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Response of Northern Populations of Black Spruce and Jack Pine to Southward Seed Transfers: Implications for Climate Change

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Abstract: A variety of responses to climate change have been reported for northern tree populations, primarily from tree-ring and satellite-based studies. Here we employ provenance data to examine growth and survival responses of northern populations (defined here as those occurring north of 52° N) of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) to southward seed transfers. This space for time substitution affords insights into potential climate change responses by these important northern tree species. Based on previous work, we anticipated relatively flat response curves that peak at much warmer temperatures than those found at seed source origin. These expectations were generally met for growth-related responses, with peak growth associated with seed transfers to environments with mean annual temperatures 2.2 and 3.6 °C warmer than seed source origin for black spruce and jack pine, respectively. These findings imply that northern tree populations harbor a significant amount of resilience to climate warming. However, survival responses told a different story, with both species exhibiting reduced survival rates when moved to warmer and drier environments. Together with the growth-based results, these findings suggest that the warmer and drier conditions expected across much of northern Canada under climate change may reduce survival, but surviving trees may grow at a faster rate up until a certain magnitude of climate warming has been reached. We note that all relationships had high levels of unexplained variation, underlining the many factors that may influence provenance study outcomes and the challenges in predicting tree responses to climate change. Despite certain limitations, we feel that the provenance data employed here provide valuable insights into potential climate change outcomes for northern tree populations.

Keywords: provenance data; climate change; northern tree populations; black spruce; jack pine; growth; survival

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1. Introduction

High latitude regions have experienced significant climate change over the past century [1]. In the Canadian Arctic region, mean annual temperature and total annual precipitation have increased by 2–3 °C and 20–50% respectively since 1948 [2]. This region is also projected to experience significant climate changes in the coming decades, including increases in mean annual temperature and annual precipitation of 2–8 °C and 10–30%, respectively [3]. Accompanying these projected changes in average conditions are changes in climate extremes, including more hot days, fewer freezing days, and more frequent heavy precipitation events [3].

Given these dire projections, numerous studies have examined plant growth and survival in relation to climate change in far northern regions. Several field- and satellite-based studies have documented a northward expansion of the Arctic tree line [4,5]. Further, climate envelope studies have projected significant northward shifts for arctic ecosystems [6]. For trees, studies of growth-ring data from northern sites have reported a range of responses to climate change that vary by region and species, with growth declines consistently reported from dry, drought-prone locations [7–9]. Studies using remotely-sensed growth index data have also reported climate change responses that vary by region and tree species [10–12].

Provenance studies represent another important source of information for elucidating tree responses to climate change [13–17]. Typically, these studies involve the measurement of growth and survival over time of various seed sources (provenances) planted at multiple test sites (common gardens) across the range of a species (see [18] for further details). Although not necessarily established with climate change research in mind, these studies allow insights into how tree populations may respond to climate change through spatial transfers that mimic a range of potential future climates. One advantage of data from provenance studies is that, if well designed, a wide range of climate conditions can be sampled across provenances and test sites, allowing insights into the limits of climatic controls on plant growth and survival. Although many studies have employed provenance data to study climate change impacts, we are not aware of any that have focused on responses of northern seed sources.

Pedlar and McKenney [19] examined the relationship between height growth and climatic transfer distance using provenance data for several boreal species, including black spruce and jack pine. They reported that southern seed sources tended to exhibit greater growth potential than more northerly seed sources—a finding widely reported in other provenance studies [14,15,20,21]. Further, they found that more northerly seed sources were generally growing at significantly cooler temperatures than optimal and thus benefitted from southward transfers. Based on these findings, we expect northern seed sources to exhibit relatively flat response curves that peak at warmer temperatures than those found at seed source origin. This pattern implies a significant amount of resilience to climatic warming by these northern populations. These expectations are illustrated for three hypothetical populations in Figure 1, which is adapted from Figures 2 and 3 in [19]. Expected responses by tree populations to other climate variables (e.g., precipitation) are less clear, although several other studies have reported growth declines from northern forests in relation to hot, dry conditions [7,8].

Here we employ provenance data to elucidate the potential response of northern populations of black spruce and jack pine to climate change. We also present responses for central and southern populations as points of comparison with these northern sources. As detailed above, we hypothesize that northern provenances will exhibit significant resilience to climate warming, though implications concerning other climate phenomena (such as precipitation and drought) are less clear. This work aims to contribute to the growing knowledge base concerning the expected response of northern tree populations to climate change.

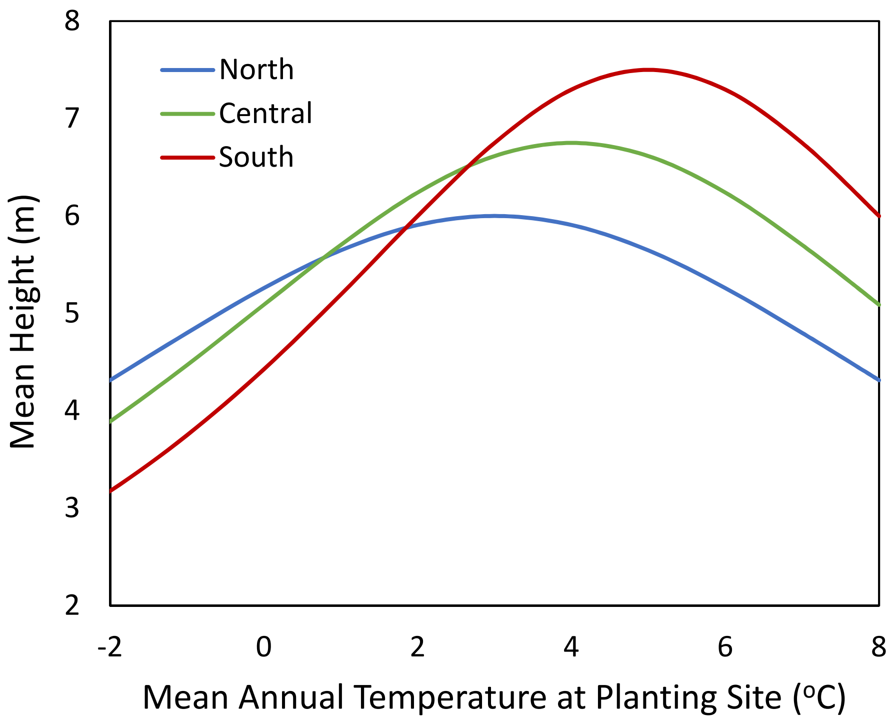


Figure 1. Expected height growth response of northern, central, and southern seed sources along a gradient of mean annual temperature (modified from Pedlar and McKenney [19]).

2. Materials and Methods

2.1. Provenance Study Data

For this effort, we define northern seed sources as populations that originate north of 52° N. We also present responses for central (located between 46 and 52° N) and southern (located at <46° N) populations as points of comparison with these northern sources.

We explored various cut-offs between 50 and 55° N for defining northern populations and found little qualitative difference in study outcomes; however, cut-offs north of 55° N resulted in prohibitively low sample sizes in the northern group.

Black spruce provenance data were obtained from measurements on a portion of the Canadian Forest Service's (CFS) long-term black spruce provenance trial, which originally incorporated 202 seed sources across 34 test sites in Canada and the United States (see [22] for details). Measurements of height and diameter of all surviving trees at each test site were made in 2003, at 33 years of age from seed (see [16] for details). In total, 192 seed sources at 18 test sites in Canada and one test site in Minnesota were included in the measurement. Based on a cut-off of 52° N, 30 of these seed sources qualified as originating from the north (Table S1, Figure 2a). These northern seed sources were planted, in various combinations, at 17 different test sites—many of which were located south of 52° N (Figure 2a).

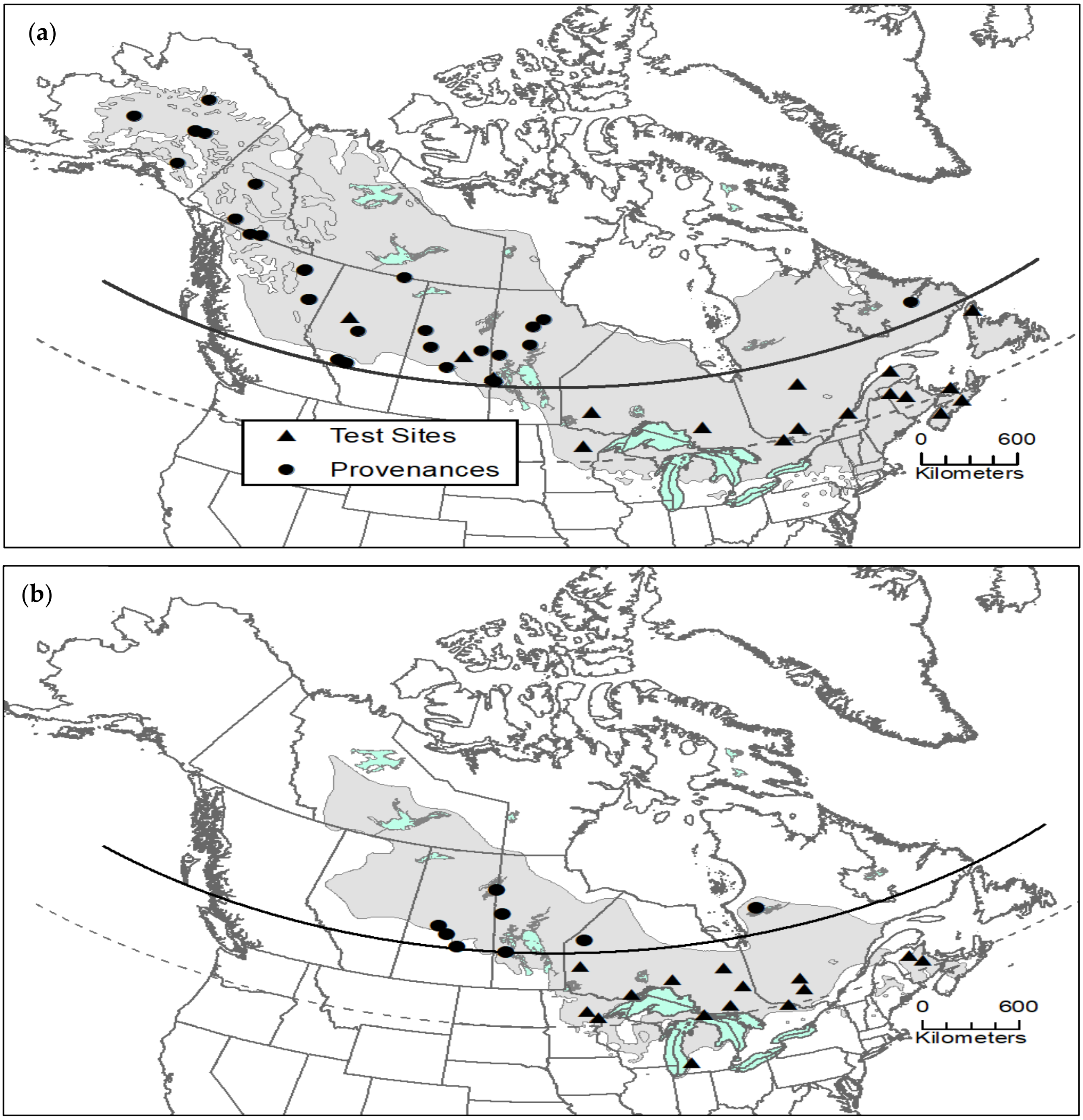


Figure 2. Locations of northern provenances (circles) and the test sites (triangles) where they were planted as part of rangewide provenance studies for (**a**) black spruce and (**b**) jack pine. The solid black line indicates 52° N, the cut-off used in the current study to define northern provenances; the dashed gray line indicates 46° N, the cut-off between central and southern seed sources. Gray shading indicates the geographic range of the species and blue shading delineates large water bodies.

Jack pine provenance data were obtained from measurements on a portion of the CFS 255 series rangewide provenance trial, which consisted of 99 seed sources planted in various combinations at test sites across eastern Canada, the United States, and Europe (see [23] for details). During the summer of 2005, at 39 years of age from seed, all 16 remaining viable test sites in Canada and the United States were remeasured (see [24] for details). Due to concerns regarding potential hybridization with lodgepole pine in the western portion of the jack pine range [25], all seed sources west of 110° W were removed from the dataset. Based on a cut-off of 52° N, eight of the remaining seed sources qualified as originating from the north (Table S2, Figure 2b). These northern seed sources were planted, in various combinations, at 15 different test sites—most of which were south of 52° N (Figure 2b).

2.2. Climate Data

We obtained historical climate estimates by interrogating spatial climate models at the location of each seed source and planting site. The climate models used here are described in McKenney et al. [26]. For seed source locations, where climate values should reflect historical conditions, we employed data for the 1961–1990 period. This period was selected because it precedes recent rapid increases associated with climate change [3] and coincides with peak weather station coverage in Canada [27]. For test sites, annual climate values were averaged over the period spanning plantation establishment to measurement, thus reflecting the climate experienced by the growing plantation.

Four climate variables were selected for modelling the relationship between tree growth/survival and climate: mean annual temperature (MAT, °C), annual precipitation (ANNP, mm), climate moisture index (CMI, cm; a measure of annual moisture balance calculated as precipitation minus potential evapotranspiration—see [28] for details), and growing season length (GSL, days). These variables were chosen because they summarize gradients in moisture and temperature and have been used in previous provenance studies [14,15,29–31].

2.3. Statistical Analyses

The use of response functions, in which seed source performance (e.g., height, survival) is modeled as a function of climate at test sites where the seed source was planted, is a well-established approach for analyzing provenance data [13,15,16,19,24]. In the current study, the limited number of test sites at which each provenance was planted (i.e., $n \leq 15$, Tables S1 and S2), necessitated the pooling of data across the northern seed sources for each species. Prior to pooling the data, we confirmed that, for all seed sources with more than 10 data points, growth patterns in relation to climate were similar among seed sources and to the grouped response (Figure S1). Several previous studies have pooled data across test sites and seed sources to elucidate patterns of growth in relation to climate [30,32].

We employed quadratic regression analyses to model the relationship between measured performance at each test site and the climatic distance that seed sources were transferred:

$$P_{ij} = \beta_0 + \beta_1 \Delta X + \beta_2 \Delta X^2 \quad (1)$$

where P_{ij} is the performance (height or survival) of seed source i at test site j, ΔX is the climatic distance between seed source i and test site j (calculated as test site climate minus seed source climate), and the β's are the fitted parameters. All terms in the model were considered fixed effects.

Assessment of regression residuals identified a suspect data point from the black spruce dataset that had a Cook's Distance value of 1.17 (nearly 40 times larger than the average distance value); this data point was removed from further analyses. Although the focus here is on northern seed sources at latitudes >52° N, we also generated pooled response functions for central and southern seed sources for comparative purposes. All analyses were carried out using R [33].

3. Results

3.1. Black Spruce

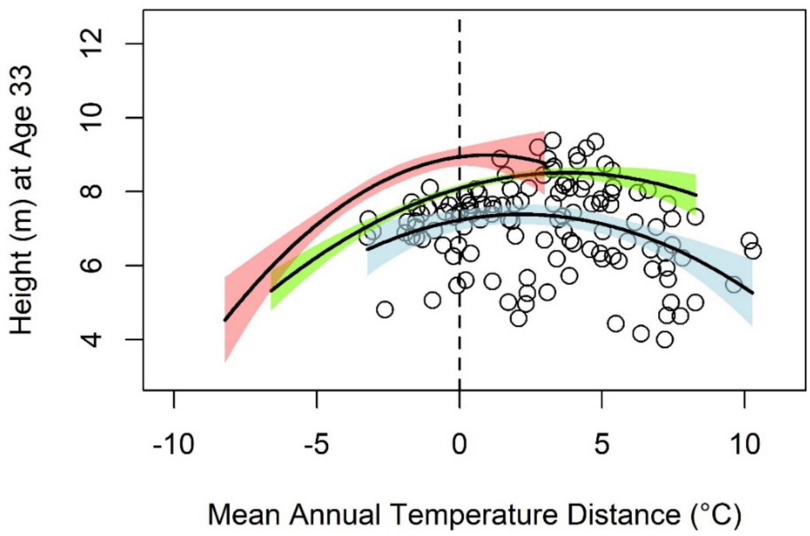
The quadratic regression model describing black spruce height growth as a function of MAT transfer distance for northern seed sources was statistically significant, although noisy, with 12% of variation explained by the model (Table 1, Figure 3a). Regression results for central and southern seed sources are presented in Table S3. The growth response by northern provenances to MAT transfer distance generally followed our expectations, with a shallow downward-facing parabolic shape, optimal growth associated with transfers to warmer environments, and lower growth potential than both central and southern seed sources. Taking the first derivative of the equation in Table 1 and solving for MAT indicated that optimal growth was associated with seed transfers to environments that were 2.2 °C warmer than seed source origin. Application of the quadratic formula revealed that height growth equal to or greater than that expected at the local planting site was associated with transfers up to 4.4 °C warmer than seed source origin.

Table 1. Parameters from quadratic regression models between climate transfer distance and height/survival of northern seed sources used in rangewide provenance trials for black spruce and jack pine. Asterisks indicate level of statistical significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Species	Climate Variable	Response Variable	N	Intercept (β_0)	Slope 1 (β_1)	Slope 2 (β_2)	R-Squared
Black Spruce	Mean Annual Temperature	Height	125	7.230	0.1418 *	−0.0325 ***	0.12
		Survival	125	74.777	−2.5179 *	−0.0702	0.21
	Climate Moisture Index	Height	125	7.075	−0.0061	0.00007	0.01
		Survival	125	70.618	0.0620	−0.0036 **	0.11
Jack Pine	Mean Annual Temperature	Height	86	13.327	0.5538 *	−0.0778 ***	0.17
		Survival	93	40.413	−4.0798 **	0.1473	0.19
	Climate Moisture Index	Height	86	14.196	0.0046	−0.0005	0.06
		Survival	93	21.809	0.5038 **	−0.0051 *	0.11

The regression model relating survival of black spruce northern seed sources to MAT transfer distance was significant (but only the linear term) and explained 21% of the variation in the data (Table 1 and Figure 3b). Survival response to MAT transfer distance differed markedly from the growth-based responses described above (Figure 3a). In this case, all seed transfers to warmer planting sites were associated with reduced survival rates. For example, predicted survival rates dropped from approximately 75% at local planting sites to approximately 60% at planting sites that were 5 °C warmer than local. Survival response curves differed for southern and central seed sources, with an essentially flat relationship for central sources and a nearly linear decline associated with northward transfers for southern seed sources (Figure 3b and Table S3).

The regression model relating CMI transfer distance to height growth of northern seed sources was not statistically significant, whereas that relating CMI transfer distance to survival was marginally significant with a low percentage of explained variation (Table 1, Figure 4). Note that most transfers were to wetter planting sites (i.e., to the right of the dashed lines in Figure 4a,b), reflecting the limited precipitation in much of northern Canada. These relationships were also weak for central and southern seed sources, despite seed transfers to both wetter and dryer planting sites (Figure 4 and Table S3)—indicating that adaptive variation between black spruce populations may not be well expressed along gradients of climatic dryness.



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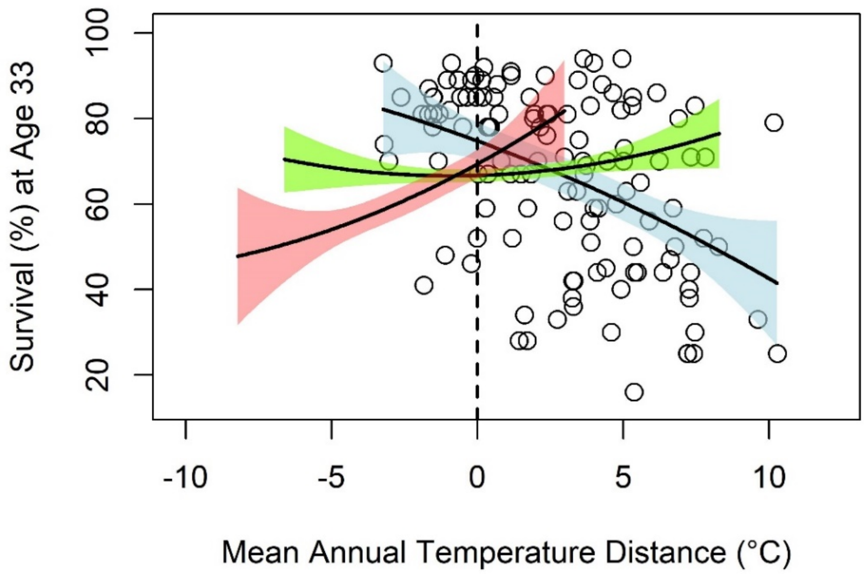
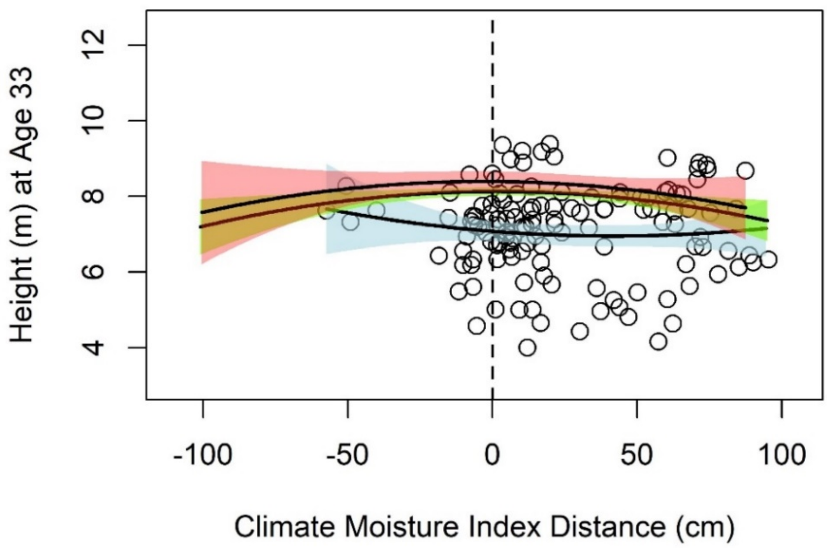


(**b**)

Figure 3. Relationship between mean annual temperature and (**a**) height and (**b**) survival of black spruce seed sources at 33 years of age. Separate regression lines and 95% confidence intervals are shown for southern (red), central (green), and northern (blue) seed sources. Data points (black circles) are shown only for northern seed sources. The vertical dashed line indicates local deployment of seed sources (i.e., a transfer distance of zero); points to the right of this line indicate seed transfers to warmer planting sites and vice versa.



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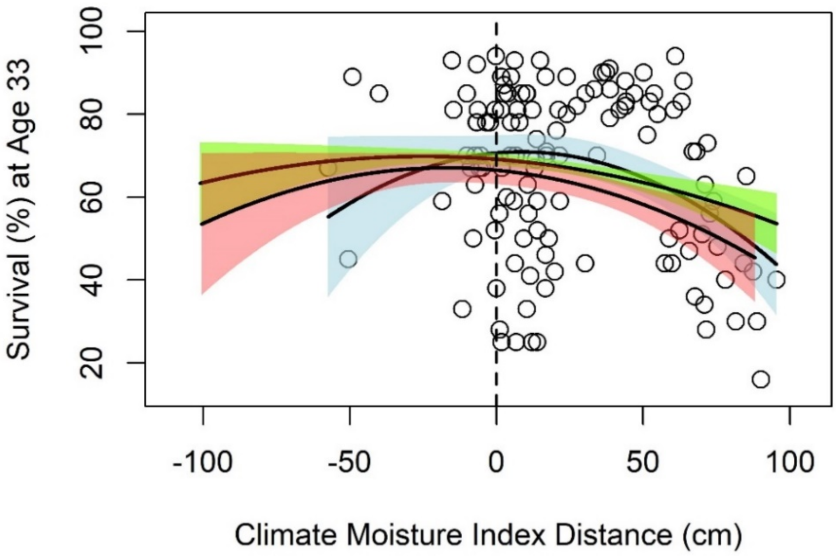

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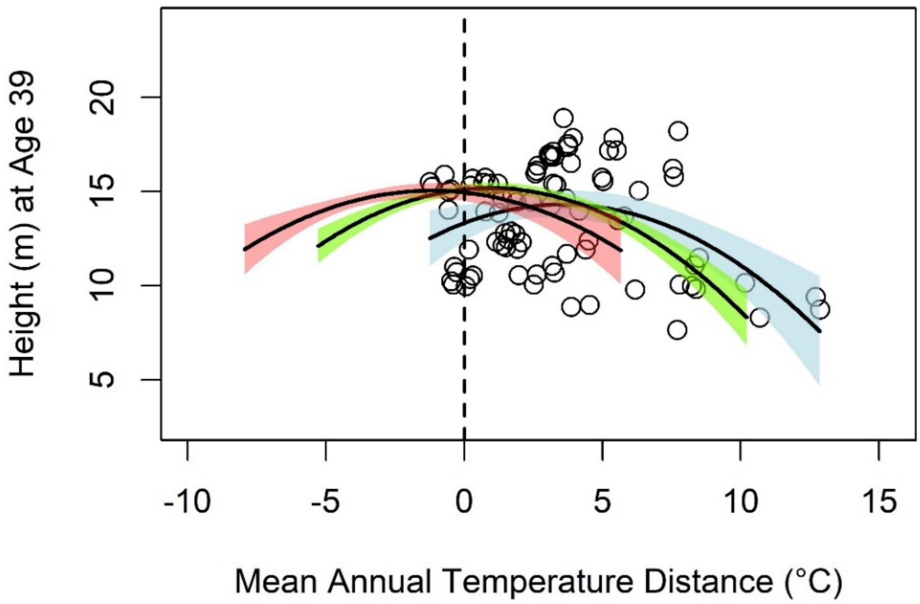
Figure 4. Relationship between climate moisture index transfer distance and (**a**) height and (**b**) survival of black spruce seed sources at 33 years of age. Separate regression lines and 95% confidence intervals are shown for southern (red), central (green), and northern (blue) seed sources. Data points (black circles) are shown only for northern seed sources. The vertical dashed line indicates local deployment of seed sources (i.e., a transfer distance of zero); points to the right of this line indicate seed transfers to wetter planting sites and vice versa.

Regression results for GSL were similar to those presented above for MAT and the two variables exhibited a Pearson correlation (r) of 0.95 across study sites. Similarly, ANNP and CMI exhibited similar regression outcomes and were highly correlated across the study area (r = 0.96). Consequently, results for ANNP and GSL are provided in the Supplementary Material (Table S3, Figures S2 and S3).

3.2. *Jack Pine*

The quadratic regression model of jack pine height as a function of MAT transfer distance for northern seed sources was statistically significant and explained 17% of the variation in the data (Table 1, Figure 5a). As expected, this growth response function had a shallow downward-facing parabolic shape and slightly lower growth potential than both central and southern seed sources. Optimal growth was associated with transfers to environments that were 3.6 °C warmer than seed source origin, and height growth equal to or greater than that expected at the local planting site was associated with transfers up to 7.1 °C warmer than seed source origin. Seed sources from central and southern portions of jack pine range also exhibited growth responses that were consistent with expectations (Figure 5a, Table S4).



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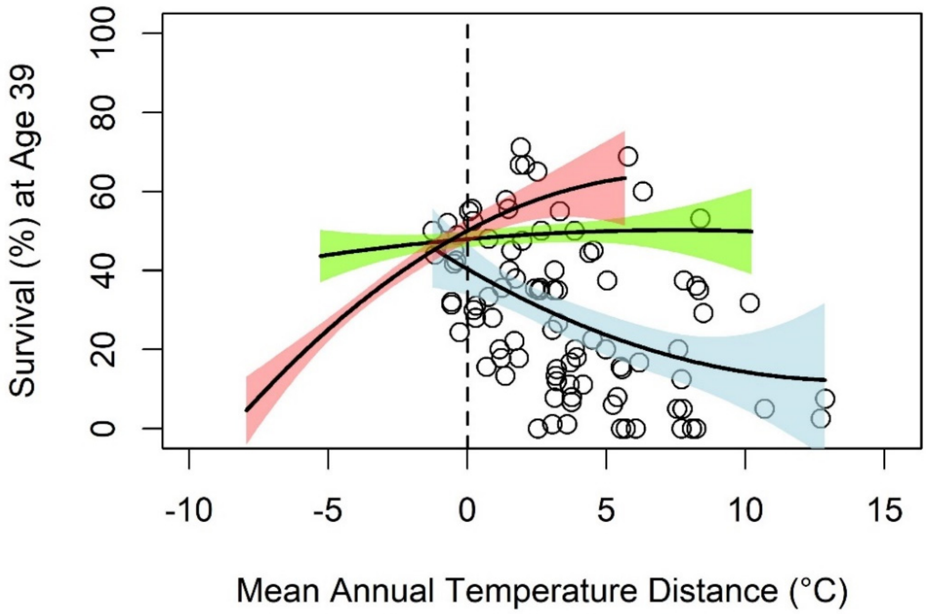
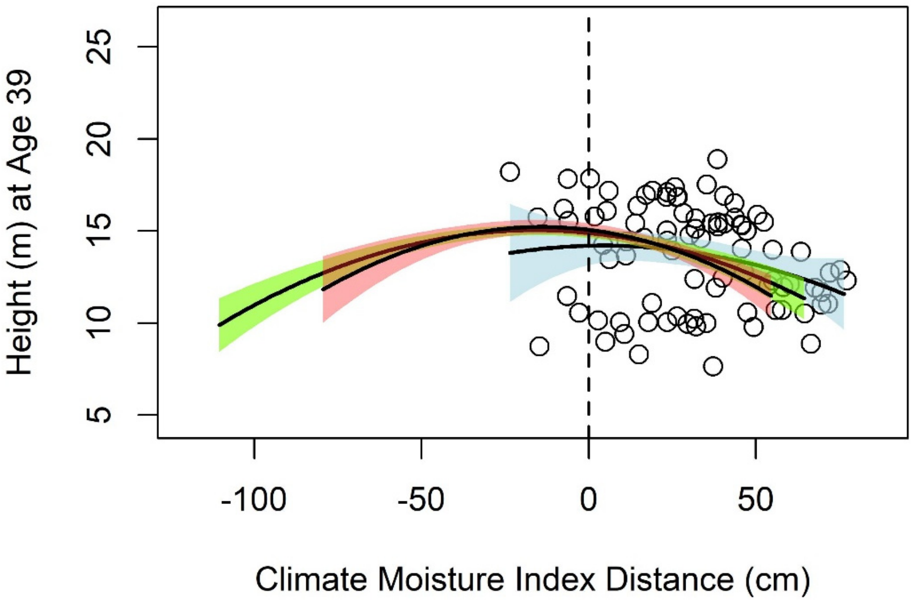


(**b**)

Figure 5. Relationship between mean annual temperature transfer distance and (**a**) height and (**b**) survival of jack pine seed sources at 39 years of age. Separate regression lines and 95% confidence intervals are shown for southern (red), central (green), and northern (blue) seed sources. Data points (black circles) are shown only for northern seed sources. The vertical dashed line indicates local deployment of seed sources (i.e., a transfer distance of zero); points to the right of this line indicate seed transfers to warmer planting sites and vice versa.

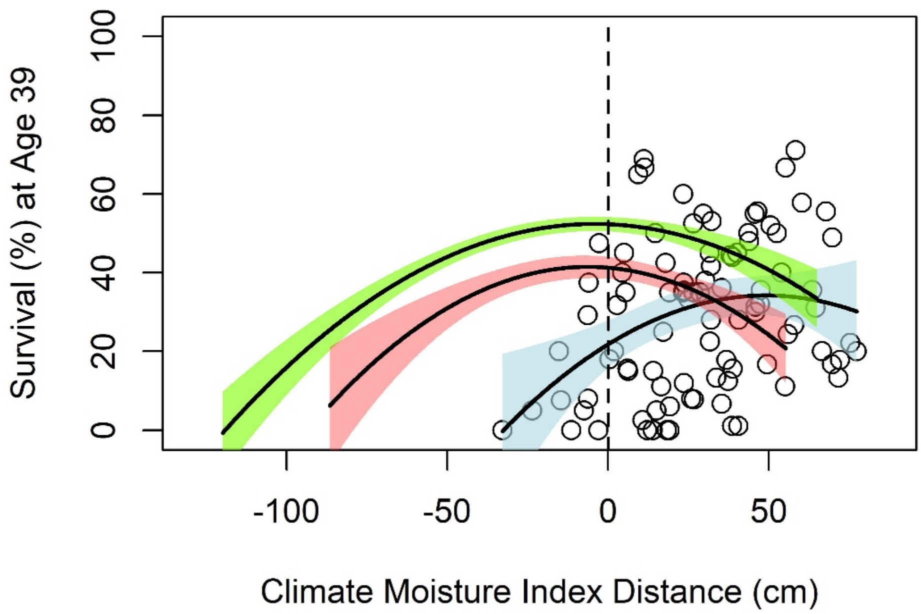
Survival of northern jack pine seed sources was relatively low, ranging from 0 to 50% across a range of transfer distances. The regression model relating survival of these northern seed sources to MAT transfer distance was statistically significant (linear term only) and explained 19% of variation in the data (Table 1, Figure 5b). Note that the number of data points in the jack pine survival regressions differs from that of the height regressions because some sites had no survival; these sites were included as zeroes in the survival analysis, but were not included in the height analysis (Table 1). Similar to black spruce, seed transfers to warmer planting sites were associated with reduced survival rates. For example, predicted survival rates dropped from approximately 40% at local planting sites to approximately 24% at planting sites that were 5 °C warmer than local. Survival response curves were markedly different for southern and central seed sources, with southern sources showing a nearly linear decline in survival with transfers to cooler environments, and central sources showing little change in survival with transfers to both cooler and warmer environments (Figure 5b, Table S4).

For CMI, the regression model relating transfer distance to height of northern jack pine seed sources was not statistically significant (Table 1, Figure 6a). This relationship was also weak for central and southern seed sources (Figure 6a, Table S4). Again, the majority of these transfers were to wetter planting sites (i.e., to the right of the dashed vertical line in Figure 6a,b), reflecting the dry conditions in the north. The relationship between survival of northern jack pine seed sources and CMI transfer distance was significant, but explained only 11% of the variation in the data (Table 1, Figure 6b). In this case, seed transfers to wetter sites were associated with survival gains, whereas transfers to drier sites were associated with higher mortality rates. Note that this finding is tentative due to the relatively few transfers to drier sites and the large amount of unexplained variation.



(**a**)

Figure 6. *Cont.*



(**b**)

Figure 6. Relationship between climate moisture index transfer distance and (**a**) height and (**b**) survival of jack pine seed sources at 39 years of age. Separate regression lines and 95% confidence intervals are shown for southern (red), central (green), and northern (blue) seed sources. Data points (black circles) are shown only for northern seed sources. The vertical dashed line indicates local deployment of seed sources (i.e., a transfer distance of zero); points to the right of this line indicate seed transfers to wetter planting sites and vice versa.

As noted above, regression results for the remaining climate variables showed similar patterns to those already discussed and are presented in the Supplementary Material (Table S4, Figures S4 and S5).

4. Discussion

We anticipated that northern populations would exhibit a downward-facing, parabolic-shaped relationship between height growth and MAT transfer distance, with a modest peak at planting sites well south of seed source origin (Figure 1). This expectation was tentatively met for both species, with northern populations of black spruce and jack pine achieving optimal growth in environments that were 2.2 and 3.6 °C of MAT warmer than local, respectively. These findings indicate that northern populations harbor a significant amount of resilience to climate warming. For example, northern jack pine seed sources could be transferred to environments that were 7.1 °C warmer than local before incurring growth declines. These findings appear to confirm previous reports that northern tree populations are often growing under suboptimal conditions and respond positively to warming temperatures [11,16,24,34,35].

Relationships between height growth and CMI transfer distance were weak for all seed sources and species considered here. These findings are consistent with previous provenance studies that have reported stronger adaptive variation along temperature gradients as opposed to moisture-related gradients [16,19,30,36]. Nonetheless, this finding is somewhat surprising given the growing evidence that hot and dry conditions may contribute to growth declines in northern forests [7,12,37].

Survival-based relationships differed markedly from those described above for height growth. Northern populations of both species exhibited reduced survival rates when moved to warmer and drier environments. This finding is consistent with several studies that have reported forest decline in response to hot, dry conditions in northern forested regions [38–40]. Together with the growth-based results, these findings suggest that the warmer and drier conditions expected across much of northern Canada under climate change [3] may reduce survival, but that surviving trees may grow at a faster rate until a certain magnitude of climate warming is reached. Cruzado-Vargas et al. [41] reported similar findings along an altitudinal gradient in Mexico. Disparity between growth and survival outcomes has been reported previously [42,43], suggesting that multiple performance metrics may be needed to fully understand climate change responses of northern tree populations.

There was a large amount of unexplained variation in our regression models, as evidenced by the low r-squared values reported in Table 1. Low levels of explained variance have been reported from a range of provenance studies [16,17,32,44]. This phenomenon may be related to a number of factors, including: variability in site conditions both within and between planting sites (e.g., soil depth, drainage, and microtopography); extreme climate events (e.g., drought, flooding, and frost) that are not well captured by long-term climate means; and herbivory impacts (e.g., deer and insects). Intra-population variation in genetic composition, phenotypic plasticity, and epigenetic effects may further contribute to this unexplained variation. This outcome underlines the many factors that may affect provenance study outcomes and the related challenges in predicting tree population responses to climate change.

The strength of provenance studies is that they substitute spatial climate variation for temporal variation, allowing for a wide range of climate impacts on tree growth and survival to be observed over a relatively short period. However, there are a number of non-climatic factors that also vary spatially and thus may confound provenance study outcomes. Soil quality, which is a critical driver of tree survival and growth [45], typically improves when moving from north to south in Canada [46]. Although efforts were made to standardize soil conditions in the provenance experiments employed here [22,23], this north–south spatial gradient in soil quality may have contributed to the growth and survival outcomes reported here.

Day length is another non-climatic factor that varies with latitude and has the potential to confound provenance study outcomes via its role in tree phenology, i.e., timing of growth initiation in spring and growth cessation in fall [47,48]. Far northern locations experience significantly longer days throughout the growing season than more southerly sites; thus, if northern seed sources are adapted to specific photoperiod cues, their performance at southern planting sites may be more reflective of photoperiod differences than climate transfer distances. However, this scenario appears unlikely for a number of reasons. First, many studies have reported that temperature plays an equal or more important role than photoperiod in controlling tree phenology, particularly with respect to growth initiation in the spring [47,49–51]. Furthermore, if the northern seed sources in the current study were entirely under photoperiodic control for growth initiation and cessation, one would expect shorter functional growing seasons (and associated growth declines) at southern planting sites as day length cues would be reached later in spring and earlier in fall at these sites relative to seed source origin. Although this pattern was not observed for either species, we do not rule out the possibility that day length may have influenced our results in more subtle ways.

Assisted migration of seed sources has been proposed as a method for establishing plantations that are well adapted to future climate at a given planting site [52,53]. For example, Kuparinen et al. [54] identified low growth potential of northern provenances as a factor that may limit the growth response of northern forests to climate change. Our results suggest that, for northern planting sites, the use of more southerly seed sources—particularly those from the central portion of the range—may result in increased growth and survival relative to local seed sources under climate change. Specifically, based on our regression models, in situ northern seed sources are expected to exhibit growth increases and survival declines under climate change, whereas central seed sources appear able to maintain higher growth rates and comparable survival rates (relative to in situ northern seed sources) with modest northward movements. The linear decline of southern seed source survival in relation to northward transfer distance indicates that extreme northward shifts would likely result in unacceptably high mortality levels.

We recognize a number of limitations to the current work. First, sample sizes were modest due to the limited number of northern seed sources incorporated into the provenance studies employed here. This limited the statistical power associated with our analyses and necessitated the pooling of regional seed sources. Furthermore, transfers of northern seed sources were predominantly to more southerly planting sites. Given our focus on climate change, this nearly unidirectional movement was less problematic for temperature transfers, which are expected to be almost exclusively toward warmer conditions under climate change. However, given the dry climate of northwestern Canada (where many of our northern provenances originated from), southward seed movements were mostly to wetter conditions, making it challenging to glean insights regarding the potential impacts of increasing dryness under climate change. Despite these limitations, we feel that this study provides valuable insights into potential climate change outcomes for northern tree populations.

5. Conclusions

Based on previous work, we anticipated that northern tree populations would exhibit positive growth responses to southward seed transfers. This expectation was generally met for both species examined here, although high levels of unexplained variance suggest significant uncertainty in the potential impact of climate warming on northern tree growth. Positive growth responses were projected for MAT increases of up to 4.4 and 7.1 °C for black spruce and jack pine, respectively; note that MAT increases of this magnitude are projected for northern regions before the end of the current century under high greenhouse gas emissions scenarios [3]. Contrary to our growth-related results, northern populations of both species exhibited declines in survival under hotter, drier conditions. Taken together, these findings suggest that northern tree populations may respond positively to a certain degree of climate warming, but only if adequate moisture levels are available. The assisted migration of more southerly seed sources—particularly those from the central portion of the range—may result in increased growth and survival relative to local northern seed sources under climate change.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/atmos12101363/s1, Figure S1: Relationship between mean annual temperature and height growth for (a) black spruce and (b) jack pine, Figure S2: Relationship between black spruce height growth and climate transfer distance of (a) mean annual temperature, (b) annual precipitation, (c) climate moisture index, and (d) growing season length, Figure S3: Relationship between black spruce survival and climate transfer distance of (a) mean annual temperature, (b) annual precipitation, (c) climate moisture index, and (d) growing season length, Figure S4: Relationship between jack pine height growth and climate transfer distance of (a) mean annual temperature, (b) annual precipitation, (c) climate moisture index, and (d) growing season length, Figure S5: Relationship between jack pine survival and climate transfer distance of (a) mean annual temperature, (b) annual precipitation, (c) climate moisture index, and (d) growing season length, Table S1: Northern seed sources used in black spruce rangewide provenance study, Table S2: Northern seed sources used in jack pine rangewide provenance study, Table S3: Parameters from quadratic regression models between climate transfer distance and height/survival of northern seed sources used in rangewide provenance trials for black spruce, Table S4: Parameters from quadratic regression models between climate transfer distance and height/survival of northern seed sources used in rangewide provenance trials for jack pine.

Author Contributions: Conceptualization, J.H.P., D.W.M.; methodology, J.H.P., A.T.; formal analysis, J.H.P.; investigation, J.H.P., A.T., P.L.; resources, D.W.M.; data curation, J.H.P., D.W.M., A.T., P.L.; writing—original draft preparation, J.H.P.; writing—review and editing, J.H.P., D.W.M., P.L., A.T.; visualization, J.H.P.; supervision, D.W.M.; project administration, D.W.M. All authors have read and agreed to the published version of the manuscript.

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