APPLICATION OF A DENDROECOLOGY APPROACH TO RED SPRUCE PROVENANCE TRIALS TO STUDY SPECIES AND POPULATION VULNERABILITY TO CLIMATE CHANGE

by

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Bachelor in Forest Engineering, Federal Rural University of Pernambuco, 2019

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

Master of Science in Forestry

in the Graduate Academic Unit of Forestry and Environmental Management

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This thesis is accepted by the
Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

April, 2022

ABSTRACT

Red spruce (*Picea rubens*) is a tree species unique to the Acadian Forest, providing numerous ecosystem goods and services, including timber for the forest industry. With the expected decline of the species due to climate change, assisted migration of more southern, warm-adapted populations could help maintain the species in New Brunswick, but empirical evidence is lacking. Here, I compared the climate sensitivity of 16 populations of 60-yr-old red spruce trees across provenance trials, using a Bayesian model relating annual growth to historical climate from 1975 to 2018, while controlling explicitly for tree-level competition and size, stand-level development, thinning, blocking design and local soil conditions. Overall, climate explained a small fraction of the interannual growth variation, while stand development, thinning events and tree size were the strongest predictors. Our results do not provide strong support for assisted migration, as all populations displayed similar phenotypical plasticity in response to 45 years of climate variations.

DEDICATION

“I dedicate this thesis to my beloved mother and grandmother. Mom, I will never understand life, but I’ll always understand your love for me. I wish you were here, you would probably make me laugh when trying to read my thesis, especially in English. Grandma, thank you for your support and for always believing in me”

“Dedico essa tese para minha amada mãe e para minha avó. Mae, eu nunca entenderei a vida, mas eu sempre entenderei seu amor por mim. Eu queria que você estivesse aqui, você provavelmente me faria rir ao tentar ler minha tese em inglês. Vó, obrigado pelo seu suporte, e por sempre acreditar em mim”

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Loïc D'Orangeville. From the beginning, he showed me that he was much more than a professor and supervisor, but a good friend. He helped me come to Canada, pursue my dreams, taught me a lot, and gave me a lot of opportunities. I wouldn't get this far without his help, patience and kindness. And not to mention all ideas, insights, suggestions and advice that he gave me on this journey. I would like to thank the members of my committee, Dr. Anthony Taylor and Dr. Neil Pederson. Anthony, thanks for helping me throughout this path with all your feedback, support, and opportunities to learn and grow. Neil, thanks for helping me understand more about tree rings and for all your ideas, support and feedback. I'm also grateful to Dr. Malcolm Itter for allowing me to improve my study with a novel methodology. Thanks for your help and for accepting to be part of this research. Thanks to Canada's Natural Sciences and Engineering Research Council (NSERC) for supporting this research. To my friend, Jacob Ravn, who helped me collect my data during a long trip over the East Coast, thanks for your help, support, insights, and for our time. Thanks to all my friends in Canada and Brazil who helped me out somehow, even the smallest gesture of sending a message helped me keep going. Thanks to the Forestry and Environment Management department for the help. Thanks to everyone that believed in me and financially supported me so I could come to Canada, I will never forget that, and I'll be forever grateful. I would like to thank my pattern, Nazareth, that was the person by my side all the time during those two years. You helped me to believe in myself, to grow, and persist. Finally, thanks to my family, even being physically apart, I could feel the love, energy, and prays you sent me. Grandma, thanks for being my cheerleader number one, and know that I'm here because you believed in me one day, and you never had doubts about me.

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List of Symbols, Nomenclature or Abbreviations

BA – Basal Area

BAI – Basal Area Increment

CFS – Canadian Forest Service

CMI – Climate Moisture Index

DBH – Diameter at Breast Height

DPI – Dots per Inch

FCM – Field Capacity Moisture

GDD – Growing Degree Days

Chapter 1 – General Introduction

Native to the temperate forest of Northeastern North America, red spruce (*Picea rubens* Sarg.) is considered a defining tree species of the Acadian Forest Region (Rowe, 1972). Red spruce is a late-successional, shade-tolerant species (Burns and Honkala, 1990) that has wood properties comparable or superior to other spruces, such as a lower percentage of less desirable juvenile wood when compared with black spruce (Morgenstern and Fowler, 1969), and denser wood than white spruce (Jessome, 1977). These characteristics make it desirable to the forestry industry and manufacturers of musical instruments (Dumais and Prévost, 2007).

The quantity available and suitability of red spruce for both lumber and pulp are the main reason for its economic importance (Morgenstern and Fowler, 1969). In West Virginia, red spruce stands show one of the highest growing stock volumes per area, almost 20% more productive than other stands (Rollins et al., 2010). Being an important tree for the Acadian Forest, red spruce is ecologically critical for its role in carbon cycling and management (Rollins et al., 2010), as well as habitat for wildlife (Menzel et al., 2006), insects and other invertebrates (Schuler and Ford, 2002), and forest diversity and dynamics.

Red spruce's range extends from the Maritime Provinces in the northeast, west to southern Ontario and as far south as North Carolina (Bourque et al., 2010; Burns and Honkala, 1990) (Figure 1). The species prefers a cold, moist climate and is well adapted to coastal and mountain regions (Burns and Honkala, 1990). Its low frost tolerance is the main reason why red spruce's natural range is restricted to the temperate forest (Dumais and Prévost, 2007). However, as a cold-adapted species, red spruce does not respond well in warmer regions, and the reason for the extension of its southern range is mainly because most are located at high-elevation sites or because of exposure to the ocean, which provides a cooler environment during the growing season and supports moisture supply (Burns and Honkala, 1990).

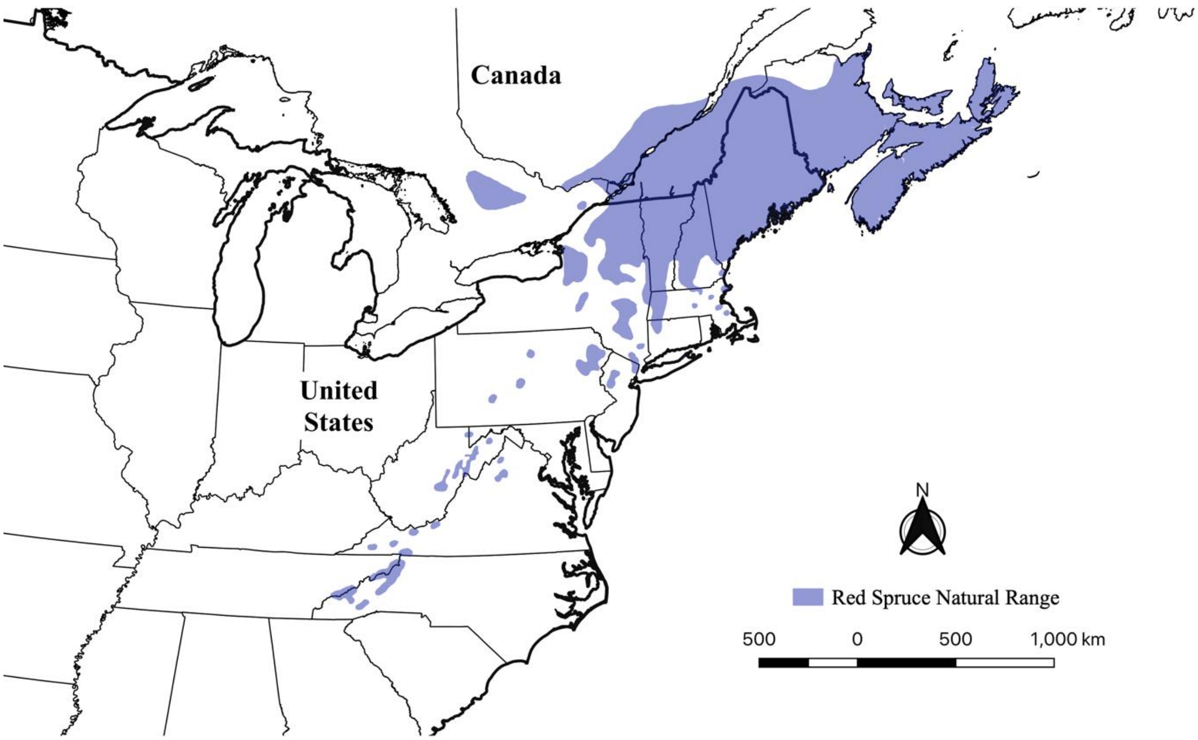

Figure 1. Red spruce (*Picea rubens*) distribution range (Little E.L., 1999)

A decline in the abundance and growth of red spruce has been reported across all red spruce range in the 1980s-1990s. This decline is mainly considered the result of atmospheric pollution (Johnson and Siccama, 1983), although the exact causes remain unclear. Other effects, such as extreme climate variations, and land-use history (Verrico et al., 2019), might have been enhanced by the impact of atmospherical pollution and increased winter injury events (Schaberg and DeHayes, 2000). Another hypothesis is that red spruce has a limited genetic diversity, that can affect genetic variability, and consequently, genetic adaptability (Capblancq et al., 2020; De Hayes and Hawley, 1992).

Even though climate change is creating new risks for red spruce and may interact with its abundance and vigour, recent studies show an increase in red spruce growth (Engel et al., 2016; van Doorn et al., 2011) and even a balance between mortality and recruitment in some areas of its range (van Doorn et al., 2011) or an expansion downslope in the northeastern US (Foster and D'Amato, 2015). However, this does not indicate that climate will not be detrimental for red spruce in the following decades.

Climate warming is expected to affect the distribution and abundance of key Acadian Forest tree species, such as red spruce (Taylor et al., 2017). The Acadian Forest region has already warmed by 0.7 ºC between 1950 and 2016 and is projected to warm another 1.5 to 5.7 degrees Celsius by the year 2100 (Zhang et al., 2019), and environmental conditions will probably change faster than plant populations can adapt or migrate (Aitken and Bemmels, 2016).

The analysis and projections of forest growth during climate change and future scenarios are fundamental to identify and quantify how climate change will impact commercial trees. The application of those analyses for commercial species is also very important because it can support management strategies that can directly affect the future economy and environment. Projections for the Acadian Forest, using the forest simulation model JABOWA, projected future climate change scenarios of maples, beech, white pine, balsam fir, red spruce, and other important species of the Acadian Forest (Ashraf et al., 2015). The projection of red spruce growth showed that its growth is sensitive to rapid changes in climate, showing a slight decrease under minimal and moderate climate change and a substantial decrease under maximum climate change (Ashraf et al., 2015). Other projections for red spruce in the Acadian Forest indicates that its abundance is projected to increase with warming temperature in the first decades of this century. Still, by the end of the century, it is expected to occupy only colder areas, reducing its distribution over its range, over time (Ashraf et al., 2015; Bourque et al., 2010, Taylor et al., 2020).

Migration and expansion of the northern part of the red spruce range are expected, but the southern part of its range is likely to contract by the end of the century (McKenney et al., 2007). In scenarios with minimal and moderate climate changes, red spruce growth is expected to slow down over time (Ashraf et al., 2015; Taylor et al., 2017).

Cold-adapted species like red spruce are expected to respond negatively to the direct effect of climate change, while temperate species are likely to respond positively (Ashraf et al., 2015; Dombroskie et al., 2010; Taylor et al., 2017). However, even with the potential to compete and adapt to future climates, temperate species are unlikely to keep pace with the loss of boreal species, causing an overall decrease in commercial timber, but forest management strategies such as assisted migration and pre-commercial thinning may help avoid this lack of future wood supply (Taylor et al., 2017).

Modelling methodologies, such as forest stand simulation models, use heat (usually mean annual, hottest, and coldest temperatures) and moisture as predictors. However, there are some limitations to this type of model because it usually does not consider that trees can show adaptive behaviours (Berger et al., 2008), and they do not consider the non-climatic factors such as competition, dispersal ability, genetic adaptation and other essential roles that also determine species distribution (McKenney et al., 2007). Overall, there is a lack of phenotypic plasticity in plant models (Grimm and Steven, 2013) that needs improvements to have accurate predictions.

Tree-ring studies can provide radial growth trends and patterns and complement standard forest mensuration metrics that help identify climate change interactions (Leland et al., 2016; Lloyd and Bunn, 2007), and there are different methods to correlate tree growth and climate, with the use of tree rings. The use of dendroclimatic analyses helps explain how growth patterns change over space and time under the influence of climatic variables (Savva et al., 2006). Provenance trials, plantation of trees with different origins and planted in different locations (i.e., common garden experiments), are another valuable source of data that helps address questions concerning climate change impacts on species performance by providing insight on how the same populations perform across broad climatic gradients (Loehle, 1998). These studies have investigated tree growth responses to climate change and indicate the need for transfer limits under human-assisted migration (Pedlar and McKenney, 2017). Using tree rings and provenance trials can provide additional information about climate adaptation, as they can provide a record of how past climate has influenced tree growth (Montwé et al., 2018). However, no studies were found with red spruce provenances trials and tree-rings together, and only a few tree-ring analyses were performed on provenance trials in North America, with a limited amount of species (Cook et al., 1998; Leland et al., 2016; McLane et al., 2011; Savva et al., 2006), and a few of them with red spruce (Conkey, 1986; Engel et al., 2016; Li et al., 2020; Morgenstern and Fowler, 1969; Yetter et al., 2021). Nonetheless, those studies showed how genetic variation is relevant to assessing climatic variations in forest productivity, and the need to understand the impact of environmental influence on forest dynamics.

This thesis aims to assess the vulnerability of *Picea rubens* to climate warming by analyzing the annual growth and health of mature red spruce trees across a climatic gradient in eastern Canada. To achieve these objectives, we developed a Bayesian hierarchical model to assess the sensitivity of *Picea rubens* with corresponding historical climate conditions of 16 range-wide populations of red spruce distributed among twelve 60-year-old provenance trials in northeastern North America and covering a 5 ºC mean annual temperature gradient.

I will test the hypothesis that red spruce is sensitive to climate moisture, where I expect growth reductions in drier years and locations (H1). As well, to support assisted migration of red spruce, I expect that red spruce provenances will display a trade-off between the local climate of origin and growth response to warming, where cold-adapted populations will have lower growth in hotter stands (H2). Our results will provide insight into the capacity of red spruce species and populations to tolerate changing heat and water stress, which will help assess its vulnerability to climate change. It will also provide growth patterns and information that may be beneficial to developing and improving forest growth model parameters.

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Chapter 2 – SIMILAR GROWTHS DECLINES WITH DRIER CLIMATE ACROSS RED SPRUCE PROVENANCES SUGGEST LIMITED ASSISTED MIGRATION POTENTIAL IN ATLANTIC CANADA

Santos, JM; Itter, M.; Taylor, AR; Pederson, N; D'Orangeville, L

2.1. Introduction

The rapid increase in average air temperature around the globe, associated with anthropogenic changes in atmospheric composition, is changing the severity, duration, and frequency of extreme climate and weather events, with region-specific impacts on forest productivity across North America (Vose et al., 2012). An accurate prediction of future changes in productivity is essential to understand future implications on sustainable forest management (Keenan, 2015; Lundholm et al., 2020).

The Acadian Forest Region of eastern Canada, mainly composed by temperate broadleaf and mixed forests (Rowe, 1972), has already warmed by 0.7 ºC and is projected to warm by 1.5 to 5.7 ºC by 2100 (Zhang et al., 2019). Such warming is expected to harm some Acadian Forest species (McKenney et al., 2007; Taylor et al., 2017). Red spruce, considered a defining tree species of the Acadian Forest Region (Baldwin et al., 2019; Rowe, 1972), has shown some decline in the abundance and growth across all its range (Dumais and Prévost, 2007; Reams and Van Deusen, 1993), most prominently in the 1980s-1990s. This decline is attributed mainly due to a combination of increased atmospheric pollution (Johnson, 1983) and land-use history (Verrico et al., 2019).

Following this decline, increasing red spruce growth has been reported from observational studies in the northeast of the US, either from tree-rings studies (Engel et al., 2016), from inventory plots (van Doorn et al., 2011), and even from remote sensing data integrated with forest inventory data (Foster and D'Amato, 2015). Those studies found improved recruitment in some red spruce's range areas and an expansion downslope in the northeastern United States. Despite these recent observations, forest simulation models indicate that the distribution and abundance of red spruce in the Acadian Forest region is expected to decline towards the end of the century (Ashraf et al., 2015; Dombroskie et al., 2010), most likely under the high climate forcing scenario (RCP 8.5; Taylor et al., 2017).

To increase the climate resilience of the Acadian forest and maintain future wood supply and biodiversity services, assisted migration of southern, warm-adapted genotypes of Acadian tree species is increasingly recognized as a valuable forest management tool (McLane et al., 2011; Pedlar et al., 2012; Sansilvestri et al., 2015). Assisted migration, i.e. the intentional movement of species to climatically suitable locations outside their natural range, is a strategy that is used to protect endangered species, increase productivity, and maintain multiple ecosystem services (Pedlar et al., 2012). However, assisted migration relies on the premise that southern genotypes have genetically diverged to match their local conditions, leading to superior phenotypic value in the face of a warmer, drier climate. However, such knowledge is currently lacking in most tree species, including red spruce. Recent comparison of diameter and height measurements across 60 year-old red spruce provenance trials revealed superior growth in cold red spruce populations moved to warmer locations, suggesting limited growth decline from moderate warming in the near future (Li et al., 2020). Such results indicate sufficient phenotypic plasticity (i.e., the ability of an organism to alter its characteristics in response to changes in environmental conditions) in northern populations to cope with increasing temperatures. A different provenance trials study showed very similar growth across range-wide populations planted in Atlantic Canada, suggesting similar phenotypical plasticity due to the small climate variability experienced by red spruce across its range, as southern populations are mainly found in high elevations areas with climates similar to Atlantic Canada (Morgenstern et al., 1980).

Despite the provenance studies cited above, the level of knowledge required to inform assisted migration of red spruce remains insufficient due to our limited understanding of how heat and moisture variation affect growth differently between populations. Dendroecological approaches, i.e. the study of annual tree-ring widths in relation to annual climate, can provide higher-resolution growth information – at the annual scale relative to standard forest mensuration metrics – which can help identify climate change effects on growth and improve our capacity to predict future impacts (Leland et al., 2016; Lloyd and Bunn, 2007). In addition, the use of dendroclimatic analyses helps explain how growth patterns change over space and time under the influence of climatic variables (Savva et al., 2006). Of the limited number of studies of red spruce provenance trials (Conkey, 1986; Engel et al., 2016; Li et al., 2020; Morgenstern and Fowler, 1969; Yetter et al., 2021), none has yet applied tree ring analyses. The use of tree rings and provenance trials can provide additional information about climate adaptation, as they can provide a record of how past climate has influenced tree growth (Montwé et al., 2018). The application of tree-ring analysis on mature provenance trials experiments (i.e., common garden) has the potential to identify and compare specific climatic sensitivities between populations under a very controlled, but in situ setting, as these experiments usually test the development of different populations to access their potential. This implementation might even be used to detect intraspecific population divergences, like drought sensitivity and local adaptation (Depardieu et al., 2020), and can be a powerful tool to support assisted migration as a management strategy.

Many methodologies exist that can inform decision-making on future management strategies, but tree ring models can be key instruments for implementing those strategies, as they can help to understand climate change effects on tree growth (Leland et al., 2016; Lloyd and Bunn, 2007; Savva et al., 2006). Usually, tree ring models use heat (e.g. mean annual, hottest and coldest temperatures) and moisture as predictors, and generally do not account for non-climatic factors such as competition, dispersal ability, genetic adaptation, and other essential variables that can be directly correlated to tree growth, distribution and abundance (McKenney et al., 2007). Overall there is a lack of phenotypic plasticity in those growth models (Grimm and Steven, 2013). Nonetheless, tree ring models that do not account for phenotypic plasticity and non-climatic factor are highly important to understanding the effects of climate on tree development; however, they usually lack the capacity to predict climate effects on growth that are applicable at large, operational scales (e.g. silviculture treatments) and needed to inform management strategies. For this reason, we decided to work with a different framework that allows us to integrate complex information, that analyzes different levels of aggregation and interactions between variables. The implementation of a Bayesian hierarchical model, fit with tree-ring information from provenance trials plantations might help us to identify differential responses and help support the idea of assisted migration of red spruce populations.

In the current study, we aim to study the climate change vulnerability of *Picea rubens* by analyzing the climate sensitivity of growth (1975-2018) in mature trees across a network of provenances trials in eastern Canada. As red spruce is a cold-adapted species having most of its distribution established in the temperate forest ecosystem, we expect that it will be sensitive to climate moisture, after controlling for size and other non-climatic influences, and that drier years and locations will be detrimental to its growth (H1). To support assisted migration of red spruce, we expect that red spruce provenances will display a trade-off between local climate of origin and growth response to warming, where cold-adapted provenances will have lower growth in hotter locations (H2).

2.2.Methods

2.2.1. Study area and Sampling design

From 1960 to 1964, the Canadian Forest Service (CFS) established two different red spruce provenance studies. The first, called series 14-95, but commonly known as the “Range-Wide" study, included 16 provenances planted at seven locations. The number of trees per plot, number of replicates, and spacing differed between trials (Table 1, and Figure A1). The second study, named series 18 and known as the "Maritimes” study, was planted a few years after, and it included 30 provenances planted in 19 trials (Morgenstern et al., 1980). Unlike the Range-Wide study, all trials had the same spacing and received the same number of provenances and replications. Each provenance was planted using a 4-tree square plot (Figure A2), replicated within ten blocks at each trial using a randomized design. A photographic example of a current Maritimes trial is shown in Figure 2.

Table 1. Characteristics of the two red spruce provenance studies, including trial identification code, establishment year and location, tree spacing, average climate (1975-2018) and soil information collected in 2013 by the Canadian Forest Service.

	Maritimes						Range-Wide			
Trial ID	**18-B2**	**18-C**	**18-D**	**18-F**	**18-E**	**18-I**	**14-A**	**14-B**	**14-C**	**95-Q**
Establ. Year	1962	1962	1962	1962	1962	1964	1959	1960	1960	1960
Location	Acadia R.F, N.B., CA	Fundy Nat. Park, N.B., CA	Iris, P.E.I., CA	E. Kemptville, N.S., CA	New Glen, N.S., CA	North Pond, N.L., CA	Acadia F., N.B., CA	Grimmer Settl., N.B., CA	Fundy Nat. Park, N.B., CA	UNB Woodlot, N.B., CA
Tree spacing (m)	1.8 x 1.8	1.8 x 1.8	1.8 x 1.8	1.8 x 1.8	1.8 x 1.8	1.8 x 1.8	1.2 x 1.2	1.2 x 1.2	1.2 x 1.2	1.5 x 1.8
Altitude (m)	75	273	31	80	96	156	62	239	273	71
Year of Thinning	2005	No thinning	1998	1987	No thinning	No thinning	1973 & 1999	No thinning	1979	- No thinning
CLIMATE (1975-2018)										
Mean Annual Temperature (°C)	5.51	4.91	6.19	6.01	7.11	4.33	5.55	2.61	4.92	5.70
Climate Moisture Index	-0.68	3.35	1.42	3.70	4.59	4.67	-0.64	4.68	3.36	-1.00
Growing Degree Days (>5 °C)	1674.86	1432.11	1660.23	1507.89	1572.43	1173.25	1678.70	1289.80	1432.02	1709.55
SOIL (0-30cm)										
Total nitrogen (%)	0.148	0.53	0.093	0.3905	0.2175	0.1375	0.1575	0.282	0.474	0.229
Field Capacity Moisture (%)	13	11	9	15	14	12	10	11	13	20
Clay (%)	2.25	2.85	2.80	2.40	1.60	0.50	3.65	4.30	3.25	10.75
Silt (%)	25.3	36.3	37.4	37.4	37.7	28.3	27.75	34.85	42.9	50.10
Sand (%)	72.45	60.85	60.2	60.2	60.7	71.2	68.60	60.85	53.85	39.15

Figure 2. Photograph of current conditions of Maritimes provenance trial (18D), located in Prince Edward Island. (Photo by Santos, J.M.)

The Maritimes and Range-Wide studies, together, have a total of 46 provenances and 12 trials. To address the first hypothesis, we collected tree core samples from 10 out of 12, excluding two trials that we could not visit due to COVID-19 restrictions (the two westernmost trials in Figure 3B). The collection of tree cores at all ten trials was essential to ensure the coverage of a sufficient temperature gradient (covering a 5ºC average annual temperature gradient) and address the tree growth response to each trial condition.

In 2020, we collected 800 growth increment cores from 16 red spruce provenances ranging from North Carolina to Nova Scotia (Figure 3B). The 16 provenances were selected to maximize the geographical distance between them and maximize the climatic gradient (Figure 2A). Eight provenances were collected from each CFS study. All cored trees (classified as study trees) had their diameter at the breast height (DBH; 1.3 m height) and canopy heights measured.

2.2.2. Tree growth

The increment cores were collected at breast height (± 1.3 m) with an increment borer (Figure 4). They were returned to the laboratory for processing, where they were glued to wood boards so they could dry without bending. The surfaces of the cores were flattened with a core-microtome, and the samples were sanded to highlight the rings when

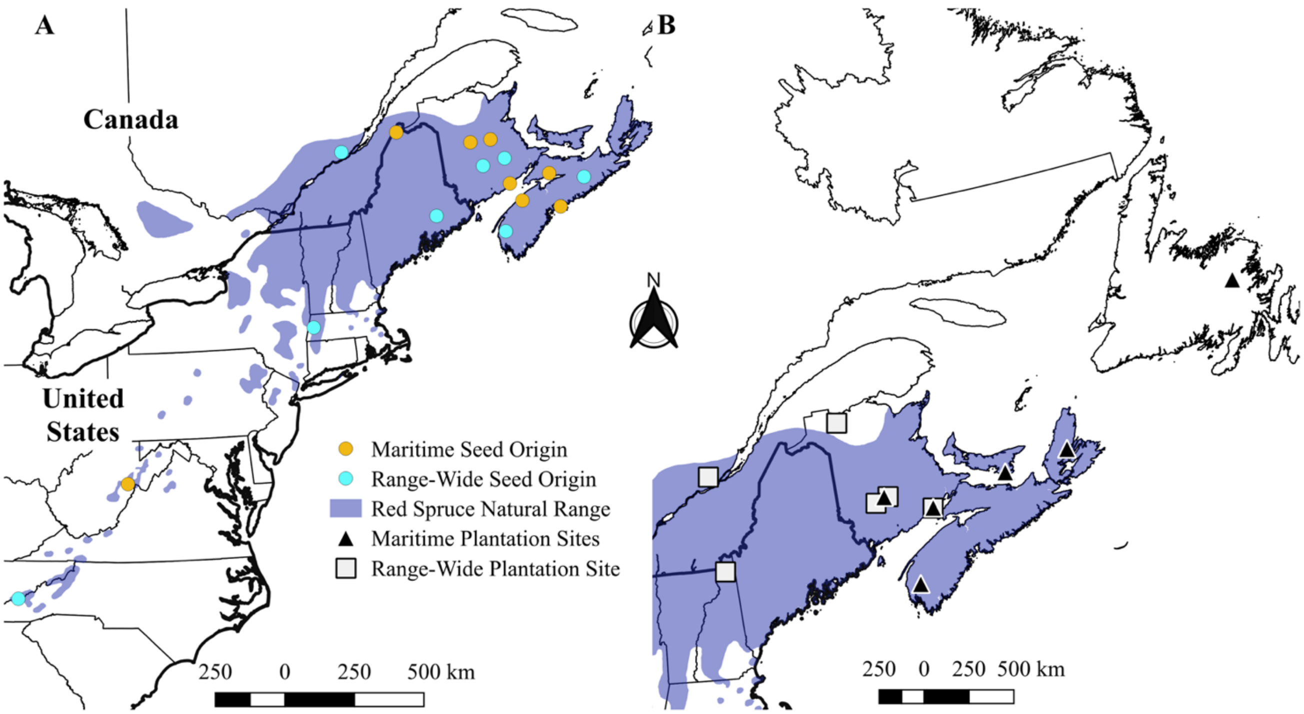

Figure 3. Location of the Maritimes and Range-Wide provenances (A) and trials (B) in Eastern North America.

needed. All samples were scanned using a stereomicroscope, with an integrated 5.1-megapixel camera (Laxco Sebacam 5.1 MP). Images were taken with a resolution of at least 3000 dots per inch (DPI).

Figure 4. Photograph showing research assistant J. Ravn collecting a growth increment core in a provenance trial located in New Brunswick. (Photo by Santos, J.M.)

Annual growth increments were then measured at 0.001mm resolution using the software CooRecorder 9.5. Cores were then cross-dated, by provenance and trial, using the Cdendro 9.5 software, using correlations between single-tree time series. A second cross-validation was made using COFECHA to ensure that all cores were aligned and that we had no missing rings. The second validation was made because the software COFECHA is well used on dendrochronology studies, and it has an easier and better visualization of the correlations, while the Cdendro has an easier interface to change the first year of a given core, or to include missing rings when needed.

Cross-dating was performed using mean series correlation (average of correlation between pairs of ring width time series for a given trial). We decided to work from 1975 because only 40% of the trees had rings from 1965 to 2018. This happened because some cores did not have the pith when collected, thus some data could not be accessed. The average inter-series correlation values on the studied years ranged from 0.52 to 0.74 (Table 2), and no missing rings were found during this period. Trials 14-B and 18-E were the ones with the lowest series correlation. The low correlations may be related to the high variation of DBH, where both trials had the biggest standard deviation (± 6%, and ± 4.7%, respectively). After the cross-dating, the ring width was transformed into basal area increment (BAI) to account for the effect of tree size on diameter growth, using annual tree diameter reconstructed by subtracting annual diameter increment from the DBH measured in 2020.

Table 2. Tree ring series details per test trial and average inter-series correlations for the studied period.

Study	Trial	# of Samples	Replicates per provenance	Mean inter-series correlation (1975-2018)
Range-Wide	14-A	80	10	0.69
	14-B	80	10	0.52
	14-C	80	10	0.73
	95-Q	80	10	0.68
Maritimes	18-B2	80	10	0.69
	18-C	80	10	0.70
	18-D	80	10	0.67
	18-E	80	10	0.56
	18-F	77[1]	8 - 10	0.68
	18-I	80	10	0.57

[1] Two provenances did not have the necessary number of trees, due to tree mortality.

2.2.3. Climate and Soil data

Monthly and seasonal Climate Moisture Index (CMI), maximum, minimum and average air temperature, and Growing Degree Days (GDD) were gathered for each trial from 1975 to 2018. The data were acquired from the Natural Resources Canada (McKenney et al., 2013), which used the BIOCLIM/ANUCLIM prediction system that uses monthly bioclimatic parameters to interpolate the climate data of a given location.

Preliminary Pearson correlations tests between standardized BAI and GDD, seasonal CMI, temperature and precipitation revealed no significant correlation with temperature or GDD, but strong correlations with summer CMI and precipitation. CMI is the difference between precipitation and potential evapotranspiration over a given period and represents the potential loss of water vapor from an area covered by vegetation (Hogg, 1997), that is directly affected by temperature. Thus, we decided to work with summer CMI because of the high correlation found with the raw data and because its also well-known to have a significant influence on tree growth in temperate forest ecosystems (Berner et al., 2017).

Soil granulometry (clay, sand, and silt percentage) was collected in 2017 for each horizon (0-15, 15-30, 30-60 cm; see Li et al., 2020 for methods). Using the granulometric content of each horizon, we calculated a weighted mean Field Capacity Moisture (FCM) applying Saxton and Rawls' (2006) equation.

2.2.4. Competition

To account for competition between each study tree and its immediate neighbors, a crowding index was calculated by measuring the DBH of all neighboring trees in a 3-meter radius around each study tree. We used the following equation to calculate the crowding index (c_i):

$$(1) \qquad c_i = \frac{\sum BA_{comp}}{BA_i}$$

Where BA_{comp} is the basal area of each tree within a 3-m radius around target tree i, and BA_i is the basal area of the ith tree. Smaller crowding values indicate less competition. As we did not have access to records of historical crowding levels, we assumed that the crowding indices calculated from 2020 observations are representative of the historical competition levels between 1975 and 2018. Under the controlled, even-aged growing conditions of tree plantations and relatively low mortality rates, such assumption appears reasonable and is supported by the strong crowding effect on growth. However, to account for the increasing competition over time as trees grow in size and resource requirements, we included a stand development variable, that was represented by stand age. After controlling for tree size and competition effects, preliminary analyses of model residuals revealed a negative, linear growth trend associated with stand development, or stand age, which was then included in the model (Figure A5). To account for varying competition over time due to recorded thinning events, we add years since thinning as another variable, as well as its interaction with stand age (see Results). Thinning treatments had been applied to some of the trials early in their development, which could have largely affected earlier levels of crowding. Existing records of past thinning events were gathered for both Maritimes and Range-wide studies. Available information included, for each trial, year of thinning, while levels of detail on the thinning design were inconsistent.

2.2.5. Spruce hybridization

Sympatric (i.e. where ranges overlap) red and black spruce trees are known to commonly hybridize, with significant implications on the phenotypic characteristics of the resulting red spruce trees, including growth rates and climatic sensitivity (Morgenstern and Farrar 1964). While no genetic information was available to quantify the level of hybridization for each studied seedlot, earlier studies had rated each seedlot's level of hybridization based on the visual assessment of 14 phenotypic traits (e.g. buds, needles, bark features), which have been previously linked with genetic hybridization level (Morgenstern and Farrar 1964). The hybridization assessment for the Range-wide trial seedlots was taken from Morgenstern et al. (1981), while the assessment for the Maritime provenances was taken from Fowler and Park (1988).

2.2.6. Data Analysis

Smooth functions were selected to properly account for the non-linear effect of climate on tree growth (D'Orangeville et al., 2018), as they don't require any a priori determination of the non-linear relationship. A Bayesian modelling framework was favored over generalized additive models (GAM) as it allowed us to better represent the complex, hierarchical structure of the random effects at the tree, block and site level. We applied the Bayesian hierarchical model to log-transformed observations of annual basal area increment of individual trees. We used log transformed of BAI in order to improve the fit of the model by normalizing the data. The model consists of a tree-level and stand-level submodel, where the tree-level submodel estimates BAI as a function of tree diameter, crowding, and a time-varying stand effect reflecting stand-level growing conditions. The stand-level submodel estimates the time-varying stand effects as a function of soil water-holding capacity, stand development, time since thinning, and climate moisture index, CMI, in addition to a site by block random effect. However, the stand-level submodel contains a provenance-specific component, where smooth functions are used to model provenance-specific responses to CMI while penalizing model complexity. Specifically, we fit the model as,

$$(2) \quad y_{ijkbt} = w_{jkt} + c_i\beta_1 + f(d_{it}; \beta_2, \beta_3) + u_{jb} + \epsilon_{ijkbt}$$

where y_{ijkbt} is the log-transformed annual basal area increment of the ith tree located in the jth stand (or plantation) from the kth provenance and located in the bth experimental block in year t. Here, w_{jkt} is the stand-by-year effect, c_i is the observed crowding for tree i at the time of increment core collection with β_1 quantifying the linear effect of crowding on annual growth, d_{it} is the diameter of tree i in year t with $f(d_{it}; \beta_2, \beta_3)$ quantifying the non-linear effect of diameter on annual growth conditional on coefficients β_2 and β_3, u_{jb} is a site-by-block random effect reflecting random variation in tree growth attributable to experimental block, and ϵ_{ijkbt} is a residual error term reflecting unexplained random variation in individual tree growth.

The stand-by-year effect accounts for the mean variation of red spruce individuals of the same provenance and co-occurring in the same stand during the same year after accounting for the effects of tree crowding, size, and experimental block. The stand-by-year effect was modeled as,

$$(3) \quad w_{jkt} = \boldsymbol{h}'_{jt}\boldsymbol{\gamma} + \boldsymbol{b}'_{jt}\boldsymbol{\eta}_k + \nu_{jkt}$$

where $\boldsymbol{h}_{jt}$ is a vector of stand-level variables including soil capacity moisture (the $'$ notation indicates the vector transpose), time since plantation establishment (reflecting stand development), time since thinning, and an interaction between time since establishment and thinning, $\boldsymbol{\gamma}$ is a set of stand-level linear regression coefficients, $\boldsymbol{b}_{jt}$ is a set of cubic regression spline basis functions of CMI, $\boldsymbol{\eta}_k$ is a set of provenance-specific, penalized basis function coefficients with dimension matching the number of basis functions, and ν_{jkt} is a residual stand-level error term reflecting unexplained variation in stand-by-year effects. Note the $\boldsymbol{b}'_{jt}\boldsymbol{\eta}_k$ term represents a provenance-specific CMI smoother term identical to those used in generalized additive models and allows for non-linear responses to CMI.

We applied a Michaelis-Menten saturating function to account for the effects of tree diameter on annual growth,

$$(4)\ \ f(d_{it};\beta_2,\beta_3) = \frac{\beta_2 d_{it}}{\beta_3 + d_{it}}.$$

Finally, all random model components were modeled using independent, normal distributions:

$$(5)\ \ u_{jb} \overset{iid}{\sim} N\left(0,\tau^2_{\text{block}}\right),\ \nu_{jkt} \overset{iid}{\sim} N\left(0,\sigma^2_{\text{stand}}\right),\ \epsilon_{ijkbt} \overset{iid}{\sim} N(0,\sigma^2).$$

The joint posterior distribution of the growth model parameters was estimated using Markov chain Monte Carlo (MCMC) simulation using RStan (Stan Development Team 2021). Three independent MCMC chains were run for a total of 5,000 iterations with a burn-in period of 1,000 iterations. All model inference was based on a total of 1,500 posterior samples (500 samples per chain) collected following model convergence. Model convergence was assessed visually and using Gelman-Rubin statistics. The tree growth model is completed by assigning prior distributions to all remaining unknown model parameters, see model implementation on Appendix B for equations and explanatory information.

Variance partitioning was conducted following model convergence to estimate the overall proportion of variance explained at different levels of the growth model (tree and stand) and to apportion this explained variance to different components of the model. We calculated Bayesian R-squared values for both individual tree growth and stand-by-year effects (as defined in Gelman et al., 2019). Equations and supplementary information can be found on Appendix B.

Explanatory analyses tested separately the effect of the hybridization index (provenance-level) and of GDD (stand-level climate variable) on growth after removing size, stand development effects, crowding, and soil effects. There was no visible effect of those variables, and they were discarded (see Figure A3 for the effect of GDD on growth).

2.3.Results

The growth model explained a large proportion of the variance (see figure A6 for predicted mean versus observed) , where crowding, tree size, block, and stand-by-year effects explained 84±0.5% (R^2±99% credible interval) of the tree-level variability in annual growth, while the stand-by-year sub-model that accounts for soil moisture capacity, stand development, thinning, and the climate moisture index (CMI) explained over 87%± 1.5 of the stand-level variability in annual growth (Figure 5).

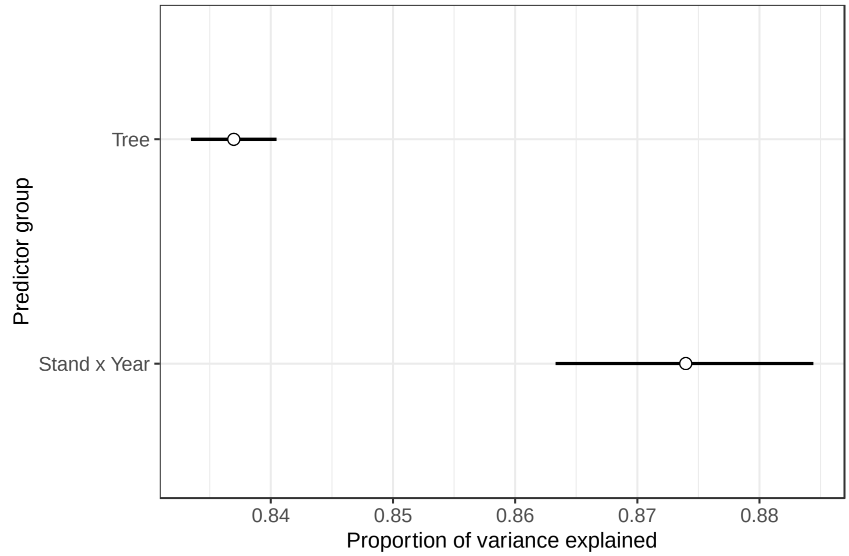

Figure 5. Proportion of red spruce tree-level and stand-by-year variance explained by the growth model. Black lines represent 99% credible interval.

At the tree-level, tree size (r^2 = 0.66) and stand-by-year (r^2 = 0.35) effects are the biggest drivers of individual growth variations in our samples, followed by the blocking effect and crowding (Figure 6). Over 95% of the stand-by-year level variability was explained by stand development, that is the stand age including thinning effects, with soil capacity moisture and CMI explaining the remaining variability (Figure 6).

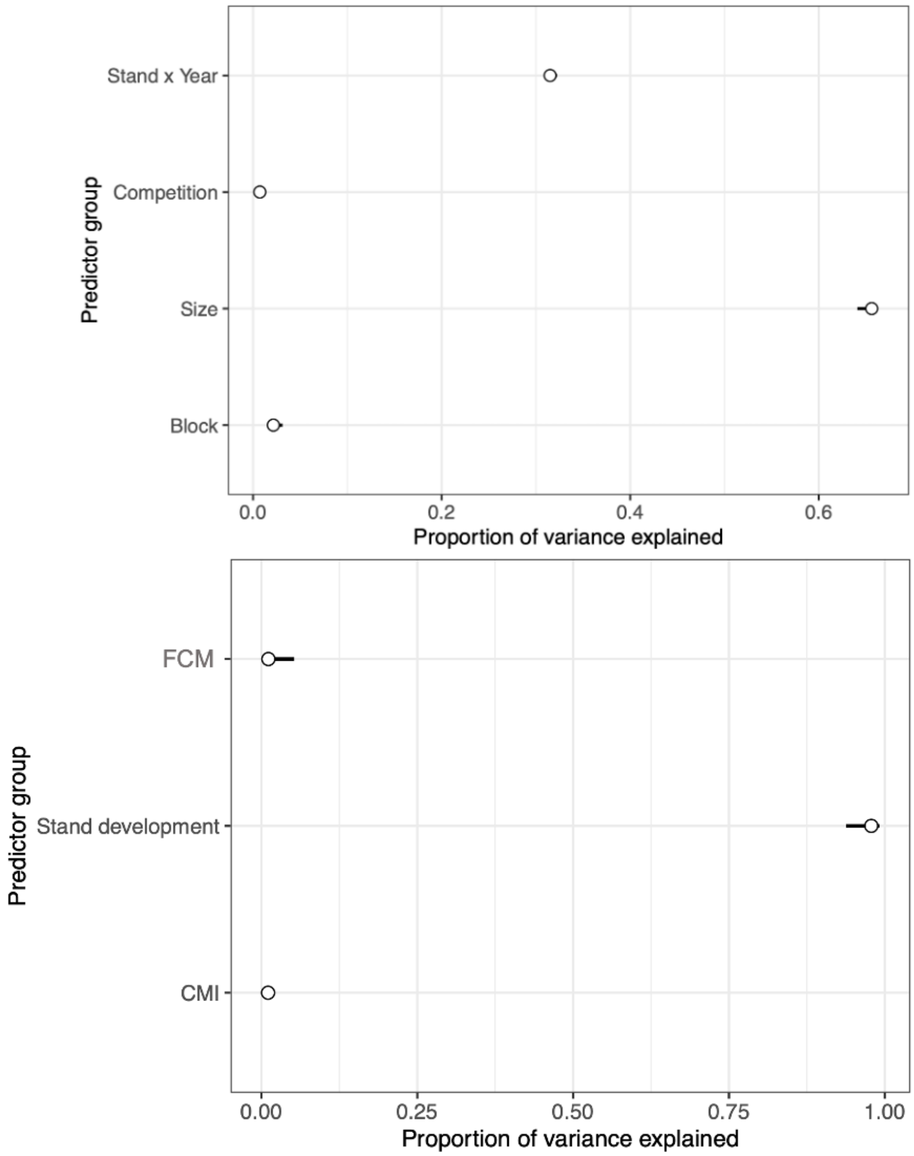

Figure 6. Proportion of variance explained by each variable on the tree-level sub-model (Top) and on the stand-by-year sub-model (Bottom) of red spruce.

Despite its low predictive power, the effect of CMI on red spruce growth followed a sigmoid curve (Figure 7; see figure A6 for annual predicted CMI effects).Controlling for other predictors, the stand-level growth response to CMI averaged across provenances is maximal at moderate, positive CMI values of 0 to 12mm, but declines under drier, negative summer CMI values, suggesting moisture limitation to growth (Figure 7). This result supports our first hypothesis of a negative growth response to reductions in available moisture. Growth patterns under wetter conditions display higher uncertainty due to lower replication.

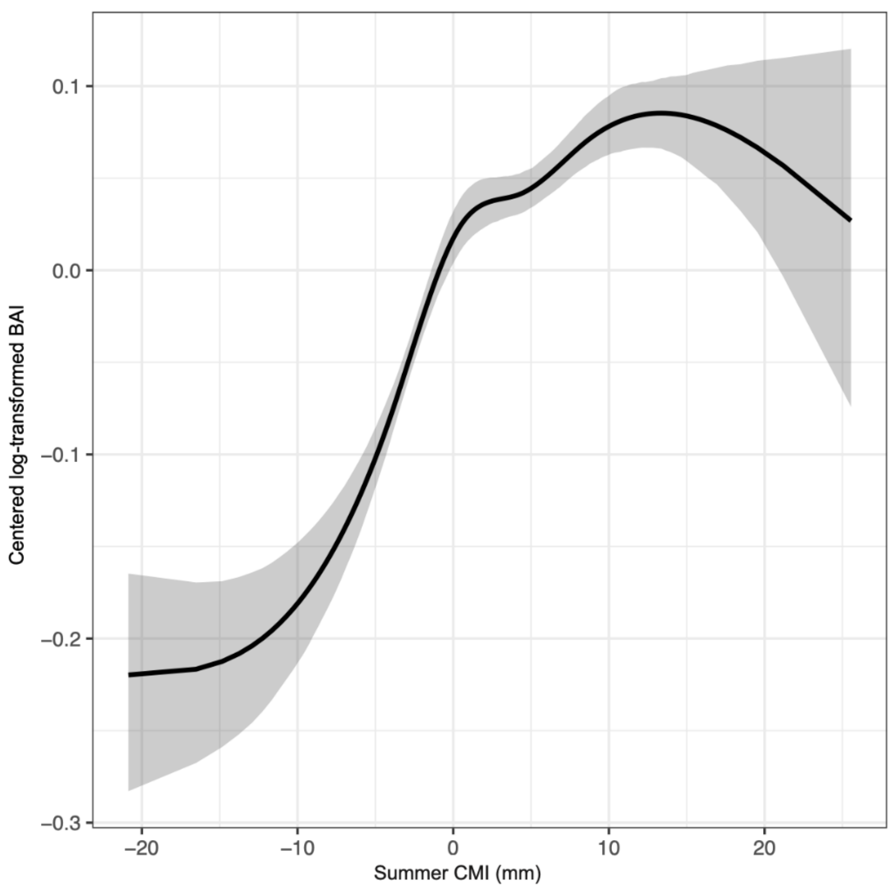

Figure 7. Posterior estimate of mean stand-level growth (centered log-transformed BAI) in response to summer CMI for red spruce. Shaded region is the 95% credible interval.

When comparing the growth sensitivity to CMI between red spruce provenances, we find similar patterns across them (Figure 8). This result does not support our second hypothesis where warm-adapted provenances were expected to display superior growth under drier conditions.

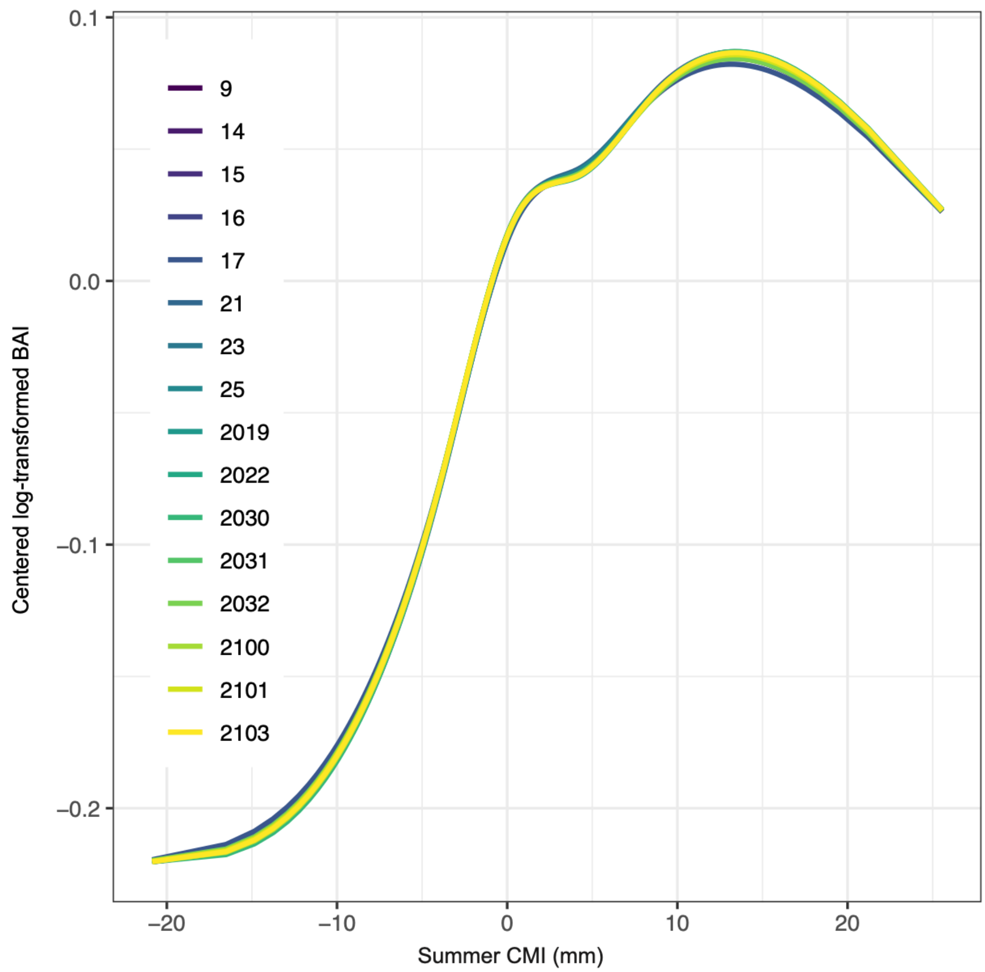

Figure 8. Posterior estimate of mean (centered, log-transformed BAI) stand-level growth in reponse to summer CMI by provenance. Shaded region is the 95% credible interval.

Red spruce trees displayed large variations in growth between trials and within each trial across provenances (Figure A4). Trials from central New Brunswick (95Q, 18B2, and 14A), despite similar climates, displayed large growth differences highlighting the influence of site conditions and other non-climatic factors on growth (Table A1). Another factor that could also explain the difference between those trials was competition. For instance, trial 95Q showed the largest average DBH and lowest mean crowding index (Table A1). At the same time, trial 18I, located at the coldest end of our climate gradient in northern Newfoundland, displayed the lowest DBH and height of all trials, but also the second-highest mean crowding index, highlighting the influence of competition and site quality on tree development.

Tree size was the strongest predictor of individual growth, showing a saturated curve response to the log-transformed BAI (Figure 9). Competition, represented here with the crowding index, displayed a negative linear effect on the log-transformed BAI (Figure 9). While that index was measured in 2020 and may not represent exactly the earlier years of growth at each trial, our results suggest that the current size of the surrounding trees generally reflects the average interaction over their lifetime.

In addition to the linear, negative effect of stand age on growth, we observed a large, linear positive growth response (+1.5 in average, log-transformed BAI) to recorded thinning events in the first five years after thinning. Even after 10 to 20 years, the mean growth response was slightly positive in relation to thinning history (+0.5 in average, log-transformed BAI). The combination of both effects reveals similar negative growth trends with time since thinning and stand initiation (Figure 10).

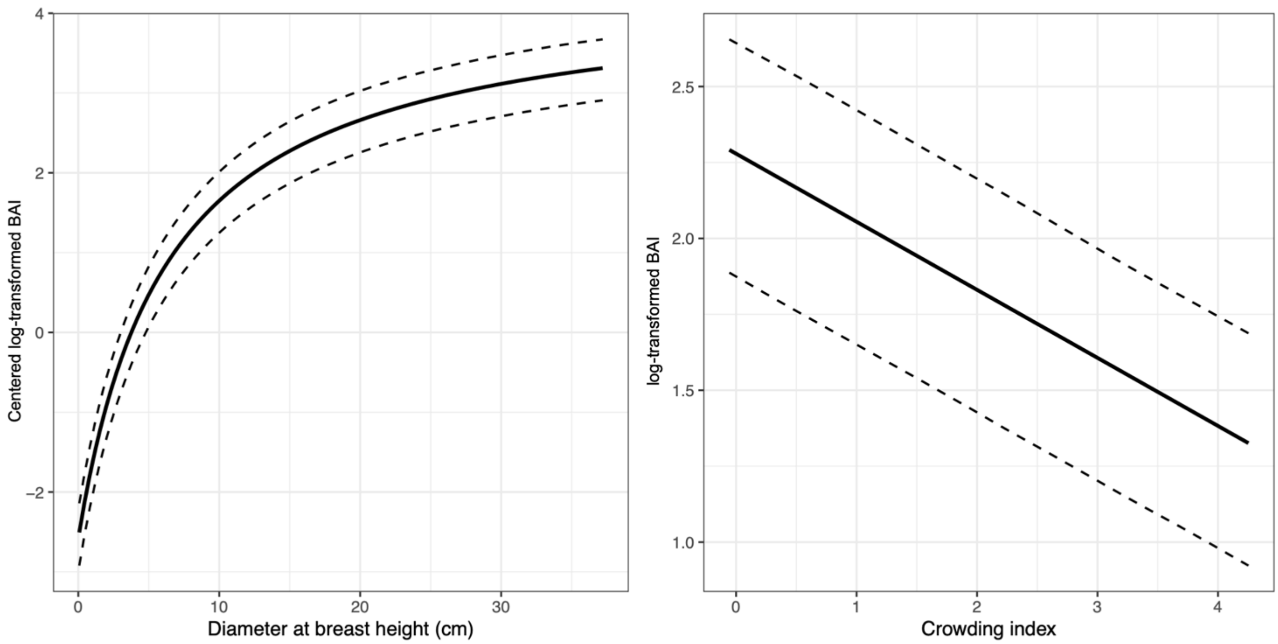

Figure 9. Posterior estimate of tree-level growth response to tree size, defined as the diameter at breast height (A), and to competition, defined as the crowding index (B). The solid line represents the posterior estimated mean while dashed lines indicate the 95% credible interval.

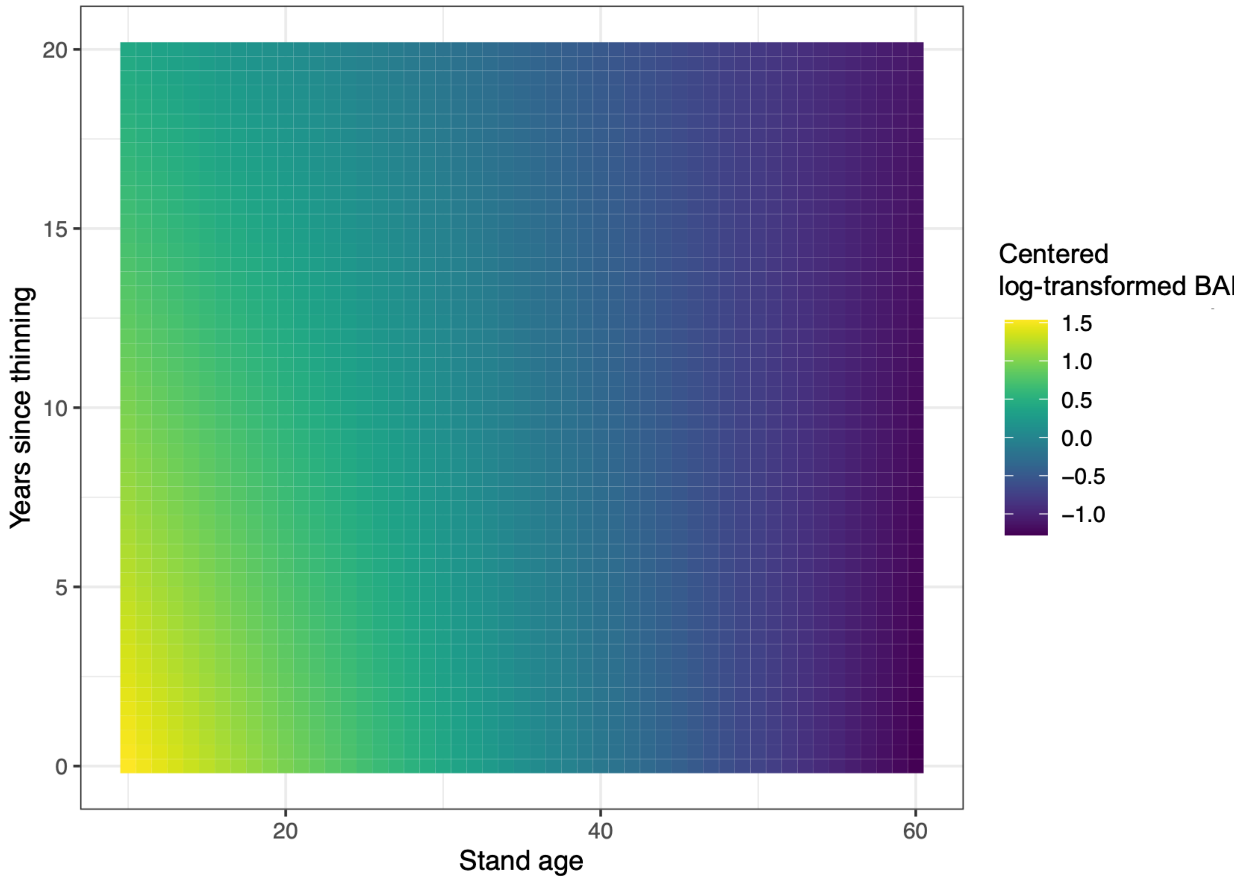

Figure 10. Posterior estimated of mean growth response (centered log-transformed BAI) to the interaction of stand age and years since thinning.

2.4. Discussion

2.4.1. Moisture sensitivity of red spruce

This study of over 40 years of annual growth rates for range-wide red spruce provenances across ten provenance trials in Atlantic Canada has identified a significant, but small, negative effect of reduced moisture availability on the growth of red spruce, in support with our first hypothesis (see Figure A6 for CMI effect on the residuals). This relatively marginal effect of climate moisture on growth, while in line with earlier studies (Day, 2000; Kosiba et al., 2018; Li et al., 2020; White et al., 2014), might suggest that the studied trees did not suffer sufficiently severe or prolonged drought to reveal larger effects. Extreme weather events have been shown to increase the susceptibility of red spruce to winter injury and reduce its growth following a lower carbon assimilation (Kosiba et al., 2018; Schaberg et al., 2011). Water availability also determines the capacity of tree species to maintain photosynthesis and transpiration under warmer conditions, as reported in boreal tree species of eastern Canada from empirical tree growth models (D'Orangeville et al., 2018). The projected increase in atmospheric vapor pressure deficit in New Brunswick under climate change (Cohen et al., 2019), expected to reduce global vegetation growth (Yuan, et al., 2019), is likely to negatively impact red spruce growth and health.

Earlier tree-ring studies of red spruce growth, which use standardized data after removal of non-climatic drivers including tree size, competition and stand development, usually show a negative response to warmer temperatures (Kosiba et al., 2018; Ribbons, 2011; Verrico et al., 2019), and to excessive spring moisture (White et al., 2014). Some of those studies also mention the effect of water availability in the development of red spruce, but generally do not find a clear relationship with growth. While the standard tree-ring approach of detrending raw growth values (i.e. removing low-frequency signal) and focusing on interannual variations is excellent at highlighting climate influences on growth (Peters et al., 2015), and is widely used for its simplicity and adaptability (Fritts 2001; Shi et al., 2020), but it limits our ability to compare climate effects with other growth predictors. Here, given the relatively simple history and structure of the plantations, we were able to model explicitly all growth predictors simultaneously, allowing better quantification of the importance of climate and other predictors on growth, while estimating uncertainty.

2.4.2. Variations in moisture sensitivity between red spruce provenances

The similar growth response to over 40 years of moisture variations found here for range-wide provenances of red spruce does not provide support for assisted migration, at least when looking at local adaptation to moisture limitations. This result might be related to the small size of the species distribution and its relatively low genetic diversity (Fowler et al., 1988; Morgenstern et al., 1981; Rajora et al., 2000), but also suggests substantial phenotypic plasticity to a range of climatic conditions. As a “younger” species (when compared with other spruces), red spruce did not have as much time to evolve (Lockwood et al., 2013), leading it to a restricted distributional range. Hence, the lower genetic variation of the species may reduce the number of climate-adaptive traits critical to locally adapting to a rapidly evolving climate (Valladares et al., 2014). However, the warmer condition that red spruce has experienced, especially on the southern part of its range, might have triggered local adaptation, supporting the exploration for locally adapted phenotypes of red spruce trees that are better able to persist under warmer climate change scenarios (Capblancq et al., 2020). For instance, the comparison of heights and diameters across red spruce provenance trials, revealed that northern red spruce populations grow well under moderate warming (Li et al., 2020). A recent provenance study about levels of genetic and plasticity variation for phenology and growth traits in red spruce seedlings also found that genetic variation in phenology and growth had a moderate heritability and differentiation, leading the authors to conclude for the existence of some potential for trait selection (Prakash et al., 2022). However, they also highlight the risk of phenological mismatch, where phenology traits (e.g. bud break in spring, bud set in fall) may become increasingly vulnerable to an earlier start of the growing season and later fall, including risks of frost injuries to foliage (Zohner et al., 2020), for which red spruce is especially susceptible (DeHayes et al., 1990). The comparison of phenotypic plasticity among tree species provenances, as reported for other conifer species like black spruce, jack pine (Pedlar and McKenney, 2017), and white spruce (Sáenz-Romero et al., 2021), is key to assessing different populations' adaptive capacity to climate change and informing the implementation of assisted migration. The climate adaptation of red spruce will mostly depend on the regional availability of genetic variation, especially in the southern, warm part of its range (Capblancq et al., 2020; Prakash et al., 2022). Here, our findings do not provide evidence supporting the management for a specific red spruce provenance in Atlantic Canada because we did not find a different response to available water among the provenances tested.

2.4.3. Management implications

Studies that are trying to access the response of tree species to climate change are key to sustainable forest management. Here, our results reveal additional information valuable for management. Notably, although reductions in available moisture within the observed range may reduce the growth of red spruce trees, such negative impacts should be one order of magnitude smaller than impacts from changes in tree size, stand density or aging, which can be modified through silvicultural interventions.

Optimizing silvicultural treatments could largely compensate for drying effects in the near-term, at least within the observed range of moisture. The optimization of silviculture treatments considering climate change effects on future productivity can be useful in mitigating economic losses on *Pinus radiata* in Europe (Gonzales-Rodrigues et al., 2021). Silviculture treatments for red spruce plantations that could compensate for the expected drying effect would be the reduction of competition by the application of thinning treatments. Another silviculture strategy would consist of longer rotations, which associated with pre-commercial thinning might maximize productivity and alleviate part of the economic losses due to the negative effects of climate change (Gonzales-Rodrigues et al., 2021).

Despite the lack of variations observed here in moisture sensitivity between provenances, assisted migration should not be discarded as a valuable management strategy for red spruce, given the moderate levels of drought recorded during this study and the risk for increasing divergences under increasing warming. Such local adaptation to higher water and heat stress, although currently unknown, will mostly depend on the regional adaptability of southern populations (Capblancq et al., 2020). However, assisted migration practices needs to carefully assess potential negative impacts from the movement of locally adapted southern populations. Specifically, the phenology (i.e. timing) of growth and dormancy may be altered under different climates, leading to phenological mismatches that can increase the risks of injuries due to frost (Zohner et al., 2020). As frost events might occur more regularly (Liu et al., 2018; Rigby and Porporato, 2008), resistance to frost events should be an important aspect to consider in future studies.

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Chapter 3 – General Discussion

In my thesis, I found that tree size and competition, not climate, were the most significant predictors of red spruce growth in Atlantic Canada. Such finding is not new, as the use of those two variables is essential to improve growth model predictions (Briseño-Reyes et al., 2020; Das, 2012; D'Orangeville et al., 2018; Tomé and Burkhart, 1989). Implementing the reconstructed diameter and tree-level competition levels allowed me to observe the exponential response of tree growth to size, and its linear response to crowding. However, as we worked with plantations, we could also include stand development (age, thinning events, age since thinning) that helped increment the model and explain the variation in growth. Those stand development variables are also known to play an important role when this type of data is available (Kimberley and Watt, 2021; Matsushita et al., 2015), which is rarely the case in natural stands.

As soil variables can also be good predictors and explain growth variations and improve models' accuracy (Buri et al., 2020; Soong et al., 2020), we include field capacity moisture, derived from the soil granulometry, as a variable to represent the influence of soil water-holding capacity on the growth of red spruce. However, the limited effect of this soil variable may be due to its limited representativity of each trial, as only one soil pit was excavated per trial. As a result, we did not pursue potential differences due to soil characteristics. However, to address other variations that could be hidden in the raw growth data, we included soil and block random effects that might represent specific growth variations that are not directly related to the site, climate variables, or the randomness around those variables (Bell et al., 2019). Another explanation is that soil variables can be more relevant when explaining forest dynamics over just the growth (Soong et al., 2020), or sometimes climate variables can be more limiting than soil fertility (Bennett et al., 2020).

Red spruce growth decline has been associated with several variables. The most recognized and evident was the reduction of growth in the mid-'90s mainly due to acid rain and the deposition of atmospheric pollutants, although the exact mechanism remains debated (Adams and Eagar, 2012; DeHayes et al., 1999; Johnson, 1983). Those events highlighted how human actions could affect the development of important tree species like red spruce. Interestingly, those events also highlighted how our society can also act when facing a rapid threat, as Canada and the US rapidly signed a treaty in the early 1990s that largely reduced acid rain impacts on our forest ecosystems. Perhaps the existence of low-cost alternatives was no stranger to such rapid action, a scenario that is different from the climate change crisis we face. After the red spruce decline, many studies were conducted to identify the causes of the decline, and more broadly the factors that influence the establishment and development of red spruce across its range. The search became even more prominent when climate change projections indicated that red spruce would probably be highly affected by the projected warming.

Understanding the sensitivity of different red spruce populations to water availability is important to support management strategies and predict how climate change might affect its growth and distribution. Moreover, the indication that lower climate moisture can be detrimental to the growth of red spruce and that different populations have similar responses to dryness highlights the importance of continued and applied studies to support the decision-making of management strategies. Understanding red spruce's genetic variability and plasticity in response to climate are necessary because populations' adaptative responses will depend on those variables (Prakash et al., 2022). However, understanding the influence of climate on the growth and distribution of one species may not be enough to predict if that species will continue to thrive in a warmer, drier climate. Even though some species might adapt to climate warming, it is also how the competing species will adapt that will be critical. Indeed, competition with warm adapted or faster-growing species might change, potentially leading to ecosystems dominated by better adapted species (Loehle, 1998). Furthermore, the change in forest composition and suppression of important ecological and commercial species, like red spruce, might directly affect the environment and economy that depends on that species' goods.

Supplementary studies can be done to increment the results of our findings. For example, the analysis of frost hardiness is one of the studies highlighting the importance of assisted migration of the red spruce population. Comparing populations with different sensitivities to frost events will improve the level of information when discussing future strategies. It might indicate populations with characteristics that can adapt or support multiple aspects of climate change. The analysis of additional populations that we did not test is also another critical study that can be done to increase the number of populations tested to support assisted migration.

While assisted migration is one of the strategies that can be implemented to save species from climate change effects, maladaptation of assisted species can cause severe growth productivity, mortality, and distribution problems. More research on dominant tree species of the Acadian Forest, especially the boreal species which are more at risk, is needed. For instance, the government of New Brunswick should invest and support more studies related to assisted migration of Acadian species red spruce, black spruce, white spruce, balsam fir, jack pine, but also trembling aspen and white birch. Investment should be made to create new provenance trials plantations of different commercial species, designed specifically to study climate vulnerability, and to better maintain existing ones. New trial plantations can create opportunities for new research that may support future strategies in the province and directly affect the economy, as forestry is one of the most significant sectors of the province.

Our most significant limitation during this study was the covid-19 pandemic. It is an understatement to say that my graduate program was impacted. We had to exclude two trials from our sample design because of covid restrictions, one in Quebec and one in the United States. I would add that many more aspects of my research were impacted.

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Appendix A – Supplementary Figures and Tables

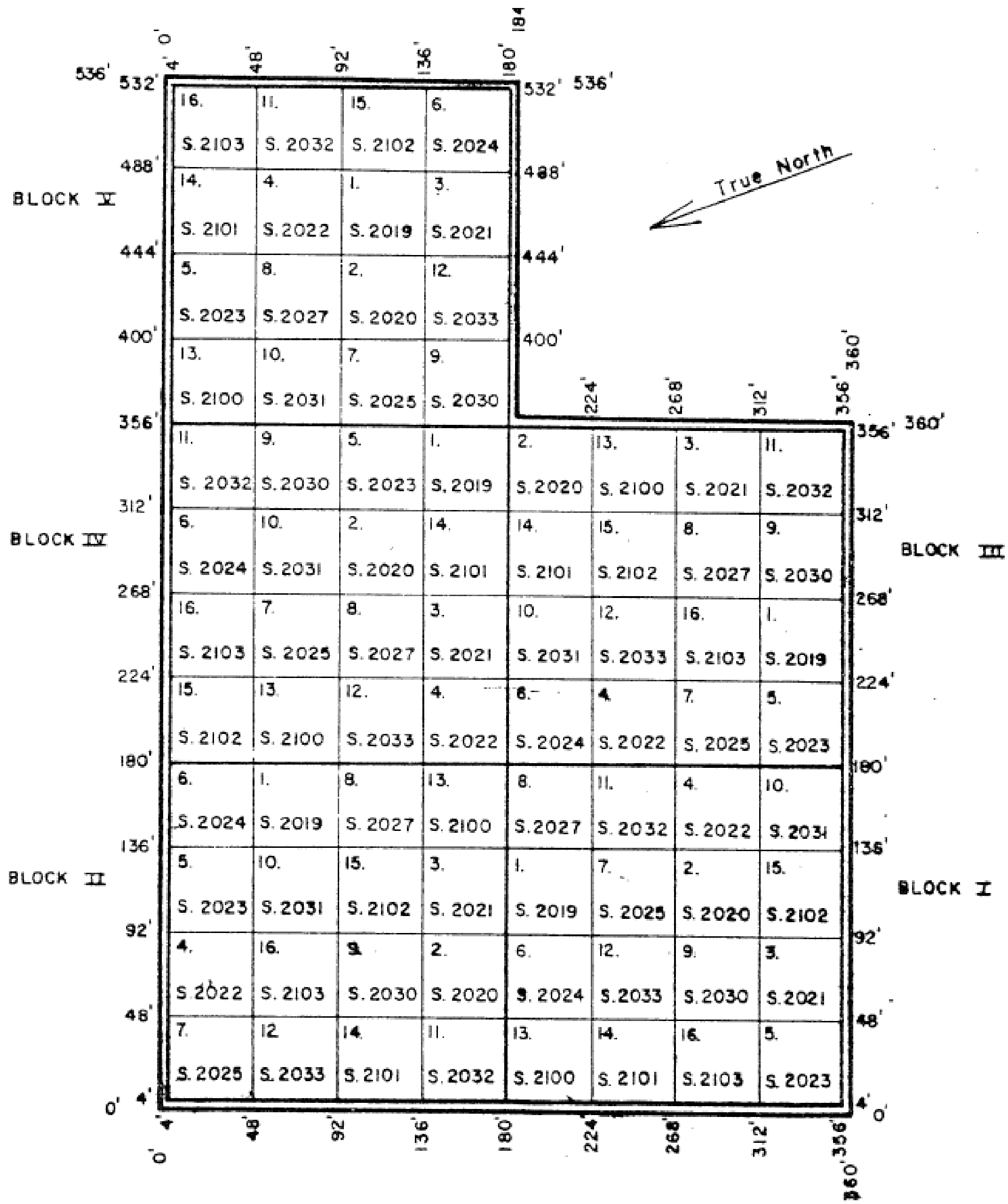

Figure A 1. Range-wide (series 14-95) red spruce plantation layout example for one trial (14A). Sixteen Provenances replicated in five different blocks.

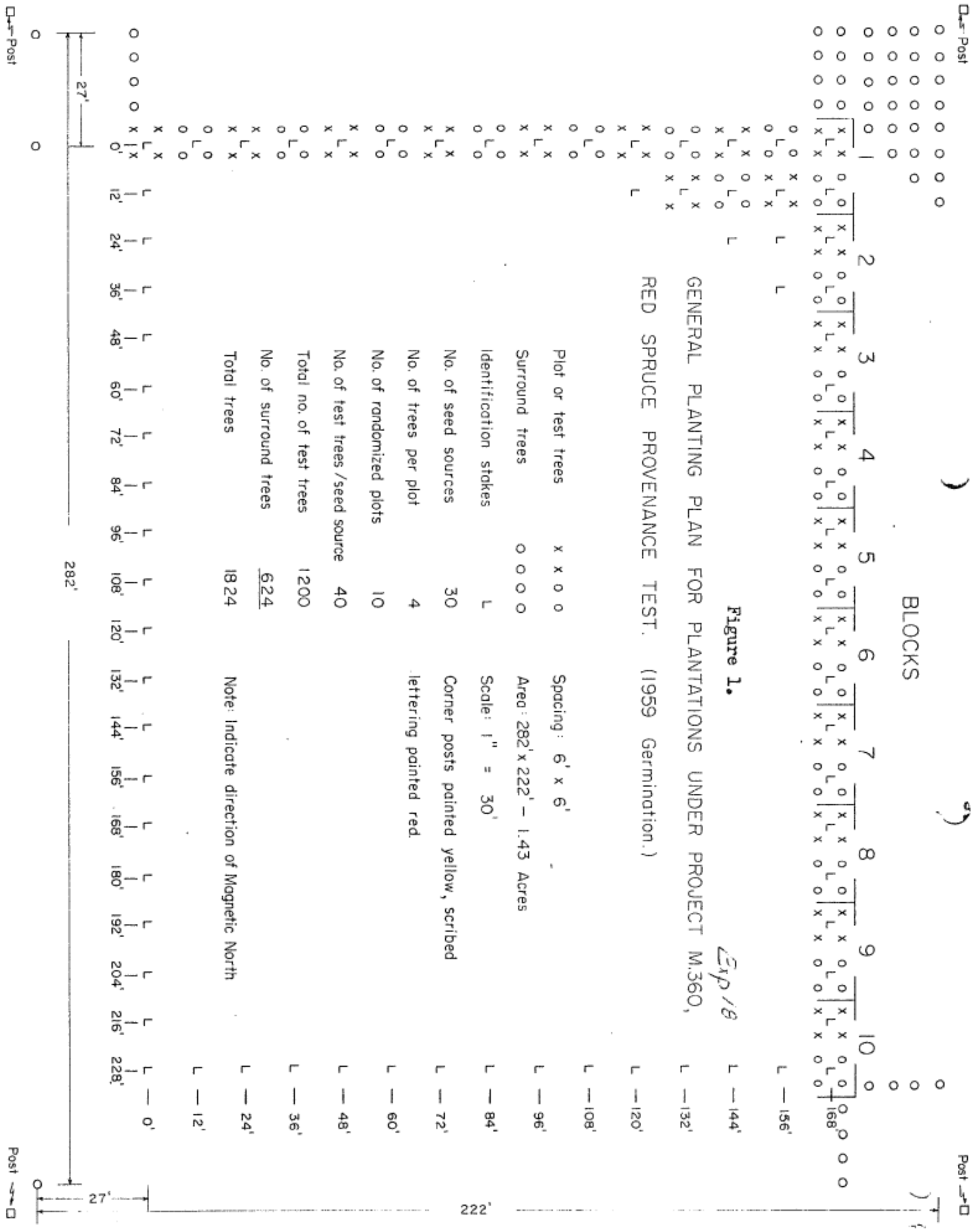

Figure A 2. Maritimes (series 18) red spruce plantation layout example for one trial. Thirty provenances were replicated in ten different blocks.

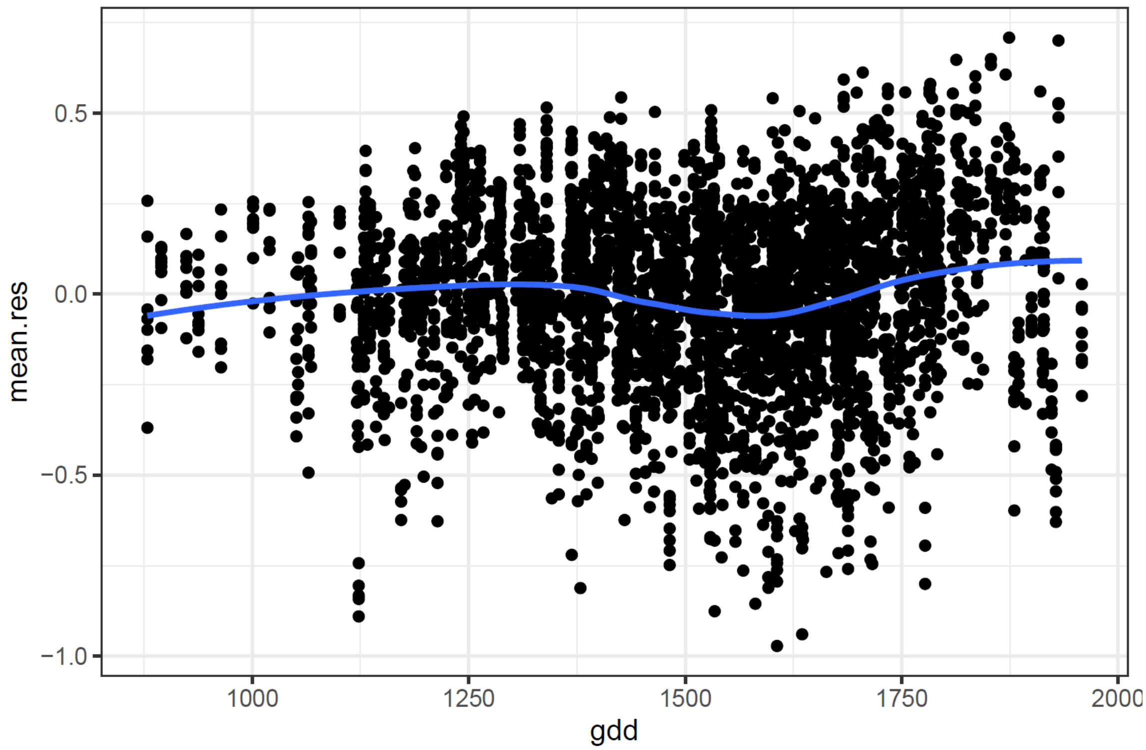

Figure A 3. Posterior mean response (log-transformed BAI) to Growing degree days.

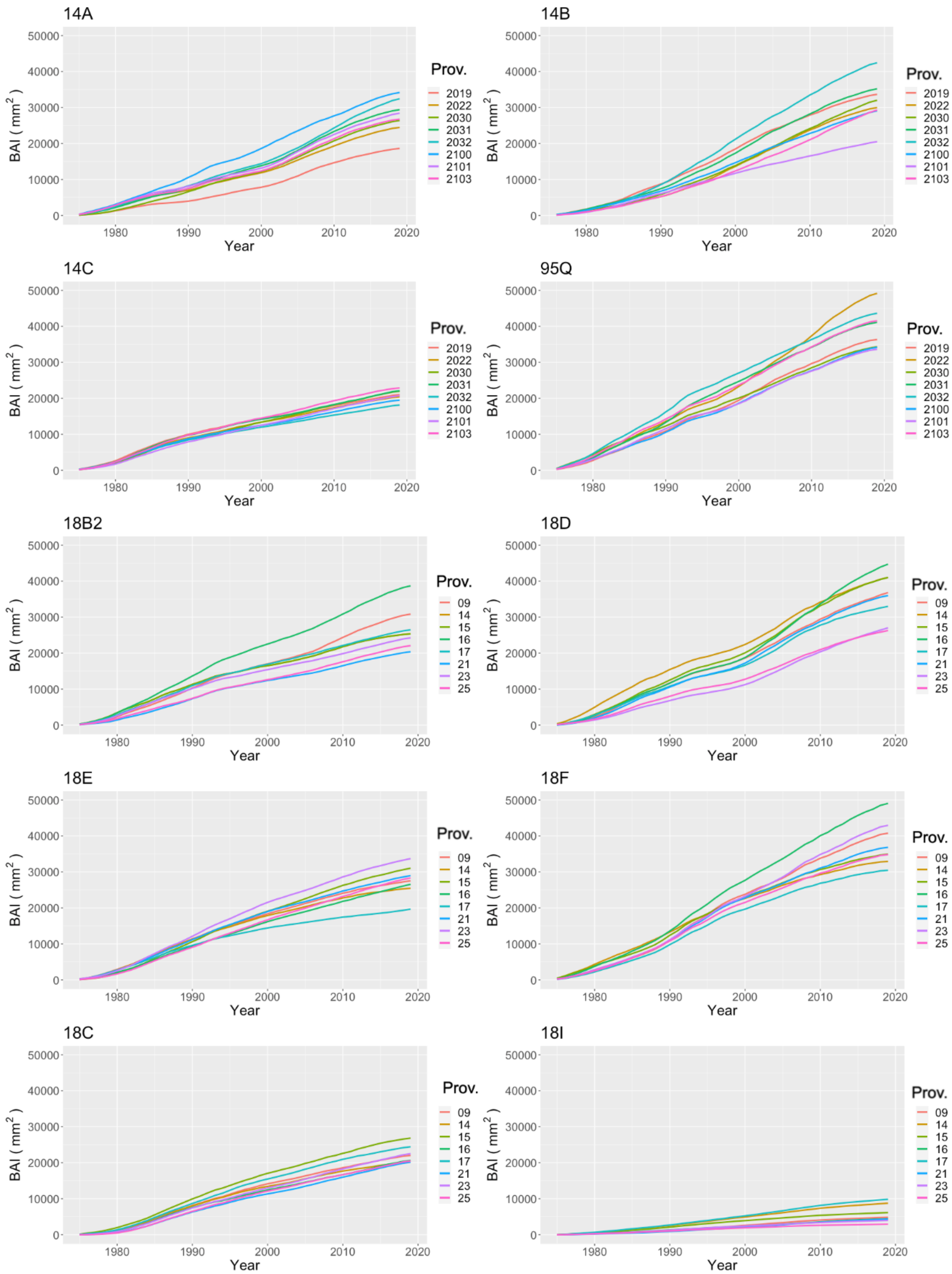
14A
BAI (mm2)
Year
Prov.
2019
2022
2030
2031
2032
2100
2101
2103
14B
14C
95Q
18B2
Prov.
09
14
15
16
17
21
23
25
18D
18E
18F
18C
18I
0
10000
20000
30000
40000
50000
1980
1990
2000
2010
2020

Figure A 4. Average cumulative basal area increment (BAI) per red spruce provenance (prov.) on each trial from 1965 to 2018.

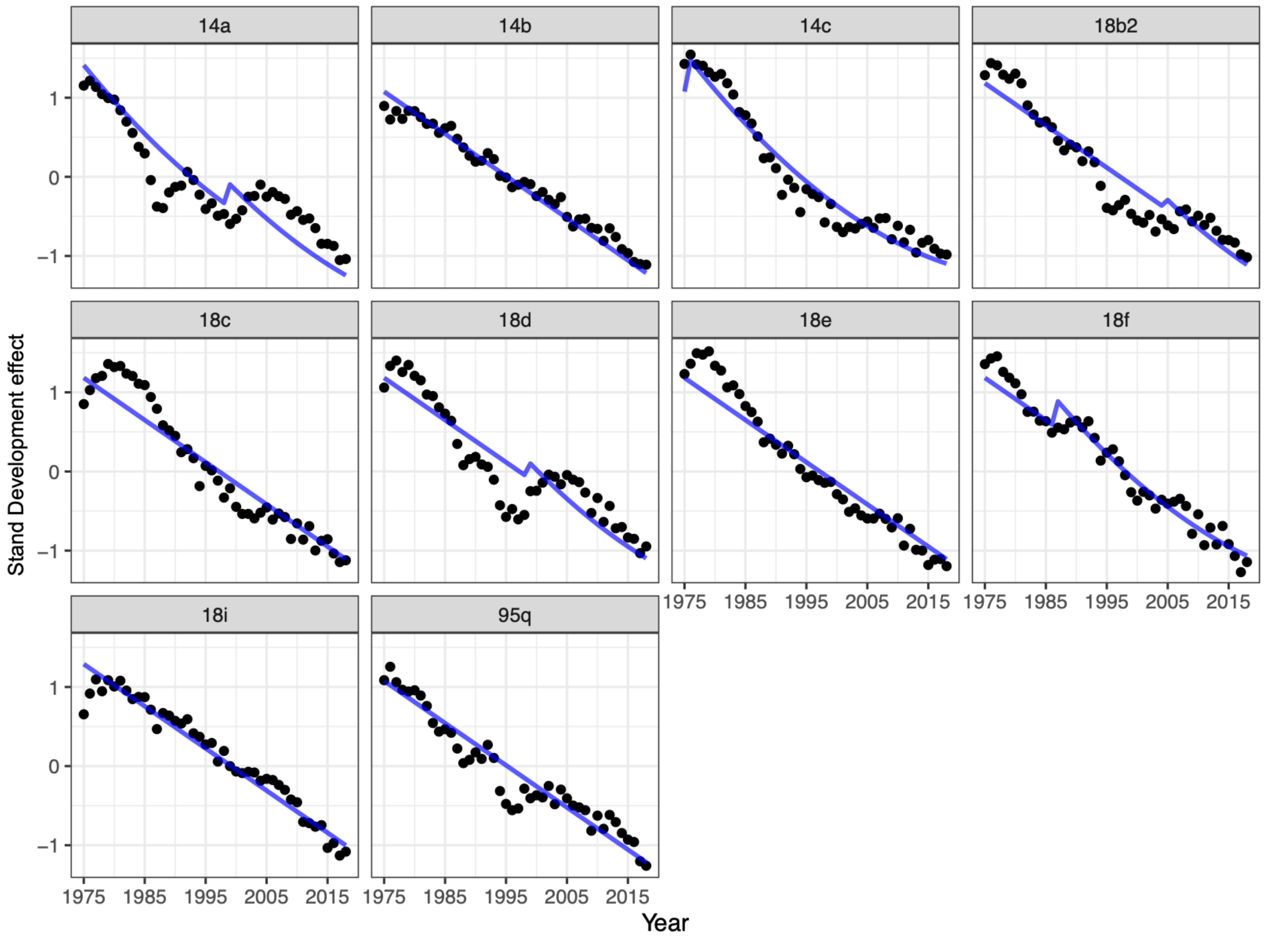

Figure A 5. Modeled stand development effect and time-varying stand effects (black) after removing the effects of fertility. All values are centered.

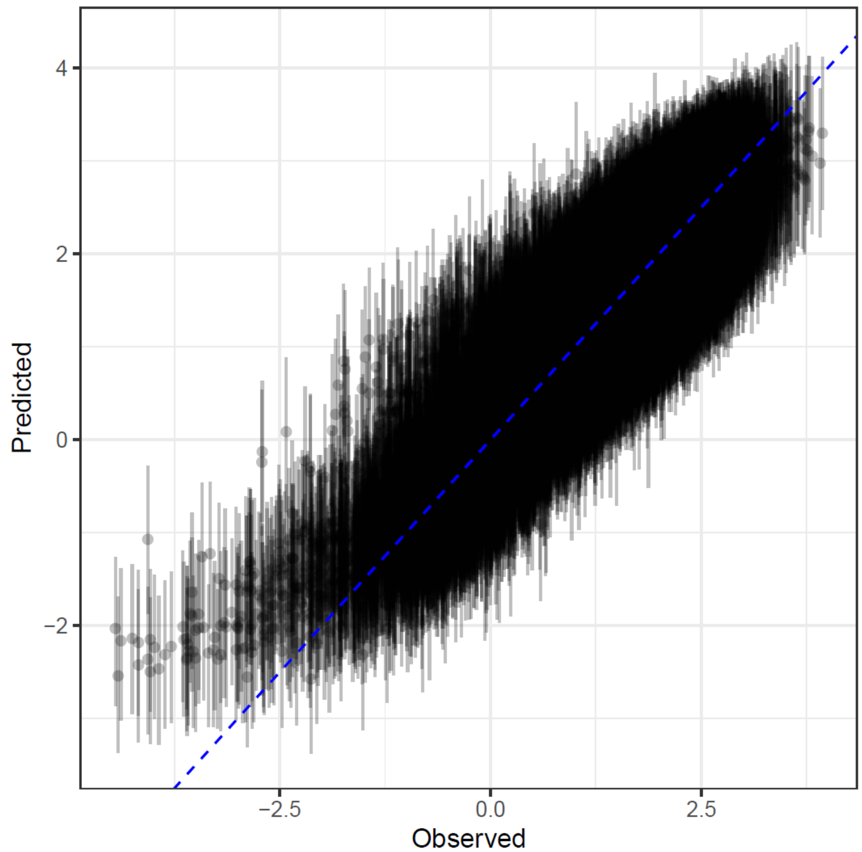

Figure A 6. Annual growth increment (log transformed) posterior mean predictions for the ~45 years of growth of red spruce. The lines represent the 95% credible intervals.

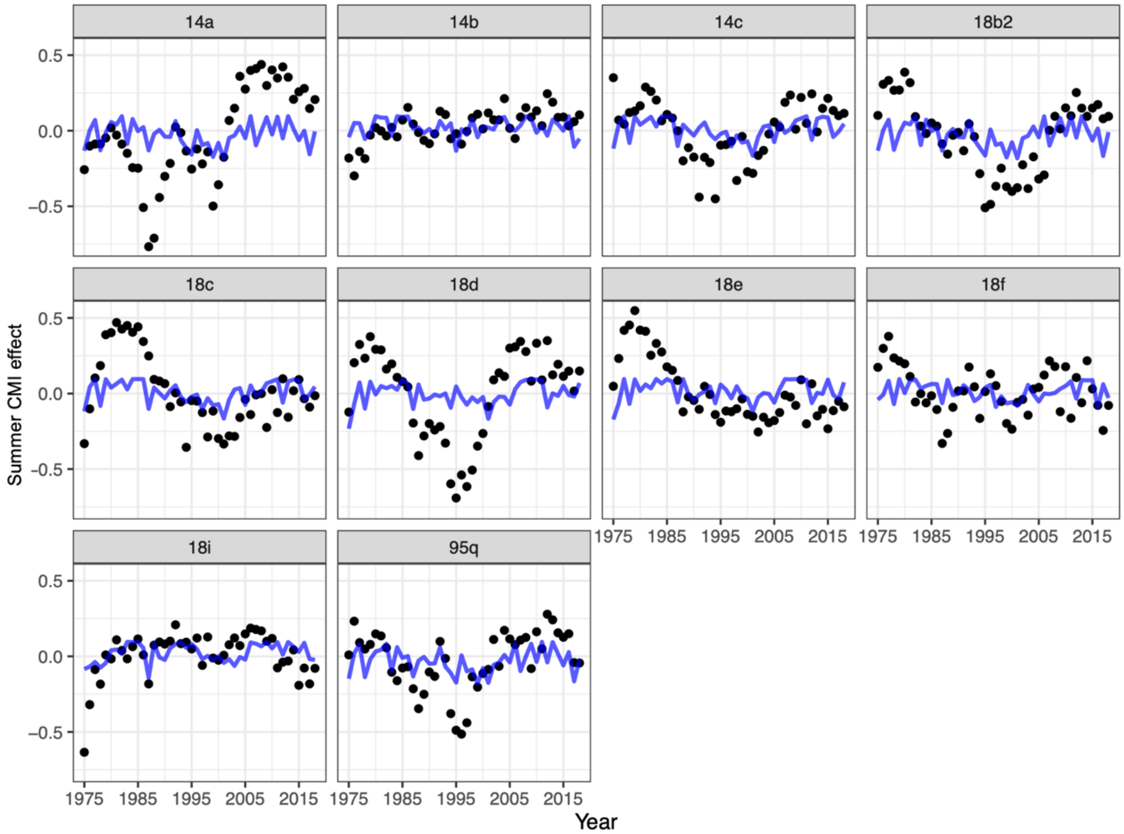

Figure A 7. Modeled summer Climate Moisture Index (CMI) effect and time-varying stand effects (black) after removing the effects of fertility and development. All values are centered.

Table A 1. Red spruce average DBH, Heights, and competition (within 3m radius) by provenance on each trial measured in 2020.

Trial	Prov ID	DBH (cm)	H (m)	Comp	Trial	Prov ID	DBH (cm)	H (m)	Comp
14A	2019	17.5 ±2.3	12.7 ±0.9	0.3 ±0.1	18C	9	18.8 ±3.4	12.4 ±1.2	0.9 ±0.4
	2022	20.9 ±3.9	14.7 ±0.9	0.4 ±0.4		14	17.9 ±4.9	11.5 ±1.6	0.9 ±0.8
	2030	20.4 ±3.9	15.1 ±1.2	0.4 ±0.4		15	19.8 ±4.0	12.5 ±1.1	0.9 ±0.6
	2031	21.7 ±3.8	14.7 ±0.8	0.2 ±0.1		16	18.5 ±1.6	12.4 ±1.3	1.5 ±1.1
	2032	23.7 ±2.6	15.1 ±1.2	0.1 ±0.1		17	20.0 ±3.6	12.5 ±1.2	0.9 ±1.0
	2100	21.7 ±3.3	14.6 ±1.0	0.3 ±0.3		21	17.8 ±3.8	11.1 ±1.3	0.9 ±0.6
	2101	21.9 ±3.7	14.4 ±1.0	0.4 ±0.4		23	18.7 ±3.5	12.1 ±1.5	0.8 ±0.4
	2103	21.8 ±3.6	14.6 ±0.4	0.1 ±0.1		25	18.0 ±2.4	12.2 ±0.7	0.8 ±0.3
	Avg	**21.2 ±3.4**	**14.5 ±0.9**	**0.3 ±0.2**		**Avg**	**18.7 ±3.4**	**12.1 ±1.2**	**1 ±0.7**
14B	2019	23.3 ±8.1	14.3 ±3.0	0.2 ±0.2	18D	9	24.2 ±3.2	17.0 ±3.6	0.2 ±0.2
	2022	22.9 ±5.4	13.9 ±3.5	0.1 ±0.1		14	24.2 ±4.9	16.8 ±1.4	0.3 ±0.3
	2030	21.8 ±3.9	15.0 ±2.3	0.2 ±0.2		15	25.4 ±3.2	17.1 ±1.0	0.2 ±0.1
	2031	22.2 ±7.6	14.2 ±3.2	0.1 ±0.1		16	27.0 ±4.1	18.0 ±1.3	0.1 ±0.1
	2032	24.9 ±6.8	14.7 ±2.8	0.2 ±0.2		17	22.6 ±3.7	16.2 ±1.1	0.3 ±0.2
	2100	21.9 ±7.9	14.6 ±3.2	0.2 ±0.2		21	24.6 ±4.1	16.3 ±1.2	0.2 ±0.1
	2101	18.8 ±2.5	14.0 ±1.2	0.2 ±0.2		23	22.2 ±3.4	16.6 ±1.3	0.3 ±0.2
	2103	22.1 ±4.4	14.2 ±2.0	0.1 ±0.1		25	20.8 ±5.3	15.7 ±1.8	0.3 ±0.3
	Avg	**22.3 ±5.8**	**14.4 ±2.7**	**0.2 ±0.2**		**Avg**	**23.9 ±4**	**16.7 ±1.6**	**0.2 ±0.2**
14C	2019	19.4 ±2.8	11.4 ±1.1	0.9 ±0.3	18E	9	21.7 ±4.6	15.2 ±1.5	0.4 ±0.3
	2022	17.5 ±3.8	11.0 ±1.6	0.8 ±0.3		14	20.6 ±4.2	15.5 ±1.3	0.5 ±0.5
	2030	19.7 ±3.3	11.4 ±1.5	0.8 ±0.4		15	23.2 ±5.6	15.3 ±2.1	0.3 ±0.3
	2031	18.9 ±3.0	11.4 ±0.9	0.6 ±0.3		16	21.2 ±4.1	15.6 ±1.2	0.5 ±0.6
	2032	17.7 ±2.7	12.1 ±0.8	1.1 ±0.6		17	18.5 ±5.6	14.3 ±2.1	0.7 ±0.6
	2100	18.0 ±3.1	11.6 ±1.5	1.0 ±0.5		21	21.3 ±4.3	15.1 ±1.0	0.4 ±0.3
	2101	19.0 ±1.6	12.0 ±0.6	0.7 ±0.3		23	24.0 ±3.2	16.0 ±0.6	0.4 ±0.4
	2103	19.0 ±3.0	12.0 ±1.0	0.8 ±0.5		25	21.5 ±5.2	15.0 ±1.7	0.2 ±0.2
	Avg	**18.7 ±2.9**	**11.6 ±1.1**	**0.8 ±0.4**		**Avg**	**21.5 ±4.6**	**15.2 ±1.4**	**0.4 ±0.4**
95Q	2019	25.2 ±5.9	16.4 ±1.4	0.1 ±0.1	18F	9	24.5 ±5.9	16.6 ±2.0	0.3 ±0.2
	2022	26.1 ±5.6	15.7 ±0.9	0.2 ±0.2		14	22.9 ±3.0	16.3 ±1.5	0.2 ±0.1
	2030	27.8 ±3.2	15.4 ±1.0	0.2 ±0.2		15	23.4 ±5.2	16.8 ±1.5	0.5 ±0.5
	2031	27.9 ±5.3	16.4 ±0.7	0.1 ±0.1		16	26.5 ±4.8	18.0 ±0.9	0.3 ±0.2
	2032	28.2 ±3.6	16.6 ±0.7	0.1 ±0.1		17	22.2 ±2.2	16.6 ±1.1	0.4 ±0.2
	2100	24.6 ±5.9	13.9 ±1.3	0.2 ±0.2		21	24.3 ±2.6	17.0 ±1.2	0.3 ±0.1
	2101	24.4 ±6.6	16.6 ±1.5	0.1 ±0.1		23	25.4 ±4.4	17.9 ±0.7	0.3 ±0.2
	2103	28.1 ±5.0	14.3 ±0.6	0.1 ±0.1		25	23.6 ±3.4	17.2 ±1.0	0.3 ±0.2
	Avg	**26.5 ±5.1**	**15.7 ±1**	**0.1 ±0.1**		**Avg**	**24.1 ±3.9**	**17.1 ±1.2**	**0.3 ±0.2**

Continued…

…Continuation

Trial	Prov ID	DBH (cm)	H (m)	Comp	Trial	Prov ID	DBH (cm)	H (m)	Comp
18B2	9	22.5 ±3.0	16.2 ±0.8	0.2 ±0.1	18I	9	9.3 ±2.2	4.6 ±1.4	0.9 ±0.6
	14	21.8 ±2.7	16.1 ±1.3	0.3 ±0.3		14	11.9 ±2.2	7.0 ±1.2	1.0 ±0.7
	15	21.8 ±3.1	16.6 ±1.5	0.3 ±0.2		15	10.3 ±2.3	5.0 ±0.7	1.0 ±0.5
	16	24.4 ±3.0	16.9 ±1.4	0.2 ±0.1		16	8.8 ±1.9	4.5 ±0.9	0.8 ±0.5
	17	21.0 ±2.9	16.4 ±1.4	0.3 ±0.1		17	11.7 ±3.7	6.4 ±1.9	0.7 ±0.5
	21	18.1 ±5.1	14.2 ±2.1	0.3 ±0.2		21	8.4 ±2.1	4.0 ±0.8	0.7 ±0.4
	23	21.1 ±3.4	15.6 ±0.9	0.3 ±0.3		23	8.7 ±1.8	3.9 ±0.8	0.6 ±0.5
	25	19.9 ±3.5	14.9 ±1.0	0.2 ±0.2		25	7.3 ±0.6	3.2 ±0.4	1.5 ±1.0
	Avg	**21.3 ±3.3**	**15.9 ±1.3**	**0.3 ±0.2**		**Avg**	**9.5 ±2.1**	**4.8 ±1**	**0.9 ±0.6**
95Q	2019	25.2 ±5.9	16.4 ±1.4	0.1 ±0.1	18F	9	24.5 ±5.9	16.6 ±2.0	0.3 ±0.2
	2022	26.1 ±5.6	15.7 ±0.9	0.2 ±0.2		14	22.9 ±3.0	16.3 ±1.5	0.2 ±0.1
	2030	27.8 ±3.2	15.4 ±1.0	0.2 ±0.2		15	23.4 ±5.2	16.8 ±1.5	0.5 ±0.5
	2031	27.9 ±5.3	16.4 ±0.7	0.1 ±0.1		16	26.5 ±4.8	18.0 ±0.9	0.3 ±0.2
	2032	28.2 ±3.6	16.6 ±0.7	0.1 ±0.1		17	22.2 ±2.2	16.6 ±1.1	0.4 ±0.2
	2100	24.6 ±5.9	13.9 ±1.3	0.2 ±0.2		21	24.3 ±2.6	17.0 ±1.2	0.3 ±0.1
	2101	24.4 ±6.6	16.6 ±1.5	0.1 ±0.1		23	25.4 ±4.4	17.9 ±0.7	0.3 ±0.2
	2103	28.1 ±5.0	14.3 ±0.6	0.1 ±0.1		25	23.6 ±3.4	17.2 ±1.0	0.3 ±0.2
	Avg	**26.5 ±5.1**	**15.7 ±1**	**0.1 ±0.1**		**Avg**	**24.1 ±3.9**	**17.1 ±1.2**	**0.3 ±0.2**

Appendix B – Supplementary methods

2.6.5.1. Model implementation

The tree growth model is completed by assigning prior distributions to all remaining unknown model parameters. The tree- and stand-level regression coefficients ($\boldsymbol{\beta}$, $\boldsymbol{\gamma}$) were assigned independent, diffuse normal priors: $N(0,1\text{E}03)$. Block and stand variance terms (τ^2_{block}, σ^2_{stand}) are assigned half-Cauchy distributions with scale 2.5 as suggested in Gelman 2006. The residual standard deviation (σ) is assigned an improper uniform prior: $\sigma \propto 1$. We applied a hierarchical prior to the provenance-specific basis function coefficients: $\boldsymbol{\eta}_k \sim N(\boldsymbol{\mu}_\eta, \tau^2_p \mathbf{I}_q)$. Here $\boldsymbol{\mu}_\eta$ is a q-dimensional vector representing the mean basis function coefficient value among red spruce provenances, τ^2_p is a scalar variance term representing provenance-specific variation around the mean basis function coefficient values, and $\mathbf{I}_q$ is a q-dimensional identity matrix (given q total basis functions). The mean basis function coefficients ($\boldsymbol{\mu}_\eta$) are assigned a multivariate normal prior: $\boldsymbol{\mu}_\eta \sim N(\mathbf{0}, \tau^2_\eta \mathbf{S}^{-1})$. Here τ^2_η is a scalar variance representing among basis function coefficient variability and $\mathbf{S}$ is a q-dimensional penalty matrix defined for the q basis functions (Wood 2017). The flexibility of the provenance-specific responses to CMI is controlled by the two variance parameters (τ^2_η, τ^2_p) with τ^2_η describing the variability among basis function coefficients and τ^2_p describing variability among provenances. Prior elicitation for these parameters is a known challenge given that resulting model complexity is highly-sensitive to the choice of prior (Simpson et al., 2017). In previous work, we have applied optimization based on out-of-sample prediction to determine variance parameter values and regularize the basis function coefficients (Itter et al., 2017). In the current analysis, we apply a combination of penalized complexity priors for the two variance parameters allowing for fully model-based estimates of CMI response (Simpson et al., 2017, Ventrucci & Rue 2016). Specifically, we assign the precision of the among-provenance variance, $\omega = \frac{1}{\tau_p^2}$, the following penalized complexity prior:

$$\frac{\theta_p}{2}\omega^{-3/2}\exp\left(\frac{-\theta_p}{\sqrt{\omega}}\right)$$

given $\theta_p = -\frac{\log(\alpha)}{U_\omega}$ where U_ω is the upper bound of the standard deviation among-provenances (τ_p) and α is the probability that the standard deviation exceeds the upper bound (as defined in Simpson et al., 2017). We assign a modified penalized complexity prior to the precision of the mean basis function coefficients ($\rho = \frac{1}{\tau_\eta^2}$) with an upper bound ($U_\rho$) defined on the number of effective degrees of freedom for the basis function expansion in CMI, $d(\rho) = \sum_{\ell=1}^{q} \frac{1}{1+\sigma^2\rho v_\ell}$ where v_ℓ ($\ell = 1, \ldots, q$) are the eigenvalues of $\mathbf{S}(\mathbf{B}'\mathbf{B})^{-1}$ where $\mathbf{B}$ is a matrix with dimension number of stand-years by q (as defined in Ventrucci & Rue 2016). This results in a prior for ρ following the same form as the penalized complexity prior above, but with ρ and θ_η replacing ω and θ_p, respectively. Under the modified penalized complexity prior $\theta_\eta = -\log(\alpha)\sqrt{d^{-1}(U_\rho)}$ (see Ventrucci & Rue 2016 for details). We set $\alpha = 0.01$ for both ω and ρ, $U_\omega = 0.1$, and $U_\rho = 3$. A simplified version of the model drops the provenance-specific responses to CMI and applies the penalized complexity prior defined for ρ to estimate a single set of basis function coefficients as: $\boldsymbol{\mu}_\eta \sim N\left(\mathbf{0}, \tau_\eta^2\mathbf{S}^{-1}\right)$.

2.7.5.2. Variation Partitioning

Bayesian R-squared values for both individual tree growth and stand-by-year effects were calculated (as defined in Gelman et al., 2019) as follows:

Tree-level: $\frac{V_{i=1}^{n}\hat{y}_i^{(s)}}{V_{i=1}^{n}\hat{y}_i^{s}+\sigma^{2(s)}}$ where $\hat{y}_i^{(s)} = w_{jkt}^{(s)} + c_i\beta_1^{(s)} + f\left(d_{it}; \beta_2^{(s)}, \beta_3^{(s)}\right) + u_{jb}^{(s)}$

Stand-level: $\frac{V_{j=1,k=1,t=1}^{m.K,T}\hat{w}_{jkt}^{(s)}}{V_{j=1,t=1}^{m.T}\hat{w}_{jkt}^{(s)}+\tau_{\text{stand}}^{2(s)}}$ where $\hat{w}_{jkt}^{(s)} = \boldsymbol{h}'_{jt}\boldsymbol{\gamma}^{(s)} + \boldsymbol{b}'_{jt}\boldsymbol{\eta}_k^{(s)}$

where $V_{i=1}^{N}x_i = \frac{1}{N-1}\sum_{i=1}^{N}(x_i - \bar{x})^2$, the variance among the N observations, s indexes the posterior sample, and n, m, K, T denote the total number of tree growth, stand, provenance, and year observations, respectively. Note that by calculating tree- and stand-level R-squared values as above, we obtain posterior samples of these statistics and thus have an estimate of their posterior distribution.

Variance partitioning is carried out applying the diagonal variance partitioning approach defined in Schulz et al., 2021. Specifically, variance partitioning is carried out at the tree scale by calculating the variance of each model component:

$$V_{\text{stand}}^{(s)} = V_{j=1,k=1,t=1}^{m.K,T}w_{jkt}^{(s)}$$

$$V_{\text{comp}}^{(s)} = V_{i=1}^{n}c_i\beta_1^{(s)}$$

$$V_{\text{size}}^{(s)} = V_{i=1}^{n} f\left(d_{it}; \beta_2^{(s)}, \beta_3^{(s)}\right)$$

$$V_{\text{block}}^{(s)} = V_{i=1}^{n} u_{jb}.$$

Then, defining $V_{\text{total}}^{(s)}(\text{tree}) = V_{\text{stand}}^{(s)} + V_{\text{comp}}^{(s)} + V_{\text{size}}^{(s)} + V_{\text{block}}^{(s)}$, the proportion of variance explained by each model component is given by the ratio of that component's variance relative to the total variance. For example, the proportion of variance explained by competition is given by: $\frac{V_{\text{comp}}^{(s)}}{V_{\text{total}}^{(s)}(\text{tree})}$.

Variance partitioning is carried out at the stand scale in a similar fashion, but now the individual variance components include soil capacity moisture effects, stand development, and CMI effects:

$V_{\text{fert}}^{(s)} = V_{j=1,k=1,t=1}^{m,K,T} h_{jt}[1]\gamma_1^{(s)}$ where $h_{jt}[1]$ is the first component of $\boldsymbol{h}_{jt}$

$V_{\text{development}}^{(s)} = V_{j=1,k=1,t=1}^{m,K,T} \boldsymbol{h}_{jt}[2:4]\boldsymbol{\gamma}_{2:4}^{(s)}$ where $2:4$ indexes the second through the fourth elements of a vector $V_{\text{CMI}}^{(s)} = V_{j=1,k=1,t=1}^{m,K,T} \boldsymbol{b}'_{jt}\boldsymbol{\eta}_k$.

2.8.5.3. Reference

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Conference Presentations: None