Climate change effects on red spruce decline mitigated by reduction in air pollution within its shrinking habitat range

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Abstract

We investigated the potential effects of projected climate change on red spruce (Picea rubens Sarg.) growth in the Great Smoky Mountains of Southeastern USA. A model called Annual Radial Increment Model (ARIM) was used to capture ecosystem complexity manifested as direct and indirect effects in multifactorial within- and across-scale interactions. The model was run under different scenarios, including projected climate change under reduced, no change, and increased atmospheric pollution. Modeled red spruce growth at end of 21st century (2080–2099) was compared to modeled growth at end of the 20th century (1980–1999). Red spruce growth at high elevations (≥1700 m) declined by 10.8% when climate change interacted with a 10% increase in air pollution, but red spruce growth increased by 8.4% when air pollution decreased by 10%. In contrast, red spruce growth at low elevations (<1700 m) declined by 11.2% with a 10% increase in air pollution, 8.9% with no change, and 6.4% with a 10% decrease in air pollution. Our results suggest that red spruce populations at high-elevation may grow more rapidly under climate change if air pollution decreases, but populations at low-elevation may decline irrespective of air pollution changes as habitats shrink.

1. Introduction

There are conflicting predictions on the effects of climate change on forest systems. Some research has reported that it could shift phenological events (Chmielewski and Rötzer, 2001; Cornelius et al., 2013), shift the ranges of organisms (Colwell et al., 2008; Doak and Morris, 2010), and shrink the habitats of alpine species (Lenoir et al., 2008). In particular, most alpine and subalpine tree species are generally more vulnerable to climate warming than other tree species because they are adapted to lower optimal temperatures and have low genetic diversity (Hörsch, 2003; Lariquneiderie and Körner, 1995). However, field experimental research (Ainsworth and Long, 2005; Norby and Luo, 2004) and ecosystem modeling research (Schimel et al., 2000) suggest that elevated CO₂ and temperature levels will have positive growth effects on most plant species. Understanding ecosystem complexity may clarify the effects of climate change on forest systems.

Krivtsov (2004) defines ecosystem complexity as being manifested in indirect effects, rather than direct effects, that result from the modification of direct interactions between two ecosystem factors by separate factors. Indirect effects have powerful influences on ecosystems’ functioning (Higashi and Patten, 1989; Salas and Borrett, 2011). For example, indirect effects contribute to the maintenance of diverse species composition through species interactions such as trophic chains and cascade (Bever, 2002, 2003) and habitat developments by interactions among species and environmental factors (Diekötter et al., 2007; Hunt et al., 1991). Such indirect effects are difficult to capture in either broad-scaled descriptive or fine-scaled experimental studies. Therefore, systems modeling, which integrates multifactorial direct and indirect interactions within ecosystems, is appropriate to study indirect effects.

Indirect effects operate both within scales (local or regional or global) and across scales (local to regional to global). Within-scale effects are processes that occur at one spatial scale. Across-scale interactions are processes at one spatial scale that interact with processes at another scale (Peters et al., 2007). For example, indirect effects contribute to species-specific habitat development (Diekötter et al., 2007). Indirect effects caused from across-scale
interactions among soil (local scale), temperature (regional scale), precipitation (regional scale), and soil biota (local scale) and within-scale interactions between soil and soil biota produced a nitrogen-enriched patch favorable to a grassland species in a temperate grassland (Hunt et al., 1991). Much research in landscape ecology and related fields has focused on within-scale interactions, often at multiple independent scales (Cowen et al., 2006; Kent et al., 2004; Wheatley and Johnson, 2009), and do not account for interactions across scales (Breckling et al., 2005; Kerr et al., 2007; Nash et al., 2014; Peters et al., 2007; Schneider, 2001). For this reason, fine-scaled studies have limited power to understand issues at regional and global scales, and global-scaled studies are also not able to predict the impacts of global environmental changes on local scales (Carpenter et al., 2006; Diffenbaugh et al., 2005; Kerr et al., 2007; Nash et al., 2014). Across-scale interactions may lead to nonlinear behavior with thresholds that cannot be predicted by observations at independent single or multiple scales (Gunderson, 2008; Peters et al., 2007; Peterson, 2000; Schneider, 2001). Failing to understand across-scale interactions has caused poor predictions of global change effects on organisms and led to ineffective management decisions (Soranno et al., 2014). Therefore, consideration of both within- and across-scale interactions is needed to improve prediction of global change effects on local species (Diffenbaugh et al., 2005; Nash et al., 2014; Peters et al., 2007; Peterson, 2000).

A challenge of revealing causation by combining direct/indirect effects and within-/across-scale interactions for many factors is that there are many incommensurable dimensions and units. Koo et al. (2011a, b) addressed this challenge by developing a model for predicting tree growth called the Annual Radial Increment Model (ARIM). ARIM is based on photosynthetic inputs, respiratory outputs and hierarchically organized environmental controls that are represented as direct and indirect interactions among biotic and abiotic factors to explain within- and across-scale interactions at global, regional and local scales. Quantifying parameters is difficult in ecosystem modeling because different methods, measurements and units are involved. To integrate different models and factors in the submodels, ARIM calculates non-dimensionalized index values for each dimensioned variable by dividing yearly average values by the corresponding long-term mean, with the non-dimensionalized index values (NIV) representing relative deviations from the long-term mean.

Red spruce is an ecologically and commercially important conifer species that is declining in eastern North America (Dumais and Prévost, 2007). In a previous study, Koo et al. (2011a) applied ARIM to assess potential causes of red spruce growth decline in the Great Smoky Mountains of the southern Appalachians in the US. Acidic rains and clouds caused by complex interactions among air pollutants, precipitation, cloud immersions and topographic factors were the dominant factors leading to red spruce decline at

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![The Great Smoky Mountains National Park in USA](image1)

**Fig. 1.** The location of Great Smoky Mountains National Park (GSMNP) in the United States and the GSMNP with state boundary between Tennessee and North Carolina following a central high elevation ridge.
higher elevations, whereas drought stress induced by interactions among high temperature, less precipitation, topographic factors and coexisting species, was the dominant processes leading to red spruce decline at lower elevations. Air pollution showed relatively minor effects on low-elevation growth. The purpose of this study is to explore the effects that different future scenarios of climate change and air pollution may have on red spruce growth while accounting for complex within- and across-scale interactions. We hypothesize that climate change will result in red spruce growth declines in the Great Smoky Mountains National Park (GSMNP) and that the climate change effects are different on high vs. low elevations in GSMNP. The potential for synergistic or antagonistic effects between climate change and atmospheric pollution is not known. This study explores the influences of these interacting factors on the red spruce ecosystem in the face of growing conservation needs.

2. Materials and methods

2.1. Study area

The study area was the (virgin) red spruce (Picea rubens Sarg.)-Fraser fir (Abies fraseri (Pursh) Spach) ecosystem in the Great Smoky Mountains National Park (GSMNP) located in the southern Appalachian Mountains of the southeastern United States (Fig. 1). The Great Smoky Mountains have a cool, temperate, rainforest climate with a mean annual air temperature of 8.5 °C and mean annual precipitation of 2300 m (Webster et al., 2004).

Fig. 2. Model structures for the high- and low-elevation models. Circles denote model parameters representing environmental factors in the equations. Solid-lined circles represent original parameters and broken-lined ones are copies of these from the original. Parameters at the arrowheads are dependent on those at the tails. Equations explaining interactions in Appendix A.
These climatic conditions result in a red spruce ecosystem with a short growing season (100–150 days) and trees that are exposed to frequent cloud immersion and high-velocity winds (Johnson et al., 1992). The Great Smoky Mountains are part of the mature Appalachian range characterized by rounded summits and ridges that drain into rugged slopes uniformly eroded by fluvial and colluvial processes. Bedrock is metamorphosed sedimentary rock (Whittaker, 1956). Soils developed from these rocks are inceptisols with high contents of organic matter and silt to sandy loam textures (Madden et al., 2004). The dominant forest species follows an elevation gradient with red spruce dominating at lower elevations (1370–1675 m), Fraser fir dominating at higher elevations (>1890 m), and both species co-dominating at mid elevations (1675–1890 m) (Nicholas et al., 1992).

The red spruce-Fraser fir stands in the Great Smoky Mountains are among the last of the old-growth stands in the southern Appalachians. The red spruce-Fraser fir forest is being impacted by several environmental stresses, including acid atmospheric pollution, extreme weather, and exotic insect infestation of Fraser fir by the balsam woolly adelgid (Adelges piceae Ratz.). These disturbances have resulted in 70% Fraser fir mortality (Rose, 2000), creating a forest community structure with large variations in stand, structure (gaps), and density of standing and fallen dead trees (Pauley et al., 1996).

### Table 1

<table>
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<th>Dependent variable: red spruce growth at high elevation</th>
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<th>Sum of squares</th>
<th>Mean square</th>
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Red spruce growth was simulated from 1940 to 2099. Baseline conditions for red spruce growth were based on simulated data from 1980 to 1999 and the future conditions were based on patterns at the high- vs. low-elevation sites (Nicholas et al., 1992). The model for each elevation has the same conceptual design but uses different combinations of parameter values. ARIM modeling found influential ecosystem factor interactions for high and low elevations (model equations shown in Appendix A). ARIM is a function of direct environmental factors such as air pollution disturbance (AP), water availability (WA) and radiation (RA) (model equations in Appendix A.1). These factors were linked to hierarchically organized submodels which depicted environmental controls (Fig. 2, Appendix A.1.1). Submodel factors indirectly influenced growth by controlling direct factors in the model equations (Appendix A) via multiple pathways. For example, spruce growth at high elevations was controlled by AP submodel including hierarchically organized interactions among air pollutants, precipitation, clouds and elevation factors. Growth at low elevations was controlled by three submodels, RA, AP and WA submodels. These submodels include complex interactions among climatic factors, air pollutants, topographic factors, such as slope, aspect, elevation, distance from stream, and co-existing species, fir mortality. Further details about model structure and parameterizations of ARIMhigh and ARIMlow and modeling processes can be found in Koo et al. (2011a).

#### 2.3. Model scenarios

Red spruce growth was simulated from 1940 to 2099. Baseline conditions for red spruce growth were based on simulated data from 1980 to 1999 and the future conditions were based on climate change or air pollution scenarios (values in parenthesis indicate actual differences in modeled red spruce growth).
Fig. 4. Simulated red spruce growth for future climate change with air pollution scenarios of (a) 10% increase, (b) no increase, and (c) 10% decrease change in atmospheric pollution at high elevations, and (d) 10% increase, (e) no increase, and (f) 10% decrease at low elevation. The x axes are years and the y axes are the radial increment index (0–2, no units). The black circles represent red spruce growth for each year, and the red lines are local regression curves (smoothed by a loess function with 0.75 of span, added by a spline interpolation between smoothed points) added to show long-term growth trends. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Simulated data from 2080 to 2099. Growth trends were investigated under three different air pollution emission scenarios for 2080 to 2099: a 10% increase, 0% increase and a 10% decrease. Local polynomial regression fitting functions and spline functions were used to create local regression curves to show growth trends.

Regional temperature and precipitation from 1939 to 1999 were measured at the airport meteorological recording station in Knoxville, TN, and air pollution (i.e., nitrogen oxides (NOx), sulphur oxides (SOx), and ozone (O3)) was estimated from data obtained from the US Environmental Protection Agency (EPA, 2000) (cf Koo
et al., 2011a). Average annual temperature was obtained by averaging daily temperature records for each year, and cumulative annual precipitation was calculated by totaling daily precipitation records for each year. Extreme cold winter temperature was calculated by averaging the lowest daily temperatures from November to February. Air pollution data for 1998 were used for both 1998 and 1999 due to a lack of data in 1999.

The future regional projections of temperature and precipitation for 2080 to 2099 were extrapolated from the 1980 to 1999 period based on the Intergovernmental Panel on Climate Change regional projections of climate change in eastern U.S.A. (IPCC 2007) including a 3.6 °C increase in annual mean temperature, a 3.8 °C increase in winter temperature and a 7% increase of annual precipitation for the 2080–2099 period compared to the values for 1980–1999. These projections, regional averages of temperature and precipitation, were the median values estimated from a set of 21 global models in the Multi-Model data for the A1B scenario (IPCC 2007). The effect of this future climate scenario on red spruce growth was also investigated using the three different emission scenarios of air pollution for 2080–2099 (i.e., 10% increase, 0% increase, and 10% decrease).

Annual values were divided by the corresponding long-term mean of the values. The long-term means were estimated using data from the 1940 to 2099 period instead of 1980–1999 because the longer time series was assumed to provide more representative average conditions. These non-dimensional index values were then applied to ARIMhigh and ARIMlow to simulate red spruce growth for the periods of 1980–1999 and 2080–2099. Annual growth for each of the 1980–1999 and 2080–2099 periods was averaged, and changes in growth between the two periods were calculated. An analysis of covariance was used to investigate the significance of effects of future climate and air pollution changes on red spruce growth that high vs. low elevations. Statistical analyses were performed in R 2.14.

3. Results

The individual effects of future climate change and air pollution scenarios are presented in Table 1. Climate change had negative effects on modeled red spruce growth at both high and low elevations, with the effects at high-elevation smaller (1.1% decline) than at low elevation (8.6%) (Fig. 3). Similarly, air pollution had negative effects on red spruce growth at both high and low elevations (Fig. 3). Red spruce growth at both high and low elevation decreased under the scenario of more air pollution and increased under the scenario of less air pollution. Specifically, red spruce growth decreased by 8.7% and 2.0% with a 10% increase in air pollution at high and low elevations, respectively, and increased by 10.3% and 2.0% with a 10% decrease in air pollution for high and low elevations, respectively (Fig. 3). Analysis of covariance analyses showed a significant effect of air pollution at high elevations only (Table 1).

The combined effects of future climate change and air pollution scenarios are presented in Table 1. At high elevation, red spruce growth under projected climate change had a variable response to the different air pollution scenarios (Fig. 4). Red spruce growth decreased by 10.8% with a 10% increase in air pollution, decreased by 1.1% with no change in air pollution, and increased by 8.4% with a 10% decrease in air pollution (Fig. 5). At low elevation, red spruce growth under projected climate change had a more consistent response to the different air pollution scenarios (Fig. 4). Red spruce growth decreased by 11.1% with a 10% increase in air pollution, decreased by 8.6% with no change in air pollution, and decreased by 6.6% with a 10% decrease in air pollution (Fig. 5). However, analysis of covariance analyses showed a significant interaction effect between air pollution and climate change at high elevations (Table 1).

The relative importance of climate change vs. air pollution effects were determined by the percent increase of combined effects over the individual effects. Fig. 5 shows that increased air pollution caused larger declines in high-elevation red spruce growth than climate change, but that climate change caused larger declines in low-elevation red spruce growth. For example, high-elevation growth under 10% increased air pollution declined an additional 2.2% more in interaction with climate change, but low-elevation growth declined an additional 9.1% more.

4. Discussion

Forests are at risk under global climate change (Thomas et al., 2004). It is important to understand the multiple interactions that operate within and across scales if we are to predict future global change effects on local tree growth (Carpenter et al., 2006; Peters et al., 2007). These multiple interactions result in nonlinear behaviors, which increase uncertainty in predicting global change effects on tree growth (Peters et al., 2007; Peterson, 2000). ARIM simulated these complex within- and across-scale interactions for a red spruce ecosystem and revealed different global change effects on tree growth at the high vs. low-elevation limits of the red spruce range in the southern Appalachians, which may explain the apparent conflicting findings from previous studies on the effects of global change on red spruce growth.

4.1. Conflicting studies on climate effects on red spruce growth

Red spruce is expected to be more vulnerable to global change than other conifers because it has low genetic diversity and is adapted to low optimal temperatures (Dumais and Prévost, 2007). Winter warming may have significant effects on red spruce growth. Chilling is an important factor required for spring bud burst (Heide, 2003). For tree species with a large chilling requirement, warmer winters might cause inadequate chilling, which will result in late bud burst in the spring (Cannell and Smith, 1986). The breaking of dormancy is related to the concentration of abscisic acid in a tree axis (LePage-Degivry et al., 1997). Abscisic acid concentrations decline during winter, stimulating bud bursts in spring. Warmer winter temperatures prevent the declines in abscisic acid, which...
results in an increase in the winter dormancy period. Alternatively, for tree species with a small chilling requirement, warmer winters may result in early bud burst in the spring (Cannell and Smith, 1986; Heide, 1993). Earlier release from dormancy can cause increased frost damage to tree buds under cold temperatures during early spring, resulting in lost foliage and consequent declines in tree growth. Red spruce has a small chilling requirement, so red spruce decreases in cold hardiness during winter thaws often lead to frost damage to trees (Dumais and Prévost, 2007).

Summer warming may also have significant effects on red spruce growth. Increased summer temperatures may cause high temperature-induced photo-inhibition to increase (Lambers et al., 1998). Red spruce seedlings and saplings showed high mortality and low growth rates under hot summer temperatures (Dumais and Prévost, 2007). Furthermore, dendroclimatological studies found that warm late summer temperature had a negative effect on annual radial growth of red spruce in the Great Smoky Mountains (Van Deusen, 1988). However, increased winter temperatures could increase the length of the growing season through earlier release from dormancy (Myking and Heide, 1995). Long-term records have shown earlier onset of several phenological events in recent years associated with warmer temperatures (Heide, 2003; Parmesan, 2006). Field surveys have also reported that red spruce photosynthesized during winter thaws (Schaberg et al., 2000), which may possibly enhance its growth.

4.2. Reconciling these conflicting studies

Inadequate attention to complex within- and across-scale interactions may explain these apparently conflicting studies. Increased CO$_2$, temperature and precipitation may have positive effects on growth by increased photosynthetic rate, but photosynthetic rate is also limited by other local habitat factors, including direct effects (e.g., resource availability) and indirect effects (e.g., topographic controls on microclimatic conditions) on tree growth (Dumais and Prévost, 2007; Geiger et al., 2009). It is important to hierarchically organize environmental controls (global to regional to local) on photosynthetic inputs and respiratory outputs (Koo et al., 2011b).

The structure of ARIM organized global to regional climate change and air pollution factors as functions of local-scale parameters such as elevation, which were in turn specified by site-specific parameters such as slope and aspect (Fig. 2 and Appendix A). Then, these factors were mediated by ecological and physiological relationships involving water, nutrients, light, and competition in interactions with co-existing species, like Fraser fir at finer scales for high and low elevations (Fig. 2 and Appendix A.1.1). ARIM was able to account for multiple direct (model equations in Appendix A.1) and indirect interactions (Appendix A.1.1) included in the submodels that improved mechanistic understanding of complex nested within- and across-scale interactions in the red spruce population and accounted for real-world complexities of habitat conditions for red spruce in the Great Smoky Mountains (Koo et al., 2011a).

ARIM analyses indicated different responses of red spruce growth in high elevations vs. low elevations populations to future climate change (3.6 ◦C warming in annual mean temperature, 3.8 ◦C in annual mean winter temperature and 7% increase in precipitation) combined with different levels of air pollution (no change, 10% increase, 10% decrease) in the Great Smoky Mountains. At high elevations, climate change led to dominance of indirect effects on red spruce growth. The mechanisms involved were (a) increased precipitation in eastern USA interacted with air pollution, which produced increased acidic rain at the regional scale (Johnson et al., 1992); (b) increased precipitation and air pollution, which are regional scale factors, interacted with elevation, which is a local scale factor, combining together to increase acidic rain (Geiger et al., 2009); (c) increased air pollution interacted with elevation and produced more acidic clouds (Borer et al., 2005; Lindens and Owens, 1992; Schier and Jensen, 1992); and (d) acidic rain and clouds interacted with ozone at the local scale (Delalays, 1992 (Appendix A.1.1). The first and the fourth interactions represented within-scale interactions, and the second and the third interactions represented across-scale interactions.

At low elevations, the mechanisms were more complicated: (a) increased temperature and precipitation, regional scale factors, interacted with elevation, a local scale factor (Geiger et al., 2009); (b) the climatic factors, regional scale factors, interacted with slope and aspect, local scale factors, (Geiger et al., 2009) and with Fraser fir mortality, also a local scale factor (Boggs and McNulty, 2010; Busing, 2004); and (c) increased winter temperature, a regional scale factor, interacted with the balsam woolly adelgid pest, a local scale factor, and controls Fraser fir mortality (Smith and Nichols, 1998) (Appendix A.1.1). All three interactions explain across-scale interactions.

The importance of considering both direct and indirect effects on ecosystems is receiving more attention (Higashi and Patten, 1989), but indirect effects are difficult to study at the whole-system level. Non-dimensionalized index values allow the synthesis of inter-disciplinary data to understand complex multi-scale phenomena by removing units and expressing spatial and temporal variation compared to long-term average values. This enables quantitative integration of all direct and indirect factors with different units, such as temperature, precipitation and air pollutants, which makes comparing different variables at different scales possible (Koo et al., 2011a). The integration of temporal variations of precipitation and air pollutants accounted for the temporal variation of acidic rains and explained red spruce growth declines at high elevations in GSMNP.

A potential constraint is that non-dimensional index values are based on relative performances of a certain spatial or temporal data point comparing to long-term mean, so long-term data are needed (at least 20 years). However, many long-term ecological research sites, such as the US LTER sites, have sufficient long-term monitoring data across multiple disciplines (Michener and Jones, 2012; Michener et al., 2011) to utilize this modeling approach.

Another potential constraint is that the non-dimensional index value approach assumes that a long-term average represents an equilibrium condition between an organism and the environment. Climate change effects do not happen in isolation. Forests will acclimate and adapt (Hamrick, 2004). The equilibrium condition could change as part of acclimation and adaptation processes (Briggs and Walters, 1997; Davis and Shaw, 2001; Hamrick, 2004). A lack of information about the acclimation range of red spruce limits our ability to predict the magnitude of global climate change effects on this ecosystem. However, uncertainty stemming from the assumption of equilibrium is likely to have less effect on alpine and subalpine tree species because they are relatively slow in acclimating and adapting compared with other lowland species (Atkin et al., 2006).

Despite these limitations, the ARIM systems modeling approach based on non-dimensional index values offers reliable predictions and comprehensive information about climate change effects on red spruce growth in support of long-term conservation policies and management of red spruce in the Great Smoky Mountains.

The initial dip in growth at high elevations was not explained by the ARIM projections (Fig. 4). This could be due to factors such as herbivory, human disturbance by logging, and physical environmental conditions, which were not considered in ARIM due to a
lack of literature information. In particular, logging could be an important factor to understand red spruce ecosystem in GSMNP between 1940 and 1979 (Harmon et al., 1984). Also, red spruce is consumed by several insects (Eveleigh and Johns, 2014; MacKinnon and MacLean, 2004). However, no research has found a specialized relationship among the insects and logging and red spruce growth declines in the GSMNP. Much ecological and physiological research for red spruce related to disturbances is needed to improve the accuracy of projections.

5. Conclusion

Systems modeling offers a reliable habitat-dependent assessment of red spruce decline and can serve as a basis for long-term conservation policies and management of this species and its ecosystems in the Great Smoky Mountains of the southern Appalachians. The Annual Radial Increment Model (ARIM) captured both direct and indirect effects on red spruce growth operating both within and across local, regional and global scales and provided an improved understanding of the effects of global change on red spruce growth in the Great Smoky Mountains National Park. Non-dimensional index values of different driving factors were used to facilitate comparisons of different factors influencing red spruce growth. Climate change alone led to reduced red spruce growth across the range of elevations. However, climate change interactions with air pollution led to antagonistic effects (leading to higher growth under a scenario of 10% lower air pollution, at high elevation only) and synergistic effects (leading to a further decrease in growth under a scenario of 10% high air pollution at both elevations). A better understanding of the ability of red spruce to acclimate or adapt to changing environmental conditions is needed to improve predictions. In summary, this study has demonstrated that a systems modeling approach, based on non-dimensional indices, can be used to examine complex ecosystem responses to global climate change.

Acknowledgments

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Appendix A.

ARIM model equations and model equations used for sub-models: (a) air pollution disturbance, (b) radiation, and (c) water availability. Detailed explanations for the equations are provided in Koo et al. (2011a). ARIM is a function of direct environmental factors such as air pollution disturbance ($AP$), water availability ($WA$) and radiation ($RA$) (model equations in Appendix A.1). These factors were linked to hierarchically organized submodels which depicted environmental controls (Fig. 2, Appendix A.1.1). Submodel factors indirectly influenced growth by controlling direct factors in the model equations in Appendix A.1 via multiple pathways.

A.1. ARIM model equations

\[
\begin{align*}
\text{ARIM}_{\text{high}} &= 0.67955AP_i + 1.55774 \\
\text{ARIM}_{\text{low}} &= 5.3397RA_i + 11.3237WA_i - 0.26971AP_i - 11.4031 \\
\end{align*}
\]

where ARIM are the annual radial growth increments at high ($\text{high}$) and low ($\text{low}$) elevations in year $i$, and $RA_i$ is solar radiation, $WA_i$ water availability, and $AP_i$ air pollution disturbance in year $i$. $AP_i$, $WA_i$ and $AP_i$ were linked to hierarchically organized submodels, (a), (b) and (c) which depicted environmental controls.

A.1.1. Submodel equations

(a) Air pollution disturbance submodel

\[
\begin{align*}
\text{AP} &= (\text{NO}_x \cdot \text{SO}_2 \cdot (0.083 \cdot 0.25CI + 0.17P) \cdot O_3 \cdot (0.17 + 0.33AC) \\
\text{P} &= (\text{Precipitation}) \cdot 1900 \text{ m was applied for Elevation of ARIM}_{\text{high}} \text{ and } 1600 \text{ m for ARIM}_{\text{low}} \\
\text{If Elevation} &< 1700 \text{ m then } P = 0.33 \text{ Precipitation (measured in the station)} \\
\text{If Elevation} &\geq 1700 \text{ m then } P = 0.67 \text{ Precipitation (measured in the station)} \\
\text{CI} &= (\text{Cloud Immersion}) \cdot 1900 \text{ m was applied for Elevation of ARIM}_{\text{high}} \text{ and } 1600 \text{ m for ARIM}_{\text{low}} \\
\text{AC} &= (\text{Acidic rains and cloud}) \cdot 1900 \text{ m was applied for Elevation of ARIM}_{\text{high}} \text{ and } 1600 \text{ m for ARIM}_{\text{low}} \\
\end{align*}
\]

(b) Radiation submodel

\[
\begin{align*}
\text{RA} &= (\text{Radiation}) \cdot 0.167AT + 0.167ST - 0.167PAC \\
\text{CI} &= 0.167P \cdot 0.167ST \times (1.317 - T) \\
\text{AT} &= (\text{Aspect}) \cdot 1 \text{ was applied for this research based on habitat conditions for tree-cores collected to construct the red spruce chronologies at low elevations} \\
\text{If Aspect} &= \text{north (315 – 45)} \text{ then } A_1 = 1; \text{ If Aspect} = \text{east (45 – 135)} \text{ then } A_2 = 2; \text{ If Aspect} = \text{south (135 – 225)} \text{ then } A_3 = 3; \text{ If Aspect} = \text{west (225 – 315)} \text{ then } A_4 = 4 \\
\text{ST} &= (\text{Slope}) \cdot 3 \text{ was applied for this research based on habitat conditions for tree-cores collected to construct the red spruce chronologies at low elevations} \\
\text{If Slope} &= 33.2 – 62.3 \text{ then } S_1 = 1; \text{ If Slope} = 26.6 – 33.1 \text{ then } S_2 = 2; \text{ If Slope} = 19.6 – 26.5 \text{ the } S_3 = 3; \text{ If Slope} = 11.7 – 19.5 \text{ then } S_4 = 4; \text{ If Slope} = 0 – 11.6 \text{ then } S_5 = 5 \\
\text{FM} &= (\text{Fir mortality}) \cdot 1900 \text{ m was applied for Elevation of ARIM}_{\text{high}} \text{ and } 1600 \text{ m for ARIM}_{\text{low}} \\
\text{If Elevation} &= 1700 \text{ then } FM = 0.33 \cdot \text{mean winter cold temperature (measured in the station)} \\
\text{If Elevation} &\geq 1700 \text{ then } FM = 0.67 \cdot \text{mean winter cold temperature (measured in the station)} \\
\text{CI} &= (\text{Cloud Immersion}) \cdot 1900 \text{ m was applied for Elevation of ARIM}_{\text{high}} \text{ and } 1600 \text{ m for ARIM}_{\text{low}} \\
\text{If Elevation} &< 1400 \text{ m then } CI = 0 \\
\text{If 1400} &\leq \text{Elevation} < 1800 \text{ then } CI = 0.5 \\
\text{If Elevation} &= 1800 \text{ then } CI = 1 \\
\end{align*}
\]

\[
\begin{align*}
\text{P} &= (\text{Precipitation}) \cdot 1900 \text{ m was applied for Elevation of ARIM}_{\text{high}} \text{ and } 1600 \text{ m for ARIM}_{\text{low}} \\
\text{If Elevation} &= 1700 \text{ then } P = 0.33 \text{ Precipitation (measured in the station)} \\
\text{If Elevation} &\geq 1700 \text{ then } P = 0.67 \text{ Precipitation (measured in the station)} \\
\text{T} &= (\text{Temperature}) \\
\text{AT} &= \text{annual mean temperature measured in the station} \\
\text{If Aspect} &= \text{north (315 – 45)} \text{ then } A_1 = 0.3; \text{ If Aspect} = \text{east (45 – 135)} \text{ then } A_1 = 0.5; \text{ If Aspect} = \text{south (135 – 225)} \text{ then } A_1 = 1; \text{ If Aspect} = \text{west (225 – 315)} \text{ then } A_1 = 0.65 \\
\text{Slope Factor} &= (\text{Slope Factor}) \cdot 3 \text{ was applied for this research based on habitat conditions for tree-cores collected to construct the red spruce chronologies at low elevations} \\
\text{If Slope} &= 33.2 – 62.3 \text{ then } S_1 = 2; \text{ If Slope} = 26.6 – 33.1 \text{ then } S_2 = 2; \text{ If Slope} = 19.6 – 26.5 \text{ then } S_3 = 3; \text{ If Slope} = 11.7 – 19.5 \text{ then } S_4 = 4; \text{ If Slope} = 0 – 11.6 \text{ then } S_5 = 5 \\
\text{FIR} &= (\text{Fir mortality}) \cdot 1900 \text{ m was applied for Elevation of ARIM}_{\text{high}} \text{ and } 1600 \text{ m for ARIM}_{\text{low}} \\
\text{If Elevation} &= 1000 \text{ then } FIR = 0.5 \\
\text{If Elevation} &\geq 1100 \text{ then } FIR = 0.9 \\
\text{If Elevation} &= 1200 \text{ then } FIR = 0.8; \text{ If Elevation} = 1300 \text{ then } FIR = 0.7; \text{ If Elevation} = 1400 \text{ then } FIR = 0.6; \text{ If Elevation} = 1500 \text{ then } FIR = 0.5; \text{ If Elevation} = 1600 \text{ then } FIR = 0.4; \text{ If Elevation} = 1700 \text{ then } FIR = 0.3; \text{ If Elevation} = 1800 \text{ then } FIR = 0.2; \text{ If Elevation} > 1800 \text{ then } FIR = 0.1
\end{align*}
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Bever, J.D., 2002. Negative feedback within a mutualism: host–specific growth of tree-cores collected to construct the red spruce chronologies at low elevations (If Slope = 33.2–62.3 then S = 5; If Slope = 26.6–33.1 then S = 4; If Slope = 19.6–26.5 the S = 3; If Slope = 11.7–19.5 then S = 2; If Slope = 0–11.6 then S = 1).

Bever, J.D., 2002. Negative feedback within a mutualism: host–specific growth of tree-cores collected to construct the red spruce chronologies at low elevations (If Slope = north (315–45°) then A = 3; If Slope = east (45–135°) then A = 2.5; If Slope = south (135–225°) then A = 1; If Slope = west (225–315°) then A = 2).


Notes.

References.


