thereby increasing the leaf photosynthetic and transpiration rates of forest trees, particularly in forests from wet regions (41). We indeed observed accelerated transpiration rates in the canopy (Fig. 2), indicating that trees require more water for photosynthesis and other physiological functions. Yet, we observed a significant but weak relationship between transpiration rate and soil moisture in the root zone ($Moisture_{root}$). This probably reflects a dynamic covariation between aboveground transpiration and belowground moisture (42), as indicated by the two-way relationship in the SEM. Specifically, higher soil moisture could support higher transpiration. However, the relationship between transpiration and soil moisture may be nonlinear, with transpiration rate decreasing above a certain threshold of soil moisture due to the saturated air or soil. Xylem cell enlargement requires sufficient water to maintain turgor pressure (18, 19). Therefore, this weak but significant effect may indicate confounding and site-specific effects of water supply in determining the cessation dates of xylem cell enlargement, which remains an open question and warrants further investigation. We also observed other important mechanisms driving the earlier termination of xylem cell enlargement under elevated soil N, which might involve shifts in C allocation between photosynthetic (leaves) and nonphotosynthetic (roots and stems) organs (39). Therefore, we stress the importance of incorporating C allocation among the different tree organs when predicting forest growth responses to climate change. This approach would provide a strong basis for predicting future leaf and wood phenological shifts, along with their impacts on global C and N cycles. This is particularly important given that most studies on tree phenology focus on leaves.

Uncertainties, Caveats, and Limitations. The microsampling technique used in our study provides high time-resolution (weekly) data of xylogenesis, offering a detailed, firsthand assessment of changes in xylem cell diameter and cell wall thickness, both of which are strongly correlated with tree-ring microdensity (31, 43). However, the process of collecting xylem phenology data is time-consuming and labor-intensive (44, 45), and we generally conducted anatomical analyses over a very short time span. As a result, we are unable to address changes in xylem autumn phenology over extended periods. One of the main limitations of using spatial analysis is that it does not account for potential time lags or carry-over effects of environmental changes on the cessation dates of xylem growth. Therefore, long-term, in situ monitoring networks of wood formation and soil N uptake are needed to strengthen the confidence in assessing the interactive effects of climate (e.g., temperature) and local factors (e.g., soil nutrients) across large scales.

The largest xylem autumn phenology dataset used in our study is still confined to temperate and boreal forests, although anatomical methods have increasingly been applied in other parts of the world, such as subtropical forests. Furthermore, research on the kinetics of xylem cell differentiation in broadleaved tree species is still limited due to the complex wood structure that is incompatible with the available modeling approaches (40). Consequently, caution is needed when extrapolating our findings to underrepresented biomes or tree species, such as conifers or angiosperms from subtropical and tropical forests.

Materials and Methods

This study used data collected from 814 trees located in 75 sites covering boreal, temperate, Mediterranean, and subtropical biomes in North America, Europe, and Asia, distributed across latitudes 23°11′ to 66°12′ N and at elevations ranging from 23 to 3,850 m a.s.l. (Dataset S1). Although the monitoring years span from 1998 to 2016, depending on the sampling sites, the cessation dates of xylem growth on the individual sites were generally collected over a very short time span (Dataset S1). This dataset is an aggregation of spatial comparisons of the cessation dates of xylem growth.

At each site, 1 to 55 adult dominant trees with upright, healthy stems were selected for extracting wood microcores (2.5 mm in diameter × 25 mm in length) at breast height (1.3 ± 0.3 m) using a Trephor borer (45). The samplings were conducted each week or, occasionally, biweekly throughout the growing season from January–April to October–December, according to the local climate conditions of the study sites. The microcores were placed in Eppendorf tubes that contained 50% ethanol and then stored at 5 °C. Microcores were then treated (sectioned, stained, observed) according to Rossi et al. (44). Further description of measurement and climate and soil data sources, and analytical procedures are described in *SI Appendix*.

Data, Materials, and Software Availability. All study data are included in *SI Appendix*, Dataset S1.

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