FORWARD MODELING OF TREE-CLIMATE RELATIONS ACROSS THE NORTHERN HEMISPHERE

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Abstract

This thesis uses the Vaganov-Shashkin model of tree ring formation, a multivariate, nonlinear, mechanistic model that directly predicts tree-ring growth using climate data, to simulate tree-ring formation across the Northern Hemisphere. Previous research has shown the model has skill in reproducing ring-width variability and climate sensitivity at local and regional scales, but its ability to simulate the major geographical differences in tree-climate relationships at a hemispheric scale has not yet been tested. In this study, we ran the model at over 7,000 locations across the Northern Hemisphere, and compared the seasonal climate responses of the simulations against a network of nearly 2,200 real tree-ring width records. We also calculated the predicted dominant factor at each location and used relative growth rates to explain these patterns.

Simulated tree-ring chronologies are consistent with the real ones in the seasonality and relative strength of the encoded climate signals, demonstrating that the model has skill in reproducing tree-ring growth response to climate variability across the Northern Hemisphere. Because the simulations were produced using only climate records and the same set of parameters, the fact that the model was able to reproduce major geographical differences in the observations suggests that climate is the primary factor in determining large-scale tree-climate relationships. We also used relative growth rates to show the sequence of events during the growing season and the possible mechanism of the climate response of tree rings. We found that temperature dominates growth at temperature-sensitive sites during most of the growing season and that at stations where temperature dominates growth at the end of growing season, summer precipitation generally has a strong positive influence on tree-ring formations, while at locations where soil moisture limits growth at the end of growing season, ring widths usually have a positive correlation with winter precipitation. Because the model has skill in reproducing ring widths and tree-climate relationships at local, regional and hemispheric scales, we suggest VSM can potentially be used as a low-cost estimator to predict tree-ring response to climate prior to sampling and to forecast long-term changes in tree-climate relationships.

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1. INTRODUCTION

Tree-ring widths are one of the most widely used proxies of past climate (Hughes, 2002; Vaganov, 1996). Because of the accuracy and precision of tree-ring dating, the large-scale common response to regional climate, and the effectiveness of simple linear models of tree-ring climate relationships, tree-ring widths are used widely to reconstruct past climates during the last several hundred or thousands of years (Hughes, 2002). Fritts (1966) established the analytical framework for tree-ring reconstruction and Cook (1987) proposed a linear aggregate model to decompose and extract different environmental signals encoded in ring widths. Since then, dendrochronologists have been using simple correlations, linear regression with climate factors or their principal components to identify monthly or seasonal climate signals in tree rings for various purposes (Fritts, 1976; Hughes, 2002; Meko & Woodhouse, 2011). Ring-width records from arctic and alpine treeline have been commonly used to reconstruct seasonal or annual temperatures at different spatial scales (D’Arrigo et al., 2006; Mann et al., 2008). Tree rings are also widely adopted to reconstruct seasonal precipitation (Cook et al., 2010) and other hydrological variables such as river discharge (Meko et al., 2007) and snowpack (Pederson et al., 2011). Recently, St. George & Ault (2014) examined large-scale patterns of tree-climate relationships within a hemispheric network of ring widths and demonstrated that the climate information encoded within tree-ring widths exhibits major regional differences.

Assessments of the climate information recorded by tree rings are still limited by the complexity and seasonality of tree-ring response to climate variability and the techniques used to remove non-climatic influences (Hughes, 2002). Simple correlation and response function are widely adopted because of the large-scale common year-to-year variability between trees and the effectiveness of simple linear models on tree-climate relations at many sites (Hughes, 2002). But they are also generally limited by assuming a linear and stationary climate–proxy relationship and neglecting other non-climatic factors (Tolwinski-Ward et al., 2011; Vaganov et al., 2011). Due to lack of complete understanding of the mechanisms of radial growth of most tree species, significant uncertainty exists in determining environmental influences and tree-climate relationships using statistical methods (Cook & Pederson, 2011).

One alternative to the standard empirical approach used to interpret climate signals within tree-ring widths is to simulate tree-ring formation with mechanistic models. Studies have proved cellular processes involved in tree-ring formation respond to both internal and environmental influences (Fritts, 1966; Vaganov et al., 2011; Vaganov et al., 2006), so a process-based model that includes only the critical processes that are minimally necessary to link climate variables to tree-ring formation may better reproduce the climatic impacts on ring widths (Anchukaitis et al., 2006; Evans et al., 2006).

The Vaganov–Shashkin model (hereafter, 'VSM') is a process-based, multivariate and nonlinear model that simulates tree-ring formation using widely-available environmental data (Anchukaitis et al., 2006; Vaganov et al., 2011; Vaganov et al., 2006). The model assumes both cambial growth rates and the duration of cellular processes are influenced directly, but non-linearly by the tree's physical environment. The model contains a growth block (environmental block) and a cambial block. Each day, the model calculates relative growth rates (ranging from 0 to 1) due to both temperature and soil moisture, and the factor that is most limiting (Fritts, 1976) drives cellular processes in the model's cambial block (Evans et al., 2006; Vaganov et al., 2006). The model uses latitude (as a surrogate for solar insolation) and records of daily temperature and precipitation as inputs, and produces relative growth rates and annual tree-ring widths. The model also requires parameters to describe biological thresholds and levels (such as minimum and maximum soil moisture, lower and upper optimal temperature and coefficient of soil melting) as well as parameters that determines the cambial activity based on known average kinetic characteristics (such as critical growth rates or cell sizes that determines the phase of a cell in the cambium). Evans et al. (2006) proved that the model is able to skillfully reproduce annual and decadal timescale variations in tree-ring widths without site-by-site tuning of parameters, but adjusting parameters based on tree species and site conditions (soil, slope, etc.) may improve the accuracy of ring-width simulations (Tolwinski-Ward et al., 2011; Vaganov et al., 2006).

Studies have intensively tested the skill of the model to reproduce variability and climate response of tree-ring widths at local and regional scale. For instance, Evans et al. (2006) simulated tree-ring widths, compared them against chronologies from North America and Russia sites and proved that VSM produces about the same skill on annual and decadal timescales as classical dendrochronological statistical modeling techniques without site-by-site tuning. They also inferred that the match between simulations and observations supported the use of both the broad-scale network of tree-ring width chronologies and VSM in paleoclimatic field reconstructions. Anchukaitis et al. (2006) applied the model to simulate regional patterns of tree-climate relationships in the southeastern United States and found consistent patterns in climate response of the simulations with those of actual tree-ring data. Therefore, they concluded that VSM has skill in reproducing broad-scale patterns of tree-climate relationships and that VSM may have further implications for nonlinear responses of tree growth to climate variability and the prediction of ecosystem responses to climate change.

In this study, we used VSM to simulate tree-ring formation during the last century at several thousand locations across the Northern Hemisphere. We then compared the climate response of simulated tree-ring width records across the network to the response displayed by a network of more than 2,200 real tree-ring records. We also used our simulations to evaluate how seasonality influences the combined effects of temperature and moisture on tree-ring formation, and explain why real tree-ring chronologies record specific climate ‘windows’ depending on local climatology. Though previous studies have test the skill of the VS-Lite (a simplified version of the VSM that uses monthly climatological records instead of daily ones and has fewer parameters than the full VSM) to reproduce tree-ring widths at a hemispheric scale (Breitenmoser et al., 2014) and tree-climate relationships at regional and continental scales (Tolwinski-Ward et al., 2011), this is the first study that applies the full VSM at a hemispheric scale and compares the hemispheric patterns of tree-climate relationships in the simulations with that in a hemispheric network of ring-width observations.

2. SIMULATING TREE GROWTH ACROSS THE NORTHERN HEMISPHERE

2.1 Data and model settings

We simulated tree growth across the Northern Hemisphere by driving the VSM with daily temperature and precipitation records from the Global Historical Climatology Network (GHCN-Daily; Menne et al., 2012). The GHCN-Daily dataset is an integrated database of daily climate summaries from land-surface stations across the globe that have passed quality-assurance procedures to detect duplicate data, climatological outliers, and temporal and spatial inconsistencies (Durre et al., 2010). These data are not adjusted for biases induced by historical changes in instrumentation and observing practices. The GHCN-Daily network contains more than 85,000 stations from over 170 countries, but its coverage is best in the United States and Western Europe (Supplemental Figure 1). Most GHCN-Daily stations in eastern and southern Asia have less than 50 years of data.

Simulations were conducted at all stations in the Northern Hemisphere with more than 30 years of climate data. At each location, years missing more than 90 days of either precipitation or temperature observations were excluded from the simulation. For all other years, missing temperature data were estimated using linear interpolation and missing precipitation values were set to zero. Daily temperature was calculated as the mean of maximum and minimum temperature. The parameters used to simulate tree-ring formation within VSM, which include optimal temperature, optimal soil moisture, and several other aspects of tree physiology and soil characteristics, were set to the model's default values (Evans et al., 2006; Vaganov et al., 2006). These values were based on the literature and on case studies at a limited number of high-latitude sites from the Northern Hemisphere (Vaganov et al., 2006). Following Evans et al. (2006), all simulations were initialized with one cambial cell and the same initial cell size and soil moisture. After each simulation was generated, its first year was excluded to reduce the influence of model initialization on the simulated tree-ring series.

2.2 Assessing tree-climate relations

Because the climate sensitivity of real tree-ring records are most commonly estimated by empirical comparisons against local climate observations (Babst et al., 2013; Fritts, 1966; St. George & Ault, 2014), we calculated simple (Pearson) correlations between our simulated tree-ring records and seasonal precipitation and temperature data. At each station, total summer (JJA) and winter (DJF) precipitation and mean summer temperature were computed from the same GHCN-Daily data used to drive the VSM. In all cases, correlation tests were adjusted for the loss of degrees of freedom due to autocorrelation (Dawdy & Matalas, 1964). We also estimated the relative influence of temperature and soil moisture at each site by computing the mean ratio (over all years) between (i) the number of days during the growing season when the total growth rate was limited by temperature and (ii) the total number of days during the growing season. For those cases where soil moisture was the principal factor limiting tree-ring formation for more than half of the total growing season, we also calculated the frequency that moisture or temperature was the main limiting factor at both the start and end of the growing season.

3. RESULTS

After applying our criteria for record length and completeness, we were able to produce tree-ring simulations at 7,003 locations across the Northern Hemisphere (Figure 1). The median length of the simulations was 65 years, and more than 900 simulations extended more than 100 years (Supplemental Figure 1b). We were not able to produce simulations at some stations that satisfied the length and completeness criteria because either temperatures or low soil moisture prevented VSM from ever reaching the critical growth rate (this issue occurred mainly at stations in northern Siberia, the Tibetan Plateau and Saharan Africa). Conversely, the model did produce simulations in treeless areas, including locations where forests have been removed by logging (such as Iceland; Blöndal, 1987) or semi-arid regions where trees are usually outcompeted by grasses (such as the Great Plains of North America; Bond, 2008).

3.1 Tree-climate relations in synthetic ring-width records

Comparisons with local climate data show that simulated ring-width records exhibit major differences in the strength and direction of association with seasonal temperature and precipitation. Across the hemisphere, nearly all simulated records are positively correlated with total winter precipitation (Figure 1a). The strongest associations were observed at stations in the American Southwest and northern Mexico, as well as select locations in the Mediterranean, central Asia and the American Gulf Coast. Only a very few (26 out of 7,003) simulations had a significant negative correlation with winter precipitation and these were restricted to locations in the eastern Tibetan Plateau, northern Canada, Alaska, and Russia.

Most simulations at low- and mid-latitude sites are significantly ($p=0.05$) and positively correlated with total summer precipitation, with the strongest associations observed in the eastern United States, northern Mexico, and east Asia (Figure 1b). In contrast, this relationship is absent in simulations from southern California and parts of the American Southwest, the central and eastern Mediterranean, central Asia, and the eastern Tibetan Plateau. At high latitudes, the connection between summer precipitation and simulated ring width weakens and, in some cases, switches sign. Most simulations in the northern half of the British Isles, Norway, and northern Sweden, Finland, and Russia are negatively (and only occasionally significantly) correlated with summer precipitation. Significant negative correlations are also present in west Alaska and coastal British Columbia.

Warm summers have a positive effect on simulated tree growth at cool sites across the high latitudes (Figure 1c). Summer temperatures are also significantly and positively correlated with simulated ring widths in the Alps and eastern Tibetan Plateau, but simulations from central Rocky Mountains do not show the same positive association with summer temperature. With only a very few exceptions, simulated ring-width records from mid- and low-latitude sites are significantly and negatively correlated with summer temperature.

Overall, the associations between simulated ring-width records and seasonal climate variables are very similar to those exhibited by the real Northern Hemisphere ring-width network (St. George & Ault, 2014). The VSM is able to produce the opposing response to summer temperature observed at mid- and high-latitude tree-ring sites, and is also able to recreate more subtle behavior, such as the observed weakening in temperature sensitivity at arctic treeline from northern Fennoscandia to central Russia. The simulations also match observations in showing the strongest winter precipitation signal at sites in southern California and the American Southwest (as well as the lack of a summer precipitation response). Likewise, both simulations and observations suggest that tree growth at high latitudes is also largely insensitive to summer precipitation. Compared to the real network, the hemispheric set of simulated ring-width records are more highly correlated with seasonal climate variables, which is likely because (i) real tree-ring sites are often far from the nearest climate station and (ii) VSM does not incorporate non-climatic phenomenon (such as soil type, ecological disturbances, aspect and slope) that are known to influence tree growth and obscure climatic signals within ring-width records (Cook, 1987). The simulations also exaggerate the clarity of winter precipitation signals, and are unable to reproduce the inverse associations between winter precipitation and ring-width observed at some records in the Pacific Northwest (which are due to the adverse influence of snowpack on tree growth; Pederson et al., 2011).

3.2 The relative influence of external environmental controls on tree growth

Because VSM calculates the daily growth rate on a given day *t* as (Evans et al., 2006)

$$G(t) = g_E(t) \times min[g_T(t), g_W(t)],$$

it is possible to determine the number of days during the growing season that tree-ring formation is limited by either temperature or soil moisture. Our simulations indicate soil moisture is the dominant control of tree growth across Mexico and most of the continental United States (Figure 2). Although soil moisture is the primary factor influencing tree-ring formation in the eastern United States, temperature becomes progressively more important towards the northeast (especially along the Appalachian Mountains) and supersedes moisture as the limiting factor in New England and eastern Canada. Temperature is also the main control on tree growth along the Pacific Northwest and high-elevation sites in the western interior. In Europe and Asia, the primary factor limiting simulated tree growth varies strongly by latitude. Soil moisture dominates at most sites south of 55ºN (except for locations in the Alps, the eastern Tibetan Plateau, and Japan), while tree growth at high-latitude sites is governed chiefly by temperature. Temperature is most consistently limiting in western Scandinavia, and its influence weakens with distance eastward, eventually being surpassed by soil moisture near 80ºE.

To understand the sequence of events in the growing season and why these major regional differences in the climate information encoded into tree-ring widths exist, we examined simulated daily growth rates at several locations across the network. These simulations were chosen because they are located close to ecotone limits which are often used as targets for dendroclimatological sampling (Fritts, 1976; Meko et al., 1993; Osborn & Briffa, 2006), were limited primarily by either temperature or soil moisture, and had a strong empirical connection to local seasonal climate that matched the signal recorded by real ring-width data in the same vicinity.

At sites close to latitudinal (Bardufoss, Norway; Figure 3a) or altitudinal treeline (Oberstdorf, Germany; Figure 3b), cool temperatures keep evapotranspiration rates low and, as a result, g_W is near maximum throughout the year. In both cases, the total growth rate is limited by g_T on every day within the growing season, which causes simulated ring-width records to be highly correlated with mean summer temperature (r = 0.93 and 0.85, respectively). In the other four simulations, the influence of temperature is usually supplanted by soil moisture, and ring width is more strongly associated with total summer or winter precipitation. Duldurga, Russia, which is located near the northern limit of Mongolian-Manchurian steppe (Olson et al., 2001), experiences dry winters and wet summers (nearly three quarters of its annual precipitation falls during June, July and August, Supplemental Figure 2c). By the time cambial activity is initiated by VSM on June 9th (Figure 3c), moisture supplied via snowmelt has been depleted and simulated tree growth depends entirely on recharge provided by summer rains. Temperature becomes limiting near the beginning of September, but during most of the growing season, growth is controlled by moisture, which leads simulated ring width to be highly correlated with summer precipitation (r = 0.81). Simulated ring width at Cascade, Iowa (Figure 3d) also tracks summer precipitation quite closely (r = 0.66) because rain is needed to replace evapotranspirative losses during the middle of the growing season. However, because Cascade receives more moisture during winter than Duldurga, this simulation also exhibits a strong correlation with total winter precipitation (r = 0.47). The synthetic tree-ring records from Ash Mountain, California (Figure 3e) and Sedona, Arizona (Figure 3f) are both highly sensitive to winter precipitation totals (r = 0.79 and 0.63, respectively). Ash Mountain has a pronounced Mediterranean climate (almost 90% of its total annual precipitation falls between November and the next April) so nearly all of the water available during the growing season is carried over from the prior winter. Sedona receives more rain than Ash Mountain during summer but because evaporatranspirative losses are so high, cool-season precipitation is again the dominant source of moisture required for simulated tree-ring formation.

3.3 Sequence of events at moisture-limited sites

In the previous section, we showed that relative growth rates can help illustrate the limiting factors and sequences of events in tree-ring formation across the year at a specific location. On the hemispheric scale, we can determine the sequence of events and intra-annual changes in the controlling climate factor using only the start and end conditions of the growing season. We mapped the hemispheric pattern in the dominant environmental control at the beginning and end of growing season at each station (Figure 4). At stations in Canada, Japan, central China, eastern United States, and between 50°N-60°N in Asia, temperature limits tree-ring growth at the beginning and end of growing season but soil moisture dominate for a longer period within the growing season. In these regions, soil moisture is abundant at the beginning and end of growing season while in the middle, because of relative high temperature and high evapotranspiration in the summer, soil moisture becomes the limiting factor. This sequence suggests summer precipitation is important for recharging soil moisture during the growing season, and depending on how much winter precipitation they exhibit, there might be a positive correlation with winter precipitation because soil moisture is the overall limiting factor. In contrast, soil moisture limits growth at both the start and end of growing season in the western Mediterranean, central Asia, southwest United States, Florida, and south and southeast Asia. At these locations, soil moisture limits growth around the year due to relative high temperature and low precipitation during the growing season. Therefore, tree-ring formation responds positively to winter precipitation at most stations within these regions and correlation with summer precipitation is positive in Eurasia and northern Mexico, where there are large amount of summer precipitation. Tree-ring formation at locations in the northeastern and central United States, southern Europe, and central Asia is limited by temperature at the beginning of growing season and soil moisture at the end, suggesting that moisture recharge during the winter is important at these locations and summer precipitation is relatively low compared with evapotranspiration. As a result, correlation with both summer and winter precipitation is generally positive at these locations. At selected locations in Alaska, Mongolia, and northern China, soil moisture dominates growth at the start of growing season and temperature limits at the end, which means that recharge of soil moisture is largely in summer. Therefore, these stations exhibit strong positive correlation with summer precipitation and relative weak response to winter precipitation.

4. DISCUSSION

Empirical comparisons suggest tree-ring formation may be influenced by a wide array of environmental factors (Cook, 1987; Fritts, 1976), and our hemispheric scale simulation suggests that climate is the primary factor of the hemispheric patterns of the tree-climate relationships. Tree-ring growth can be influenced by the age of trees, aspects and ecological conditions (Fritts et al., 1965), natural disturbances (Swetnam & Betancourt, 2010), and non-climatic factors such as volcanic eruptions (LaMarche & Hirschboeck, 1984) and CO_2 fertilization (Gedalof & Berg, 2010). Research also showed that at a hemispheric scale, climate information encoded within a hemispheric network of tree-ring widths exhibits major regional differences (St. George & Ault, 2014). Here we simulated ring widths and encoded seasonal climate signals at more than 7000 locations over the whole Northern Hemisphere using a simple mechanistic model that directly simulates conifer tree-ring growth using only climate records and uniform default set of parameters. Overall, the set of simulated tree-ring width records correlated positively with winter and summer precipitation and negatively with summer temperature at mid-latitudes, while at high-latitude and high-altitude regions, simulations exhibited negative correlation with precipitation and positive correlation with summer temperature. These patterns largely agree with the tree-climate relationship showed by the real hemispheric tree-ring network (St. George & Ault, 2014). Because the model does not include genetic differences in different tree species, the effects of ecological disturbances, or non-climatic factors like volcanic eruptions, we conclude that these hemispheric patterns of tree-climate relationships are primarily due to differences in regional climate and that other factors play a secondary role. In addition, because the model is a simple mechanism model of tree-ring formation, this fact further proves that tree rings are good proxy for climate variability and that it is possible to use climate records alone to predict tree-climate relation at a certain location.

Due to the large spatial scale of the simulations and mismatch between the locations of tree-ring sites and climate stations, certain problems exist with our comparisons, but we were still able to prove the skill of the model to reproduce large-scale patterns in tree-climate relationships. Firstly, in this study, we used the default parameters (Evans et al., 2006), so this simulation does not include information about soil, aspect, ecological settings, and many other factors known to influence the association between climate and tree growth. Prior studies using the VSM and VS-Lite showed that the climate thresholds for optimal growth can vary by species or by site (Breitenmoser et al., 2014; Tolwinski-Ward et al., 2011; Vaganov et al., 2006); as a result, it is likely that adding more detailed information about local site conditions and forest composition would produce more accurate simulations. This problem may also cause prediction of unrealistically early, late or long growing seasons, which generally happens at stations in the Mediterranean type of climate, for instance, stations in California. Secondly, we used Pearson correlation for equal comparison with empirical studies (St. George & Ault, 2014). Due to the large number of comparisons in this project, false discovery may cause overly strong significance (Benjamini & Hochberg, 1995). Though this problem exists in comparisons using both simulations and observations, because of the larger number of the simulations, the significance of the correlations and therefore the importance of climate factors may be exaggerated. Thirdly, we did not examine the magnitude or the significance of the similarity between the hemispheric patterns of tree-climate relationships in the observations and those in our simulations. Due to the mismatch between the locations and elevations of tree-ring sites and those of the climate stations and the spatial scale of this study, it is hard to perform a spatial comparison between the observations and the simulations or transformations like PCA. But we were able to conduct tree-ring simulations at more than 7000 locations over the Northern Hemisphere to achieve complete spatial coverage and the simulated tree-climate relationships are able to reproduce major geographical differences and transitions in the observations. Therefore, even though there are limitations with these simulations, our results suggest that the model has skill in reproducing large scale patterns in tree-climate relationships and may be useful as a forecasting tool. For example, the simulations could be used to estimate the likely climate sensitive of tree-ring width records prior to sampling at places that are yet to be sampled, such as locations in the ecotones in central Asia and eastern Europe, and potentially places with different climatic conditions within a small spatial scale, such as a range of sites along an elevational gradient or watershed.

We also used the relative growth rates simulated by the VSM to diagnose how seasonal climate response patterns emerge from the underlying climate. In general, simulated ring-width records that are highly correlated with mean summer temperature are the result of temperature being the dominant factor limiting tree-ring formation throughout (or nearly throughout) the growing season. These are usually high-latitude or high-altitude regions where precipitation is relatively abundant due to low temperature and evapotranspiration. In contrast, records that are highly correlated with total precipitation during either or both winter and summer often incorporate climate information through a more complex or variable sequence. Sites where temperature is the dominant factor during the growing season are generally sensitive to summer temperature in the simulations, while moisture-limited sites normally exhibit combined influence of both summer and winter precipitation. Examining the annual cycle of relative growth rates at six exemplar stations showed simulations that are positively correlated with summer temperature are produced by a relatively consistent sequence of events, in contrast, moisture sensitivity can arise from a number of potential combinations and factors such as the carry over effect caused by snow melting, water capacity of soil, and evapotranspiration-induced loss. At stations where temperature dominates growth at the end of growing season, summer precipitation generally has a strong positive influence on tree-ring formations, while at locations where soil moisture limits growth at the end of growing season, ring widths usually have a positive correlation with winter precipitation. This pattern still needs to be validated against observations of tree-ring formation and dormancy, but phenological studies based on species-level observations and field experiments have showed that phenological events in tropical or moisture-limited regions are sensitive to seasonal changes in soil moisture (Eamus, 1999; Peñuelas et al., 2004; van Schaik et al., 1993) whereas in temperate zones, plant phenology respond only to temperature and not to precipitation changes (Kaye & Wagner, 2014; Sherry et al., 2007).The relative importance of temperature and precipitation at the beginning and end of growing season can help explain how different combination of summer and winter precipitation may influence tree-ring growth. These combined influences also require caution in using sites where negative tree-ring response to summer temperature presents for temperature reconstruction.

5. CONCLUSION

In this study, we used a process-based model to simulate radial growth of tree rings in the Northern Hemisphere. Although the skill of the model to reproduce tree-ring variability and tree-climate relationship at certain locations has been intensively tested (Anchukaitis et al., 2006; Evans et al., 2006; Vaganov et al., 2006), our results proved VSM has skill in reproducing hemispheric patterns in tree-climate relationships. We also showed the simulated patterns of ring-width response to climate agree well with patterns drawn form a network of observations over the Northern Hemisphere, suggesting that climate is the primary factor that influences large-scale climate response in tree rings. These results also imply that, although there are biological and statistical uncertainties in reconstructing climate using tree rings (Cook & Pederson, 2011), at regional or larger scale, ring widths are efficient predictors of climate variation. We also used relative growth rates to show the sequence of events happened in the growing season and the possible mechanism of these tree-climate relationships. Temperature dominates growth at temperature sensitive sites during most of the growing season, and the relative importance of summer and winter precipitation to tree-ring formation can be derived from the climate conditions at the beginning and end of growing season. Because the model has skill in reproducing ring widths and tree-climate relationships at local, regional (Anchukaitis et al., 2006; Evans et al., 2006; Vaganov et al., 2006) and hemispheric scales, VSM might be useful as a low-cost estimator to predict tree-ring response to climate prior to extensive field sampling.

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APPENDICES

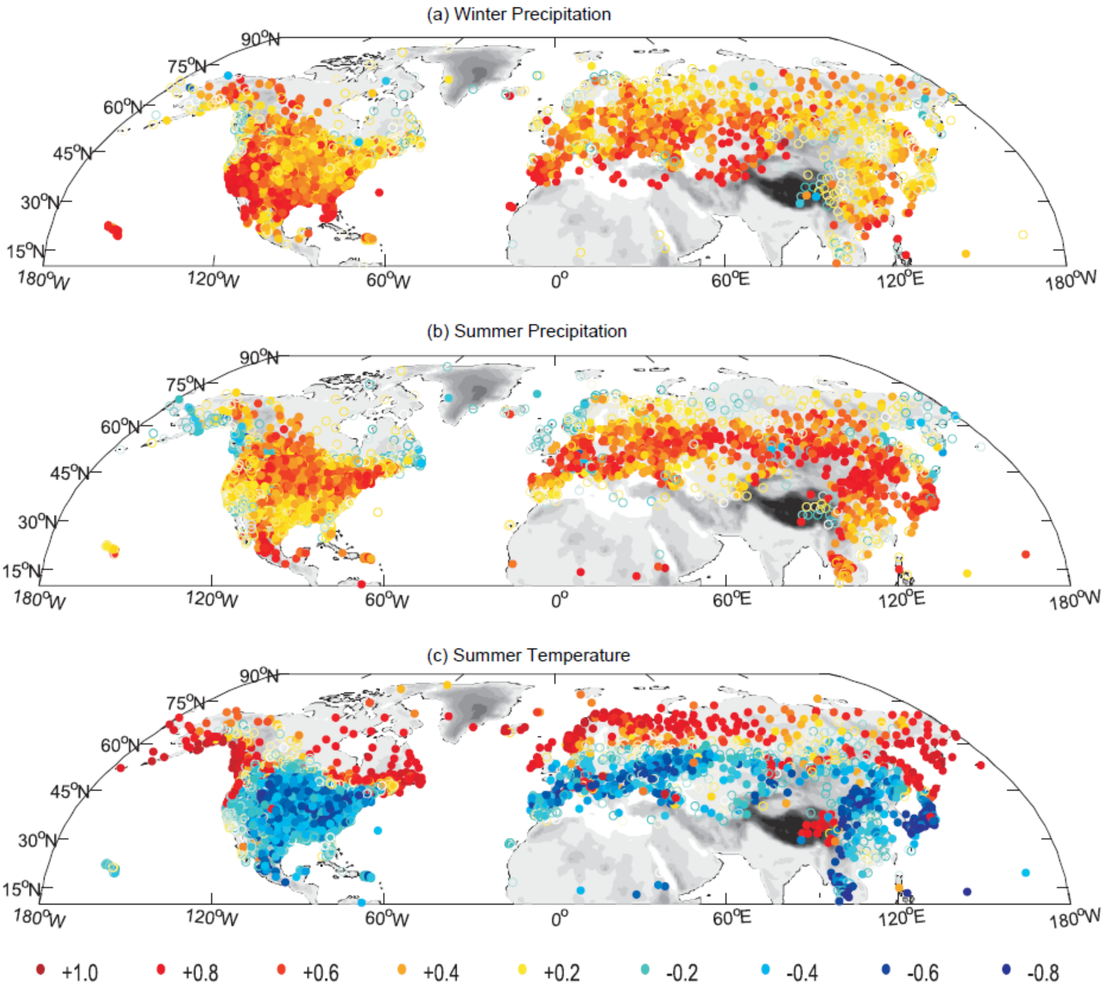


Figure 1 Maps showing the magnitude and sign of correlation coefficients between seasonal climate variables and simulated tree-ring widths at climate stations across the Northern Hemisphere. Circles represent coefficients at each location between simulated ring-width and (a) total winter (DJF) precipitation, (b) total summer (JJA) precipitation, and (c) mean summer temperature. Open circles represent correlation coefficients that are not significant at the $p = 0.05$ level.

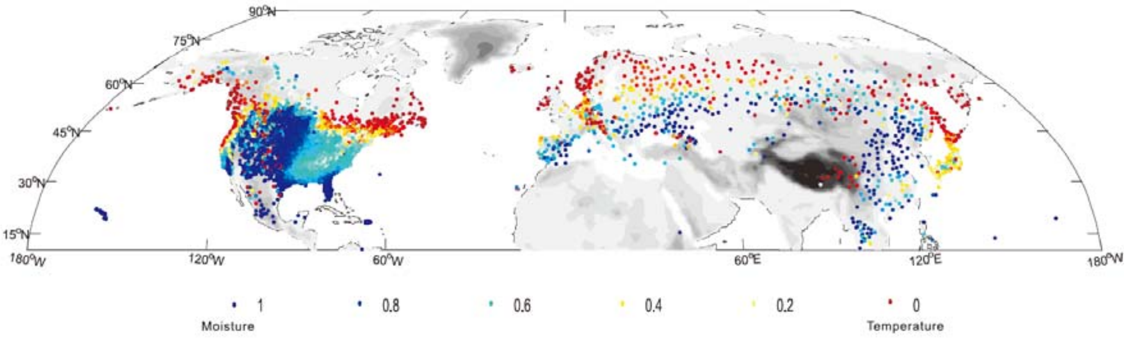


Figure 2 Map showing the relative influence of soil moisture and temperature on simulated tree growth across the Northern Hemisphere. Circles represent the mean ratio over all simulated years of (i) the number of days in the growing season when tree growth is limited by soil moisture and (ii) the total number of days in the growing season.

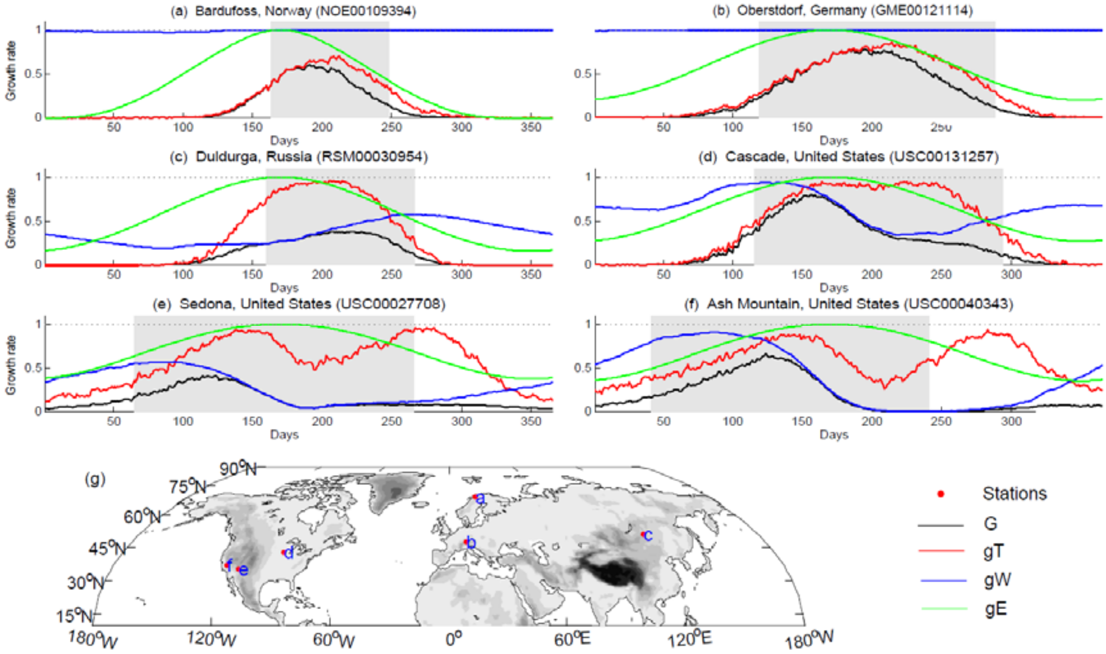


Figure 3 Simulated mean daily tree growth at several exemplar locations. In panels a-f, the daily growth rate (G) is calculated as the product of the growth rate due to solar radiation (gE) and the minimum of the relative growth rate due to either surface air temperature (gT) or soil moisture (gW). The grey shading represents the mean growing season simulated at each location.

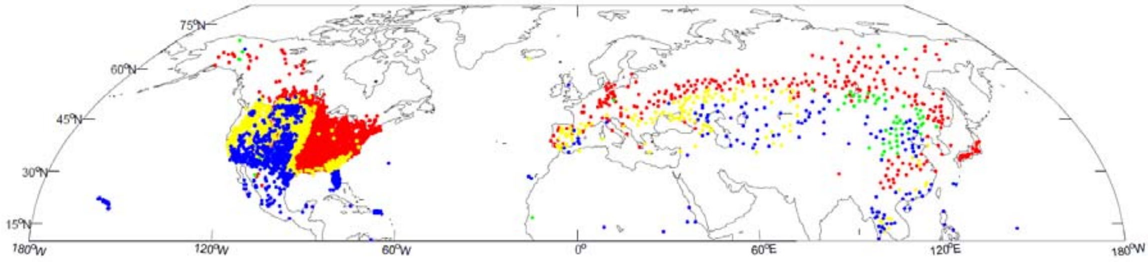
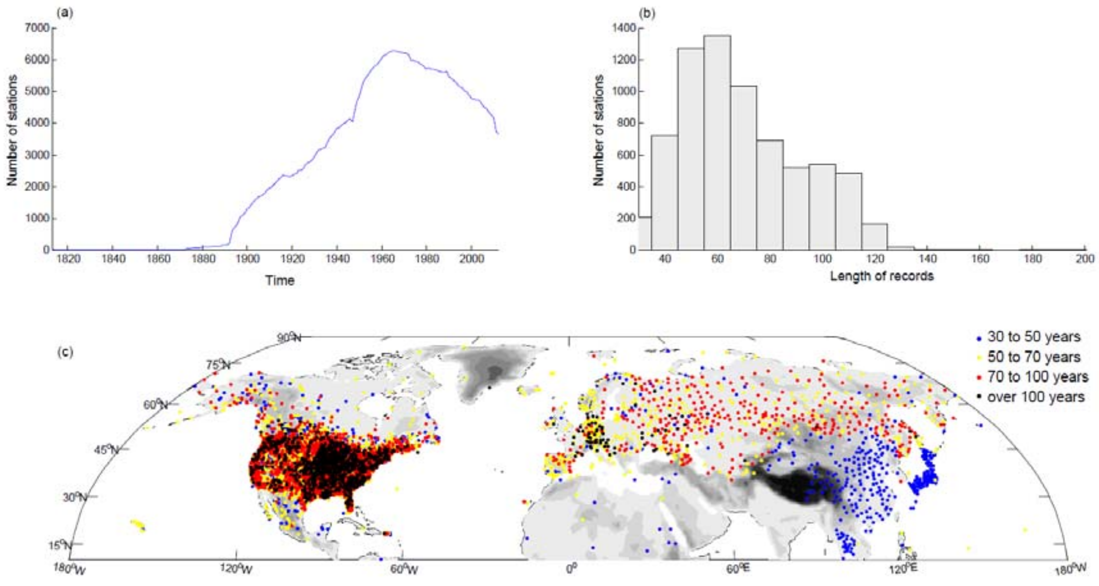
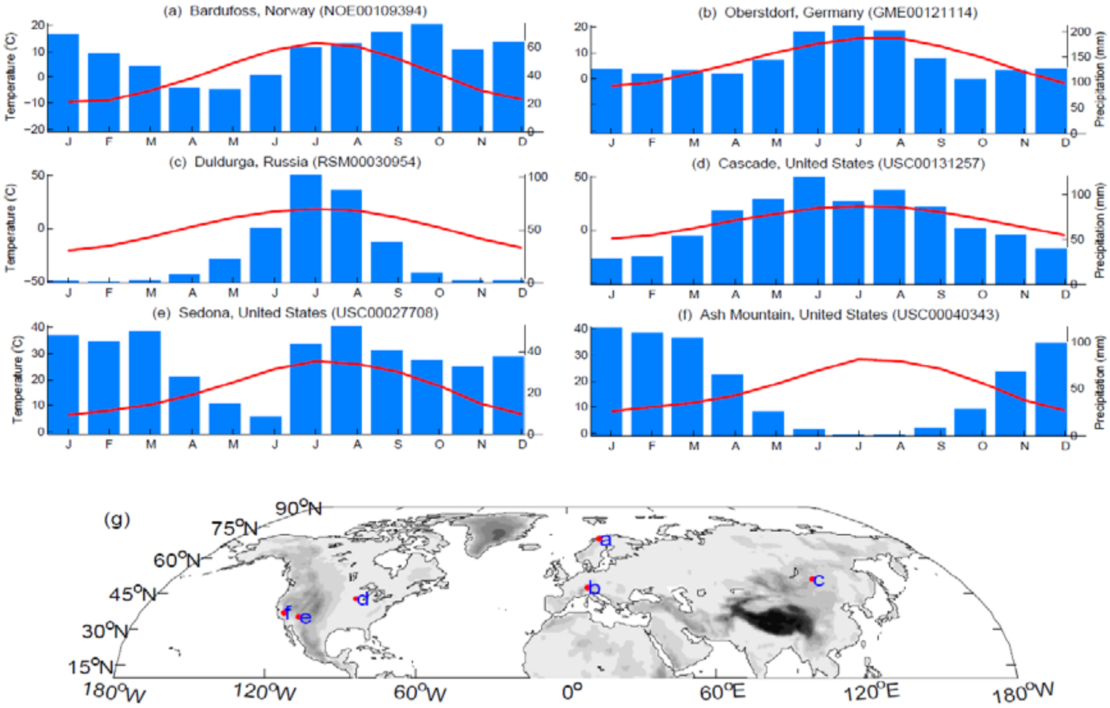


Figure 4 Map showing the relative influence of soil moisture and temperature at the start and end date of growing season across the Northern Hemisphere. Red circles represent stations where temperature limits growth at the beginning and end of the growing season. Yellow markers represent stations where growth is initially limited by temperature but switches to moisture-limited at the end of growing season. Green circles represent the opposite situation, where soil moisture is limiting at the start of growing season and temperature is the dominant control at the end of growing season. At sites shown in blue, tree growth is limited by soil moisture at the beginning and end of growing season.



Supplemental Figure 1 Daily data from the Global Historical Climate Network (Menne et al., 2012) used to simulate tree growth across the Northern Hemisphere. (a) Total number of climate stations available by year through the period of record. (b) Histogram showing the number and length of climate records used to produce the tree-ring simulations. (c) Map showing the location and length of daily climate records used to simulate tree-ring formation.



Supplemental Figure 2 Climographs at the exemplar locations. In panels a-f, blue bars represent mean total precipitation in each month at each station. Red lines show annual changes in monthly mean temperature. Panel (g) shows the location of the six exemplar stations.