

ON PREDICTING THE RESPONSE OF FORESTS IN EASTERN NORTH AMERICA TO FUTURE CLIMATIC CHANGE

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Abstract. Our ability to accurately predict the response of forests in eastern North America to future climatic change is limited by our knowledge of how different tree species respond to climate. When the climatic response of eastern hemlock is modeled across its range, we find that the assumed climatic response used in simulation models is not sufficient to explain how this species is presently responding to climate. This is also the case for red spruce growing in the northern Appalachian Mountains. Consequently, simulations of future change to forests that include eastern hemlock and red spruce may need to be improved. We suspect that similar findings will be made when other tree species are studied in detail using tree-ring analysis. If so, our present understanding of how individual tree species respond to climate may not be adequate for accurately predicting future changes to these forests. Tree-ring analysis can increase our understanding of how climate affects tree growth in eastern North America and, hence, provide the knowledge necessary to produce more accurate predictions.

1. Introduction

By the middle of the next century, significant global and regional climatic changes are expected from warming caused by increased concentrations of CO₂ and other radiatively active gases in the atmosphere (Manabe and Wetherald, 1980; Hansen *et al.*, 1986). Although the regional patterns of CO₂-induced climatic change are uncertain (Schlesinger and Mitchell, 1985), both general circulation model (Mitchell, 1983; Rind *et al.*, in press) and climatic data scenarios (Wigley *et al.*, 1980) indicate that the seasonal climates of eastern North America will be significantly affected. These climatic changes should have a large impact on the mixed deciduous/evergreen forests of this region, which comprise the eastern deciduous forest biome (Braun, 1950). Vegetation/climate classification schemes (e.g. Emanuel *et al.*, 1985) and forest stand simulations (e.g. Solomon, 1986) suggest that there will be substantial changes in the range limits of many tree species, concomitant changes in species composition and importance in forest communities, and, for some areas, significant declines in live tree biomass. If these studies are correct, the ecological consequences will be enormous.

To accurately predict how eastern forests will respond to future climatic change, we must know how climate presently affects the establishment, growth, mortality, and range limits of tree species in these forests. In stand simulation models such as FORENA (Solomon, 1986), the climatic response of sapling and mature trees is modeled as a combination of accumulated growing degree days (GDD) and the

number of drought days per growing season (DD). The selection of GDD and DD as predictors of tree growth was based on physiological studies of how temperature, heat sums, and water availability affect the growth and development of woody plants (e.g. Kozlowski, 1971; Kramer and Kozlowski, 1979). We do not argue with the general validity of GDD and DD for this purpose. Indeed, the FORENA model and closely related variants, such as JABOWA (Botkin *et al.*, 1972) and FORET (Shugart and West, 1977), have been reasonably well validated by comparing the simulated assemblages of tree species with those observed in the real world. Rather, we question the *sufficiency* of these variables for predicting climatically-induced changes in the growth and development of sapling and mature trees in these forests.

To this end, we have empirically modelled the tree ring-climate relationships of eastern hemlock (*Tsuga canadensis* Carr.), growing on 42 sites in eastern North America, using monthly climatic data. We will also review some recent results of modeling the climatic response of red spruce (*Picea rubens* Sarg.), a species that is presently declining for unknown reasons. These dendroclimatic models indicate that important climate variables apparently unrelated to GDD and DD are probably missing from the simulation models due to an incomplete understanding of how these species respond to climate.

We are only studying the ring-width patterns of mature trees here and do not claim that our results necessarily generalize to the way in which climate affects the establishment, mortality, and range limits of eastern hemlock and red spruce. However, we note that GDD and DD used in simulating the growth of sapling and mature trees also play an important role in determining the probability of mortality when certain thresholds are exceeded. Therefore, improved models of how mature trees respond to climate should also improve our understanding of how climate predisposes some trees to die and contributes to the establishment of range limits.

2. The Climatic Response of Eastern Hemlock

Eastern hemlock is an evergreen tree species native to eastern North America. Its present northern and western range limits (see Figure 1) were reached around 1000–2000 years ago based on pollen evidence (Davis, 1981). The lack of more recent migration suggests that hemlock is at equilibrium with climate and non-climatic factors such as competition that affect its distribution (Davis *et al.*, 1986).

Hemlock typically grows in cool, humid environments where adequate soil moisture is often available. In most cases, the soils are thin or nutrient poor (Rogers, 1978). It is one of the most shade-tolerant tree species (Fowells, 1965) and can grow for decades as a suppressed understory tree before attaining full canopy status. The foliage of eastern hemlock is extremely dense, allowing little light to penetrate to the forest floor. Thus, the environment beneath a well-developed hemlock canopy is cooler and damper than that found under hardwood canopies in the same region (Fowells, 1965). As a result, the microclimate within hem-

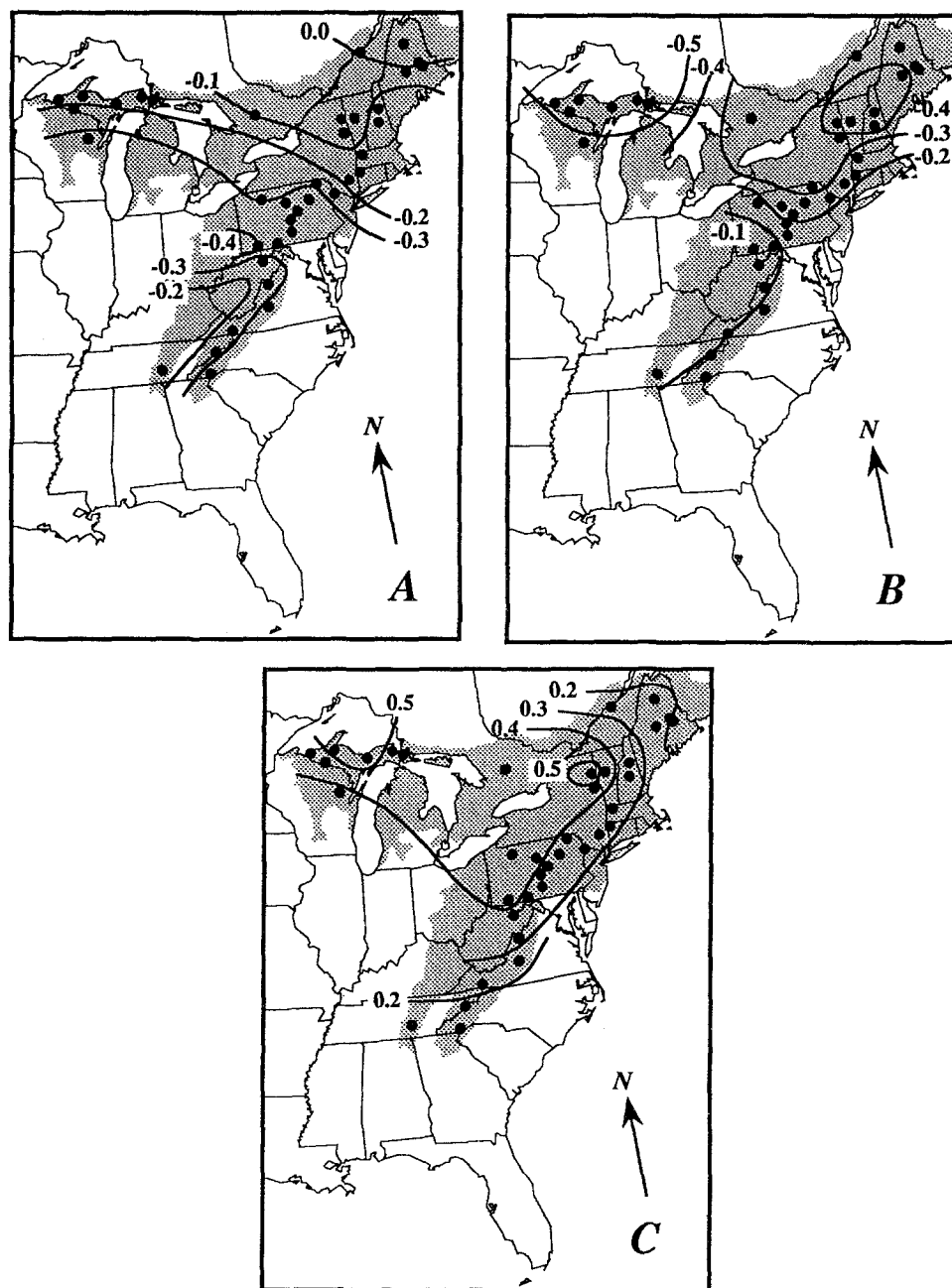


Fig. 1. Maps showing the spatial patterns of correlation between eastern hemlock tree rings and prior-June (A), prior-July (B), and current-March (C) temperatures. The range limit of eastern hemlock (stippled shading) and the site locations (●) of the 42 hemlock chronologies are also indicated. Note that some of the sites have more than one chronology.

lock stands may be much different from the macroclimate of the region in which it grows. Fowells (1965) also notes that the microclimate produced by hemlock canopies can be remarkably uniform over large geographic areas.

How much climate affects the growth and present range limits of eastern hemlock is difficult to infer from the available studies of the species. In the Great Lakes region, Davis (1981) suggested that the halt of hemlock migration south of Lake Michigan about 6000 years ago was due to excessive dryness in the Midwest. Solomon (1986) used as the potential northern and southern limits of hemlock range a growing degree day (GDD) minimum of 1324 GDD and a maximum of 3800 GDD, respectively. The minimum and maximum GDD values roughly follow the current northern and southern range limits of the species (see Figure 1). However, Kavanagh and Kellman (1986) proposed that competition is more important than temperature as a limiting factor along the northern range limit because of evidence of poor recruitment in some age classes and the preference of hemlock to grow on cooler northerly and westerly facing slopes. As an additional variable for delimiting the present range limits of hemlock, Solomon (1986) included a minimum January temperature tolerance of -12°C in the FORENA model. Below this threshold, bud damage is assumed to occur which results in no growth the following summer. Two or more consecutive years of damage then increase the probability of mortality. Given that January temperatures in the northern areas of the range often fall below -12°C , this threshold may be too high. In the Southern Appalachians and for disjunct stands in the Midwest, hemlock may be limited as much by the existence of suitable microsites controlled by physiography and soils as by any special set of macroclimatic variables (Friesner and Potzger, 1936; Oosting and Hess, 1956; Adams and Loucks, 1971).

Over the past several years, 42 precisely dated eastern hemlock tree-ring chronologies have been developed from sites scattered over most of its natural range (Figure 1). These chronologies were originally developed for reconstructing past climate from tree rings and are typically 300 or more years in length. Each chronology is a mean-value function of standardized tree-ring indices obtained from 15 to 30 trees on a site. See Fritts (1976) or Cook (1987) for details regarding the necessary procedures for developing valid tree-ring chronologies. Although the stands are not a true random sample, there was no selectivity in choosing sites having defined intrinsic characteristics such as slope aspect, soil type, or elevation. Rather, the principal criterion for site selection was that the stand was 'old-growth'. The tree-ring sites are highly variable in character with some being extremely well-drained and others being bog-like. However, the majority of sites are mesic with moderate drainage.

Prior to statistical analysis, the hemlock chronologies were prewhitened with autoregressive-moving average (ARMA) models (Box and Jenkins, 1970) to remove autocorrelation due largely to internal biological processes of the trees. The prewhitened chronologies have the advantage of being cleaner reflections of the original environmental inputs that affect tree growth than the original chronologies.

In addition, the lack of autocorrelation greatly simplifies statistical significance tests between tree rings and climate. See Monserud (1986) and Cook (1987) for detailed descriptions of ARMA modeling as applied to tree-ring chronologies.

Monthly temperature and precipitation records obtained from the Historical Climatology Network (Boden, 1987) were used to model the climatic response of each hemlock chronology. We chose not to seasonalize the data because our experience indicates that trees often respond most strongly to climate in a narrow time window that is usually better resolved with monthly data. This resolution could be lost by first seasonalizing the climatic data. In addition, we rarely know *a priori* what the true physiological seasons are for the tree species and stands being studied. Without such knowledge, climatic data might be seasonalized incorrectly and the climatic signal in the tree rings either obscured or lost. Finally, we chose not to use for modeling an integrated climatic variable like the Palmer Drought Severity Index (Palmer, 1965), which incorporates the influence of temperature and precipitation simultaneously to produce an index of relative wetness or dryness. At certain times of the year when available soil moisture is not limiting to tree growth and metabolic processes, temperature alone may be the most important growth limiting variable. As will be shown, the results of our hemlock analyses support these arguments for using monthly temperature and precipitation records.

We used a 'nearest neighbor' approach in pairing meteorological station records with the tree-ring chronologies. That is, we used the records of stations closest to our tree-ring sites. In most cases, we were able to use unique pairs of chronologies and station records. However, in some areas like Maine, the small number of suitably located meteorological stations forced us to use the same climatic data for several chronologies. This reduced the number of unique pairs to 36 or 85.7% of the total number of chronologies.

The product-moment correlation coefficient was used to characterize the climatic response of hemlock. A dendroclimatic year beginning in May of the previous year and ending in September of the current year of growth was used in the correlation analyses. This 17-month year includes two radial growth seasons and the intervening cold season months when climatically-induced physiological preconditioning may occur (Fritts, 1976). The simple correlations were computed for the 1931–1976 period common to all of the meteorological records and tree-ring chronologies. With these degrees-of-freedom ($df = 44$) and a two-tailed hypothesis test, we considered a correlation exceeding $|\pm 0.25|$ ($\alpha < 0.10$) as potentially meaningful. This is a somewhat liberal α -level, but one that we felt was justified at this exploratory level of data analysis.

In judging the true significance of our climatic correlations we relied on redundancy of results. Since most of our correlations were based on independent data sets, we looked for monthly correlations that both exceeded ± 0.25 and occurred across tree-ring sites in a spatially consistent pattern.

The correlation analyses revealed spatially coherent patterns of negative correlation (< -0.25) between temperature and tree growth for prior-June (16 out of 42

cases) and prior-July (23 out of 42 cases). These negative correlations are consistent with an expected drought response in trees related to increasing evapotranspiration demand as temperature increases. When evapotranspiration demand is low because of cooler than average growing season temperatures, hemlocks may be able to maintain a better internal water balance and, therefore, grow better. This is a classic component of the drought response of trees, although it must be viewed as an indirect effect because of the 1-year lag in its effect on hemlock ring widths. Because of the 1-year lag, it is also plausible that warmer temperatures are increasing dark respiration faster than photosynthesis, thereby reducing the net supply of carbon available to hemlocks for growth the following year.

The prior-June response is concentrated in Pennsylvania and northern Virginia (Figure 1a), while the prior-July response is concentrated north of Pennsylvania from Wisconsin to New Hampshire (Figure 1b). The geographic shift from June to July temperatures probably reflects differences in the timing of growth initiation from south to north and, therefore, the time when warm air temperatures become, in some sense, limiting to growth. There is also a trend towards increasingly negative prior-July temperature correlations in the Great Lakes region. Presumably this reflects the approach of hemlock towards its drier western range limit in the northern Great Plains.

More surprising was the appearance of strong positive correlations (>0.25) between hemlock growth and March temperatures in 33 out of 42 cases. These significant correlations are especially apparent for sites in the central and northern parts of the range where the correlations sometimes exceed 0.50 (Figure 1c). Above-average March temperatures may improve the thermal conditions at the hemlock sites by more quickly removing snow cover and by allowing for an earlier-than-normal resumption of photosynthesis.

The spatial consistency of the July and March temperature correlations extends across regions having different climatologies (Karl and Koscielny, 1983). Thus, it is unlikely that spatial autocorrelation in the temperature and hemlock fields is forcing these spatial relationships. Rather, it is more likely that eastern hemlock is predisposed by genetics and its control over stand microclimate to respond to temperature in a similar way over much of its range. Given the considerable diversity in the site characteristics (especially site hydrology) of the sampled stands, such high spatial consistency was unexpected.

The results of the precipitation analyses were markedly different. Only one weak geographic pattern of positive correlations concentrated in the Great Lakes region was indicated for June of the current growth year (8 out of 42 >0.25). However, this pattern of correlations suggests that the importance of June rainfall increases as the northwestern range limit is approached. This may reflect increasing drought sensitivity of eastern hemlock as it approaches the eastern margin of the northern Great Plains.

The relative weakness of the precipitation results may have been due, in part, to using single-station records instead of regionally averaged records, which have

been shown to be better correlates with tree rings (Blasing *et al.*, 1981). The reason for this is the generally poorer spatial representativeness of single-station precipitation records compared to single-station temperature records. For this reason, we recomputed the correlations using regionally averaged precipitation records from the climatic divisions in which the hemlock sites were located. The results did not change appreciably. Some correlations improved, while others declined. But, there was no indication of any new or more distinct geographic patterns.

Unlike the temperature correlations, the precipitation correlations appeared to be related to differences in site hydrology. Hemlock chronologies from well-drained sites often correlated more highly with various prior and current growing season (May–July) precipitation months compared to those from more mesic or poorly-drained sites. This effect is characterized in a histogram in Figure 2, which was derived by stratifying the sites into four site drainage classes: poor, fair, good, and excellent. The bar in each drainage class is the average maximum correlation found between any of the six prior and current growing season (May–July) months of rainfall and hemlock growth. This stratification was based solely on visual evaluations of the sites. Therefore, it is arguable that some sites would be moved into different drainage classes if physical measurements of site hydrology were available. Regardless, the sites in the poor and excellent drainage classes were unequivocally different, with the poor-class sites having abundant water supplies and associated hydrophytic vegetation near the trees and the excellent-class sites having

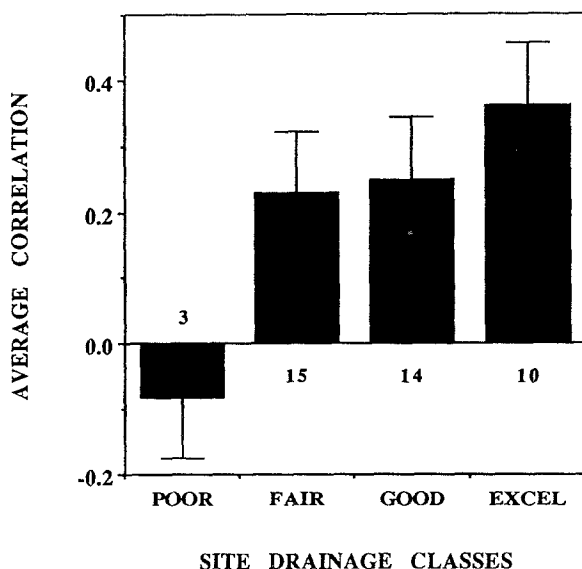


Fig. 2. The average maximum correlation between eastern hemlock tree rings and current or prior growing season months of May, June, and July. The 42 hemlock chronologies were stratified into 4 drainage classes based on visual impressions of the sites. The error bars are derived from the pooled standard error for all 42 correlations. The sample size in each drainage class is shown by each class.

superior drainage and associated xerophytic vegetation. The trend towards higher positive maximum correlations as site drainage improved suggests a link between site hydrology and sensitivity to current or prior growing season rainfall. Since differences in site hydrology are more or less randomly distributed among the 42 sites, the virtual lack of spatial patterns analogous to those found for temperature is, therefore, not surprising.

The differential influence of site on the response of hemlock to temperature and precipitation is more clearly illustrated in the patterns of monthly correlations for three proximal sites in the Shawangunk Mountains of southeastern New York state. Two sites, Mohonk Lake Talus (MLT) and Rock Rift Road (RRR) are southwest-

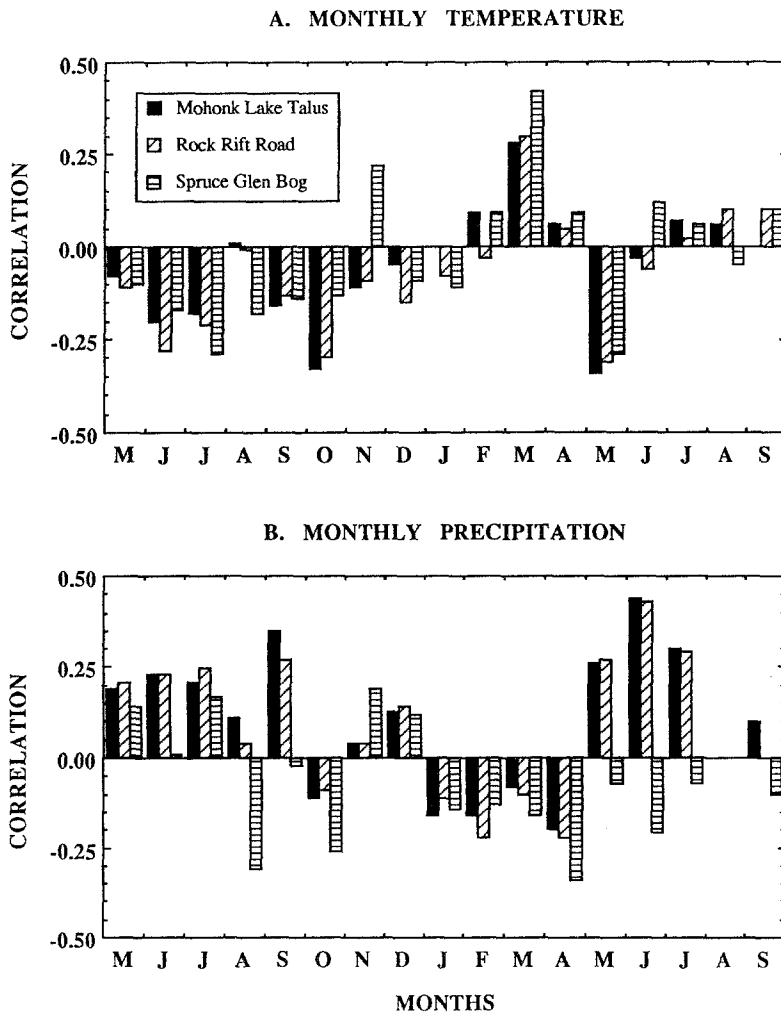


Fig. 3. The monthly correlations between eastern hemlock tree rings and monthly temperature and precipitation from prior-May to current-September of growth. Mohonk Lake Talus and Rock Rift Road are extremely well drained conglomerate talus slopes. Spruce Glen Bog is a poorly drained bog site.

facing and north-facing quartzite conglomerate talus slopes, respectively, which are extremely well drained. The third site, Spruce Glen Bog (SGB), is a small, poorly-drained sphagnum bog that also supports red spruce. The MLT and RRR sites are within two kilometers of each other at elevations of 335 and 320 meters, respectively. The SGB site is about ten kilometers south of the other sites at an elevation of 550 meters. The hemlock chronologies developed from these sites were correlated with monthly meteorological data from the Mohonk Lake cooperative weather station located within about one kilometer of the MLT and RRR sites at a comparable elevation.

Figure 3 shows these monthly temperature and precipitation correlations for the three sites. The patterns of temperature correlation (Figure 3a) are extremely similar for all three sites even though SGB is drastically different from either MLT or RRR with respect to drainage. Only in the precipitation correlations (Figure 3b) do we see the effects of site hydrology on climatic response. This is especially apparent for the current growing season months of May, June, and July. These correlations are strongly positive for MLT and RRR hemlock and weakly negative for SGB hemlock. Thus, the effect of site on the climatic response of eastern hemlock appears to manifest itself mainly through its influence on precipitation and moisture supply, not temperature and evapotranspiration demand.

3. Discussion and Conclusions

From our detailed analyses of the climatic signals in eastern hemlock tree rings, it is apparent that the theoretical climatic response model used in stand simulation models for all tree species (i.e. growing degree days and drought days per growing season) is incomplete for this species. Eastern hemlock ring widths show some strong relationships with monthly temperature that appear to be largely independent of site characteristics. These relationships are mainly found in June and July of the previous growing season and March of the current growing season. The broad spatial consistency of these relationships suggests that a combination of genetic predisposition and control over site microclimate is responsible. Only when the influence of precipitation is modeled does the influence of site hydrology become apparent in affecting the growth of eastern hemlock.

The June and July temperature correlations are consistent with what we know about the effects of air temperature on evapotranspiration demand and the development of internal water deficits in trees when available soil moisture is in limited supply. They also support the validity of using drought days per growing season as a component of the climatic response of eastern hemlock in simulation models. We can only conjecture about the physiological meaning of the March temperature effect on hemlock growth. However, its broad spatial consistency suggests that it has a true physiological basis that we do not yet adequately understand. There is a tendency for March temperature correlations to increase as the tree-ring chronologies approach the northern and western range limits of eastern hemlock (see Figure

1c). This suggests that March temperatures may in some way influence the northern range limits of this species or at least affect hemlock's competitive status in those regions. Incorporating this kind of information in simulation models could affect the projected outcome for eastern hemlock in some climatic change scenarios.

With regards to how future climatic changes may affect the growth and range limits of eastern hemlock, our results suggest that much will depend on how monthly and seasonal patterns of temperature and precipitation change and co-occur. Given the broad spatial consistency in the temperature relationships, changes in climate that principally affect March, June and July temperatures should have a large-scale impact on eastern hemlock growth. The worst-case scenario would be for warm-dry summers and unusually cold March temperatures. Whether or not an equal warming in March temperatures would offset a warming of June and July temperatures is unclear, and would probably depend on how much precipitation was received by the trees and on site hydrology. The variable influence of site hydrology on precipitation sensitivity suggests that boggy sites, where hemlocks show little correlation with growing season rainfall, could serve as refugia within the present range limits of the species should future droughts become more frequent and severe.

While some of the properties of hemlock's response to climate may be unique to that species due to its impact on site microclimate, how likely is it that other tree genera or species will also respond to climate in unique and unexpected ways? We suspect that many important and unexpected relationships between radial growth and climate will be found when other tree species in the eastern deciduous forests are investigated in a similar broadscale fashion. For example, red spruce ring widths from numerous sites, age-classes, and elevations in the northern Appalachian Mountains are negatively correlated with previous summer (mainly August) temperatures and positively correlated with early winter (mainly December) temperatures preceding the growing season (Cook *et al.*, 1987; Johnson *et al.*, 1988; Federer *et al.*, 1989; Cook and Johnson, 1989). That is, when previous August temperatures are below (or above) average and December temperatures are above (or below) average, radial growth the following growing season will increase (or decrease).

Similar to hemlock, these climatic effects on red spruce growth appear to reflect some fundamental interaction between tree genetics and the climatic environment that has not been explicitly incorporated in forest simulation models. If incorporated in a simulation model, this kind of information could also alter the outcome for red spruce in climatic change scenarios. This likelihood is also suggested by the correlation between past occurrences of adverse August and December temperatures and historical declines of red spruce (Johnson *et al.*, 1988). In addition, physiological models of climate effects on red spruce growth, which included growing degree days, estimated soil-water deficits, and estimated seasonal accumulations of daily net photosynthesis, showed poor predictive skill compared to the empirical temperature response model derived from tree rings (Federer *et al.*,

1989). These findings add more support to our thesis that the basic climatic response model presently used in forest simulators like FORENA is probably not sufficient for accurately predicting the response of some tree species to climatic change.

Tree-ring analysis provides an unique means of investigating and characterizing the climatic response of tree species. Although the climate modeling presented here is statistical and empirical, this fact should not be viewed as a weakness. Our understanding of how climate affects the growth and range limits of different tree species in the eastern deciduous forest biome is incomplete and in need of additional data and insights. We believe that the results of our study illustrate the rich potential of tree rings for this purpose. Tree-ring analysis can provide useful information without being constrained by *a priori* biological theory. If such information is consistently strong, it should be valuable for augmenting existing theories and models of how climate affects the growth and development of trees in natural environments. While we do not claim that our analyses presented here have contributed much yet to a theoretical understanding of how future climatic change will affect the eastern deciduous forests, the accumulation of this kind of empirical knowledge should provide a fertile substrate upon which such theory can grow and develop.

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