

PLANT TRANSLOCATIONS AND CLIMATE CHANGE:
BIOASSAY, SURVEILLANCE AND SOLUTION TO A GLOBAL THREAT?

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Critical seed transfer distances for selected tree species in eastern North America

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Abstract

1. Forest planting events present key opportunities to enhance forest adaptation and growth through the selection of appropriate growing materials (seeds and seedlings). Critical to such efforts is knowledge of the climatic distance that seed sources can be moved before significant growth forfeitures are incurred. These limits, referred to here as critical seed transfer distances (CSTD), can be used to identify a potential seed procurement region for any given planting site and can readily incorporate climate change projections.
2. We assembled provenance trial data from a variety of sources and employed transfer functions to derive CSTDs for five major tree species in eastern North America.
3. Optimal height growth at test sites was associated with modest warm-to-cold (i.e. northward) seed transfers of 1.6°C on average. Calculated transfer limits were large, indicating that seed sources could be moved significant climatic distances before height growth was less than 90% relative to that of the local seed source. These broad relationships, which were relatively consistent across species, would allow considerable flexibility in resulting seed transfer systems; however, given the significant uncertainty surrounding climate change—particularly in the location and timing of extreme weather events—prudent application of seed transfer limits may be appropriate.
4. *Synthesis*: We assembled and analysed a significant amount of provenance data to derive novel information on seed movement limits for five tree species in eastern North America. This information will support forest managers in ongoing efforts to incorporate climate change into forest regeneration operations.

KEYWORDS

assisted migration, climate change, critical seed transfer distance, forest regeneration, provenance data, seed zones, trees

1 | INTRODUCTION

Climate change is expected to have significant impacts on forest growth and mortality (Boulanger et al., 2017; Girardin et al., 2016; Taylor et al., 2017). A key driver of these impacts is the disparity between the velocity of climate change, which is projected to shift

tree climate envelopes more than 500 km northward by the end of the current century (McKenney et al., 2007, 2011), and tree migration, which typically occurs at rates less than 50 km per century (McLachlan et al., 2005). As a result, tree populations are expected to become increasingly maladapted to local climate conditions as the century progresses (Aitken et al., 2008).

In anticipation of these impacts, many jurisdictions are reviewing and revising their seed transfer systems, which provide guidance regarding movements of growing materials (seeds and seedlings) for forest regeneration (e.g. O'Neill et al., 2017). Many seed transfer systems are based on a series of contiguous fixed zones, with seed movements constrained such that seeds are deployed within the zone from which they originate (Bower et al., 2014; Castellanos-Acuña et al., 2018; Johnson et al., 2004). This constraint reflects one of the basic tenets of forest genetics—that sites should be planted using local seed sources, thus ensuring a match between the climate at the planting site and the climate to which the seed sources are adapted (Ying & Yanchuk, 2006). However, as climates rapidly shift under climate change, local seed deployment no longer ensures this match.

Central to any seed zone system is an understanding of how tree growth and mortality respond to climate. Provenance studies—which measure growth and mortality through time of various seed sources (provenances) planted at various test sites (common gardens)—provide data to help address this topic. As such, these data have been integral to the development of numerous seed transfer systems (Campbell, 1986; Hamann et al., 2011; Johnson et al., 2004; Parker & van Niejenhuis, 1996). Though not typically designed with climate change in mind, provenance studies also afford insights into potential climate change impacts and related opportunities for climate change adaptation through strategic seed movements (Isaac-Renton et al., 2014; Klisz et al., 2019; Wang et al., 2010; Yang et al., 2015). The terms seed source, provenance and population have been used interchangeably in the scientific literature to describe genetic material that originates from a certain geographical location; here we employ the term seed source, though we retain the well-established phrases 'provenance data' and 'provenance study' where appropriate.

Critical seed transfer distance (CSTD) refers to the maximum distance (measured in geographical, adaptive or climatic units) that seeds can be moved before displaying unacceptable levels of maladaptation (Ukrainetz et al., 2011). Various approaches have been used to derive CSTDs, including the calculation of a risk index based on the degree of genetic mismatch between local and distant populations (Campbell, 1986) and the calculation of least significant differences between discernible populations (Rehfeldt, 1994). Recently, CSTDs have been calculated from transfer functions that use provenance data to relate population transfer distance to population growth and/or survival at a given planting site (O'Neill et al., 2014, 2017; Ukrainetz et al., 2011); this approach has the advantage of defining transfer limits in relation to growth and/or survival forfeitures—measures that are familiar to most forest managers.

Here we report on an effort to calculate CSTDs using provenance data for five major tree species in eastern North America: Black Spruce (*Picea mariana*), White Spruce (*Picea glauca*), Jack Pine (*Pinus banksiana*), White Pine (*Pinus strobus*) and Yellow Birch (*Betula alleghaniensis*). We detail significant efforts involved in assembling provenance data for these species, then develop univariate transfer functions for several common climate variables at each test site,

from which we derive CSTDs. Finally, spatial patterns in CSTD values are explored using regression analyses that relate calculated CSTD values to test site climate. The analysis undertaken here is aimed at providing accessible, baseline information regarding climatic transfer tolerances for a selection of tree species. Such information, in combination with projections of future climate, will support forest managers in ongoing efforts to incorporate climate change into seed transfer systems.

2 | MATERIALS AND METHODS

2.1 | Provenance study data

Provenance data were obtained from both published reports and directly from forest genetics researchers. Below, we briefly describe the data for each species examined here. Many of the datasets consisted of average height values for each seed source at each test site, so all datasets were summarized at this level of detail prior to analysis.

Black spruce provenance data were obtained from remeasurements 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 Selkirk, 1974 for details). The remeasurements were carried out in 2003 (33 years of age from seed) and involved measuring height and diameter at breast height (DBH) of all surviving trees at each test site (see Thomson et al., 2009 for details). In total, 192 seed sources at 18 test sites in Canada and one test site in Minnesota were measured (Figure 1a). These data were obtained through a collaborative research agreement with William H. Parker at Lakehead University, Thunder Bay, Ontario.

White spruce provenance data were obtained from a variety of sources. Data from a 2001 remeasurement of Ontario test sites in the 410-series white spruce range-wide provenance trial were provided by William H. Parker (see Lu et al., 2014 for further details). Jean Beaulieu (emeritus research scientist at Laurentien Forestry Centre, Quebec) provided data from remeasurements of the 93-, 194- and 410-series provenance trials in Quebec (see Andalo et al., 2005 for further details). Similarly, data from the 93-, 194- and 410-series white spruce provenance trials in the Maritime Provinces were provided by Dale Simpson (Manager of the National Tree Seed Centre in Fredericton, NB). A final source of white spruce provenance data was obtained from the literature for a single test site in central Maine (Wilkinson, 1962). In total, data for 324 seed sources at 39 test sites were obtained (Figure 1b).

Jack pine provenance data were obtained from remeasurements on a portion of the CFS 255 Series range-wide Jack pine provenance trial, which consisted of 99 seed sources planted in various combinations at test sites across eastern Canada, the United States and Europe (see Rudolph & Yeatman, 1982 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

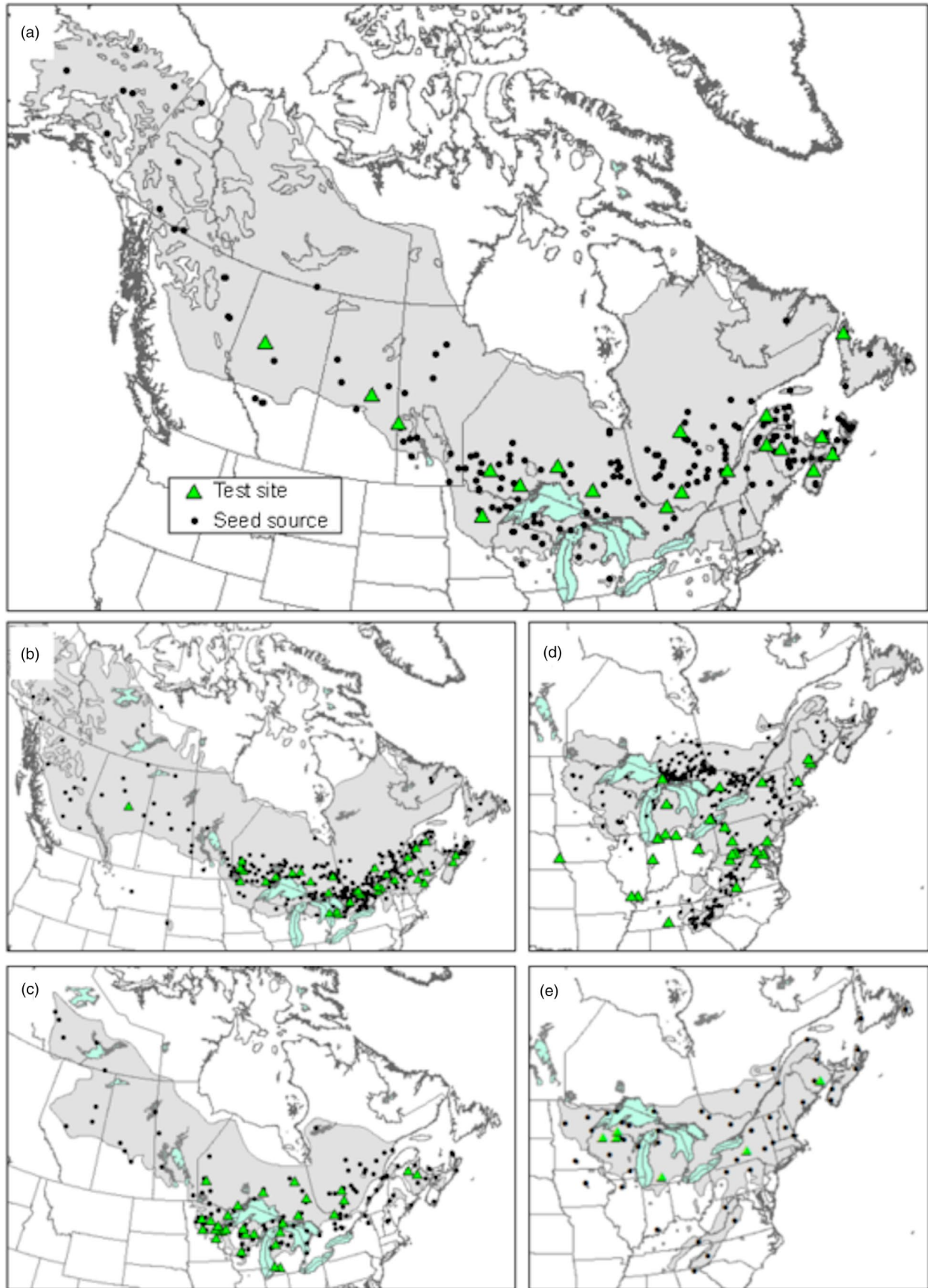


FIGURE 1 Spatial distribution of test sites and seed sources included in provenance data for (a) black spruce, (b) white spruce, (c) Jack pine, (d) white pine and (e) yellow birch. Grey shading indicates each species' geographical distribution (Little, 1971)

Thomson & Parker, 2008 for details), and the data were provided by William H. Parker. A second Jack pine provenance dataset was obtained from a trial that covered the Great Lakes region of the United States and included 26 seed sources and 17 test sites (see Jeffers & Jensen, 1980 for further details). This trial was remeasured in 1973 (at 20 years of age from seed) and average seed source height values at each test site were made available (see table 4 in Jeffers & Jensen, 1980). In total, data for 125 seed sources at 30 test sites were obtained (Figure 1c).

White pine provenance data were obtained from three sources. The first was a provenance trial initiated by the US Department of Agriculture (USDA) in 1955 at 13 test sites in the northeastern US and two in Ontario, Canada (see King & Nienstaedt, 1969 for details). Regional remeasurements of these test sites were reported at age 16 for 10 test sites in the northeastern US (Demeritt & Kettlewood, 1976); at age 16 for three test sites in Maryland (Genys, 1983, 1987); and at age 28 for two test sites in southern Ontario (Abubaker & Zsuffa, 1990). The second source for white pine data was a provenance trial initiated by several cooperating agencies in 1964 (Wright et al., 1979). This trial included 41 seed sources from the southern Appalachian region that were planted at one or more of 11 test sites. Height growth was measured at ages ranging from 7 to 11 years depending on the test site (Wright et al., 1979). Finally, Pengxin Lu (Provincial Forest Geneticist at the Ontario Forest Research Institute in Sault Ste Marie, Ontario) provided measurements for two white pine test sites in Ontario—Turkey Point and Sault Ste Marie. In total, data for 295 seed sources at 28 test sites were obtained (Figure 1d).

Finally, yellow birch data were obtained from published reports of provenance trial measurements in eastern North America (Clausen, 1975), northern Wisconsin (Clausen, 1980) and New Brunswick (Fowler & Park, 1988). In total, data for 57 seed sources at 7 test sites were obtained (Figure 1e).

2.2 | Climate data

Historical climate estimates were obtained by interrogating spatial climate models at the location of each seed source and planting site. The climate models were developed by interpolating temperature and precipitation data from over 12,000 stations from across Canada, Alaska and the contiguous United States. Withheld errors associated with annual temperature and precipitation models are approximately 1°C and 20%, respectively (see McKenney, Hutchinson, et al., 2011 for details).

For seed source locations, where climate values should reflect historic conditions, we employed data for the 1961–1990 period. This period was selected because it precedes recent rapid increases associated with climate change (Zhang et al., 2019) and coincides with peak weather station coverage in Canada (Mekis et al., 2018). 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.

The following five climate variables were selected for this work: mean annual temperature (MAT), annual precipitation (ANNP), climate moisture index (CMI; a measure of annual moisture balance—see Hogg, 1994 for details), extreme minimum temperature (XMINT) and growing season length (GSELENGTH). These variables were chosen because they summarize gradients in moisture and temperature, are relatively uncorrelated and have been used in previous provenance studies (e.g. Andalo et al., 2005; Leites et al., 2012; Rehfeldt et al., 1999; Wang et al., 2006, 2010).

To illustrate the use of CSTDs under climate change, we averaged projections from the Canadian Earth System Model (CanESM2; Chylek et al., 2011) for the 2040–2050 period under a moderate emissions scenario (i.e. RCP4.5; van Vuuren et al., 2011); see Price et al. (2011) for details on the downscaling of these spatial products. This time period was selected because it is approximately 25 years in the future (or roughly 1/3 the length of a harvest rotation in much of Canada), thus striking a reasonable balance between near-term mortality risk and longer-term growth potential (see O'Neill et al., 2014 for further discussion).

2.3 | Statistical analysis and calculations

Various approaches have been used to model provenance data, including transfer functions (Andalo et al., 2005; Ukrainetz et al., 2011), response functions (Thomson & Parker, 2008; Thomson et al., 2009; Wang et al., 2006), mixed effects models (Leites et al., 2012) and universal transfer/response functions (O'Neill et al., 2008; Wang et al., 2010; Yang et al., 2015). Previous efforts to identify CSTDs have employed transfer functions, which model tree growth as a function of the climatic distance between seed source and test site (O'Neill et al., 2014; Ukrainetz et al., 2011). O'Neill et al. (2014) employed a half-normal curve-fitting approach for identifying CSTDs for two tree species in British Columbia, Canada. One limitation of this approach is that, by definition, the optimum occurs at a climate transfer distance of zero (i.e. local seed sources are always best), which also implies that northward and southward seed transfer limits are identical. Given that preliminary analyses of our data indicated that this was not always the case, we opted to use a quadratic regression approach, which allows for more flexibility with respect to the location of the optimum and associated transfer limits.

We generated univariate quadratic transfer functions for each test site to model population mean tree height as a function of the climatic distance between the test site and the seed source:

$$Ht_{ij} = \beta_{0j} + \beta_{1j}\Delta X + \beta_{2j}\Delta X^2 \quad (1)$$

where Ht_{ij} is the height of seed source i at test site j , ΔX is the climatic distance between seed source i at test site j (calculated as test site climate minus seed source climate), and the β 's are the fitted parameters. Transfer functions were considered valid for CSTD calculation if they defined a downward-facing parabola with a significance level of $p < 0.10$ for all terms in the model. Optimal transfer distances were

calculated by taking the first derivative of Equation (1), setting it equal to zero, and solving for ΔX .

Critical seed transfer distances identify the climatic distance from which seed can be procured before exhibiting a specified forfeiture in productivity. For the current work, CSTD values associated with a 5% and 10% forfeiture in height (as compared to height expected with the use of local seed sources) were calculated by solving the quadratic formula:

$$\text{CSTD}_j = \frac{-\beta_{1j} \pm \sqrt{\beta_{1j}^2 - 4 \cdot \beta_{2j} \cdot \beta_{0j} \cdot \alpha}}{2 \cdot \beta_{2j}} \quad (2)$$

where the β 's are as defined above and α defines the tolerance for height growth forfeiture (i.e. 5% or 10%). Note that Equation (2) provides two CSTD values when solved (because of the \pm sign in the equation); one CSTD value is for 'negative' transfers (i.e. movements of warmer/wetter seed sources to cooler/drier test sites) and the other is for 'positive' transfers (i.e. movements of cooler/drier seed sources to warmer/wetter test sites).

We explored the possibility of combining data across test sites to produce a single regression model for each species and climate variable. However, preliminary analyses consistently identified significant interactions between test sites and climatic transfer distance, indicating that the relationship was more appropriately modelled at the scale of individual test sites (see also O'Neill et al., 2014). Therefore, for each species and climate variable, we calculated positive and negative transfer distances for each site, then calculated mean and standard deviations for positive and negative transfer distances for each species and climate variable. To explore how CSTD values varied in relation to climate, we ran simple regressions between CSTD values and test site climate for each of the five climate variables considered here.

3 | RESULTS

3.1 | Black spruce

Transfer function results for individual black spruce test sites and each climate variable of interest are provided in Table S1 and Figures S1a–e. Sample transfer functions, with CSTD values displayed, are shown for MAT and ANNP in Figure 2. Across climate variables and test sites, the proportion of explained variance (i.e. r -square value) was low, averaging 0.17–0.29 (Table 1). Regressions involving ANNP had the highest average r -square value (0.29) and generated statistically significant, Gaussian-shaped transfer functions at 15 out of 19 test sites (79%); CMI regressions had a slightly lower average r -square value (0.26) and were significant at 89% of test sites. MAT regressions explained the least amount of variation (0.17) and were significant at 68% of test sites. CSTDs were large for all climate variables; for example, on average, seed sources could be moved to planting sites that were up to 455-mm drier or 6.1°C of MAT cooler than conditions at their climate of origin before exhibiting height forfeitures greater than 10% relative to the local seed

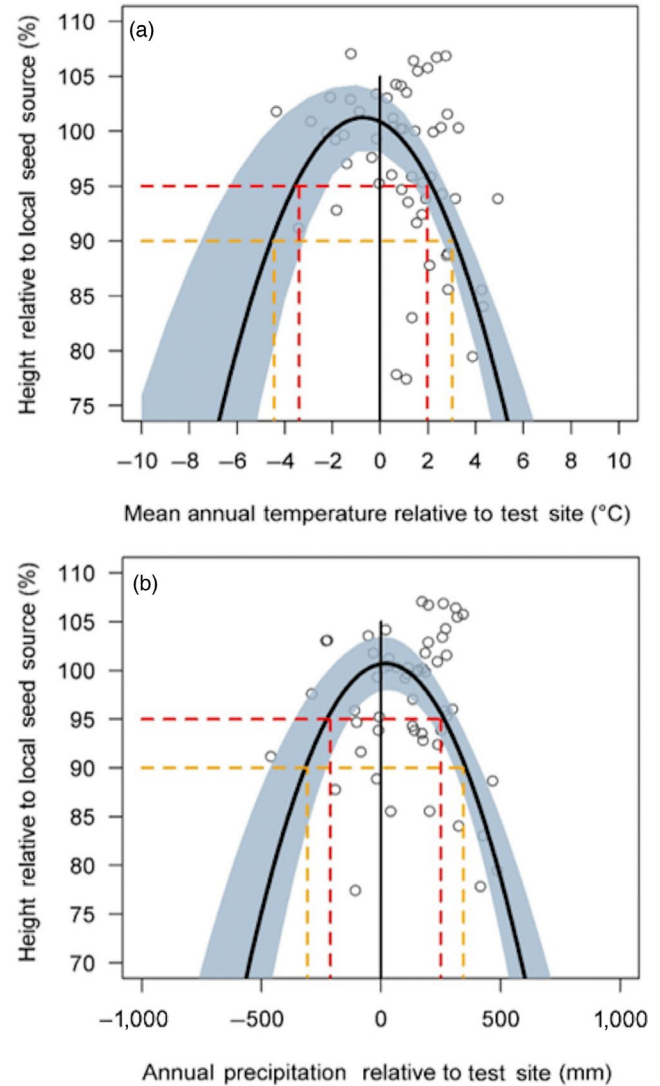


FIGURE 2 Sample transfer functions for black spruce at a test site in Petawawa, Ontario. Plots show the relationship between height and climatic transfer distance (calculated as test site climate minus seed source climate) for (a) mean annual temperature and (b) annual precipitation. Orange and red dashed lines indicate critical seed transfer distances that would maintain growth rates equal to or greater than 90 and 95% of expected height of a local population, respectively. Grey shading around each regression line indicates the 95th confidence interval

source (Table 1; Figure 3a,c). With a height forfeiture tolerance of 5% relative to local, transfer limits were somewhat narrower at 350 mm and 4.9°C for ANNP and MAT, respectively (Table 1; Figure 3a,c).

3.2 | White spruce

Transfer function results for individual white spruce test sites are provided in Table S2 and Figure S2a–e. Again, r -square values were low, ranging from 0.16 to 0.23 across climate variables and test sites (Table 1). Regressions involving GSELENGTH had the highest average r -square value (0.23) and generated statistically significant transfer

TABLE 1 Summary of critical seed transfer distances calculated using transfer functions for each of five North American tree species

Species	Climate variable	N test sites	N significant	Mean R^2	Growth > 90% of local				Growth > 95% of local			
					Cooler/drier transfers		Warmer/wetter transfers		Cooler/drier transfers		Warmer/wetter transfers	
					Mean	SD	Mean	SD	Mean	SD	Mean	SD
Black Spruce	ANNP	19	15	0.29	-455.3	213.6	476.8	260.6	-350.4	230.1	371.8	242.3
	CMI	19	17	0.26	-46.6	24.5	51.9	23.4	-35.1	25.1	40.4	22.4
	GSLENGTH	19	13	0.22	-48.9	21.3	23.7	12.1	-40.9	21.0	15.7	11.0
	MAT	19	13	0.17	-6.1	2.7	3.9	1.3	-4.9	2.6	2.7	1.2
	XMINT	19	15	0.19	-12.5	3.7	11.1	5.8	-9.5	3.8	8.0	5.1
White Spruce	ANNP	40	17	0.18	-471.5	276.7	294.5	170.8	-390.6	267.9	213.6	158.3
	CMI	40	15	0.16	-48.3	30.1	35.9	25.2	-42.3	27.3	29.0	22.4
	GSLENGTH	40	17	0.23	-53.1	18.4	20.9	6.0	-45.0	17.4	12.8	4.5
	MAT	40	15	0.22	-5.7	3.0	2.8	1.2	-4.9	2.4	1.9	0.6
	XMINT	40	16	0.17	-7.6	4.1	8.0	5.5	-6.2	3.4	6.7	5.4
Jack Pine	ANNP	30	14	0.15	-424.4	139.0	583.1	210.8	-291.2	117.7	449.8	208.2
	CMI	30	17	0.2	-45.2	20.0	56.7	27.0	-31.4	15.7	42.9	23.3
	GSLENGTH	30	11	0.21	-51.6	23.9	25.7	16.8	-44.4	19.2	10.2	30.9
	MAT	30	12	0.23	-6.6	3.0	4.0	3.0	-5.5	2.8	2.9	2.8
	XMINT	30	12	0.16	-11.6	5.1	11.3	6.3	-9.2	3.4	8.9	5.0
White Pine	ANNP	28	12	0.2	-1,206.8	548.4	219.9	145.1	-1,116.8	556.7	129.9	94.2
	CMI	28	9	0.14	-86.9	44.7	27.3	26.1	-78.8	44.8	19.2	25.7
	GSLENGTH	28	13	0.32	-97.3	36.6	32.2	18.5	-85.4	34.9	20.4	15.3
	MAT	28	13	0.32	-9.0	4.5	3.8	2.2	-7.7	4.4	2.5	1.8
	XMINT	28	9	0.29	-11.4	6.1	9.8	7.5	-9.2	5.3	7.6	7.6
Yellow Birch	ANNP	7	0	0.11
	CMI	7	0	0.11
	GSLENGTH	7	5	0.19	-70.7	21.4	33.4	16.3	-58.9	24.1	21.7	12.6
	MAT	7	3	0.14	-7.8	3.0	3.4	2.2	-6.7	3.3	2.2	1.7
	XMINT	7	2	0.09	-13.5	3.7	14.8	1.7	-9.5	3.3	10.7	2.1

functions at 17 out of 40 test sites (43%), while CMI regressions explained the least amount of variation (0.16) and were significant at 38% of test sites. CSTDs were large for all climate variables; for example, on average, seed sources could be moved to planting sites that were up to 472-mm drier or 5.7°C of MAT cooler than their maternal climate before exhibiting height forfeitures greater than 10% (Table 1).

3.3 | Jack pine

Transfer function results for individual Jack pine test sites are provided in Table S3 and Figure S3a–e. *R*-square values were low, ranging from 0.15 to 0.23 across climate variables and test sites (Table 1). Regressions involving MAT had the highest average *r*-square value (0.23) and generated statistically significant transfer functions at 12 out of 30 test sites (40%), while ANNP regressions explained the least amount of variation (0.15) and were significant at 47% of test sites. CSTDs were large for all climate variables; for example, on average, seed sources could be moved to planting sites that were up

to 424-mm drier or 6.6°C of MAT cooler than their maternal climate before exhibiting height forfeitures greater than 10% (Table 1).

3.4 | White pine

Transfer function results for individual white pine test sites are provided in Table S4 and Figure S4a–e. *R*-square values were relatively low, ranging from 0.14 to 0.32 across climate variables and test sites (Table 1). Regressions involving MAT and GSLENGTH had the highest average *r*-square values (0.32) and generated statistically significant transfer functions at 13 out of 28 test sites (46%). CMI regressions explained the least amount of variation (0.14) and were significant at 32% of test sites. CSTDs were notably larger than those of the other species examined here; for example, on average, seed sources could be moved to planting sites that were over 1,200-mm drier or 9.0°C of MAT cooler than their maternal climate before exhibiting height forfeitures greater than 10% (Table 1).

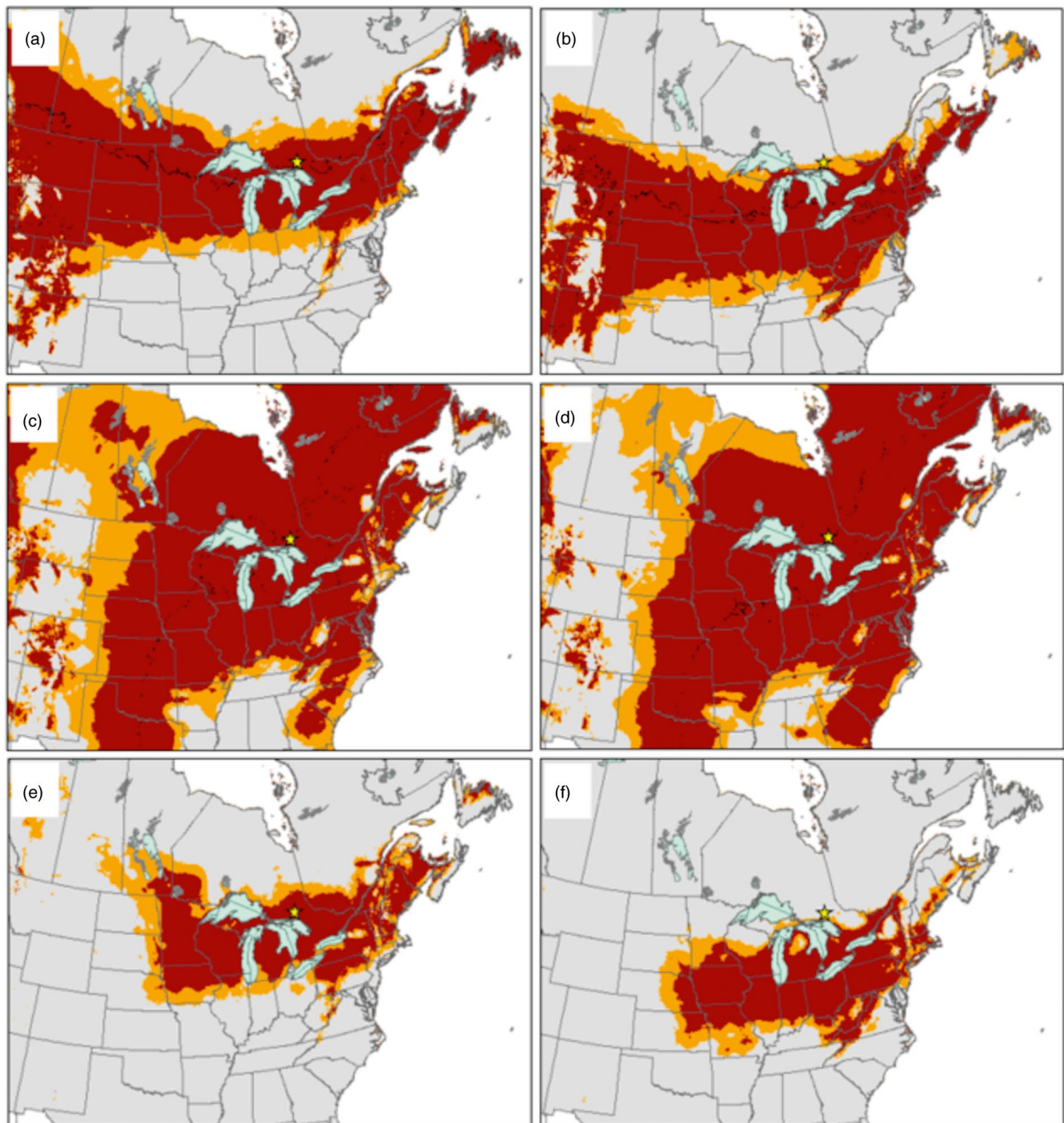


FIGURE 3 Black spruce seed collected from the red (or orange) procurement area and planted at a hypothetical site near Sudbury, Ontario (yellow star) is expected to yield trees with average height greater than 95 (or 90)% relative to the local seed source. Results are shown for mean annual temperature under (a) current climate (i.e. with no assisted migration) and (b) future climate (i.e. with assisted migration); and similarly for annual precipitation (c and d), and an overlay of all five climate variables considered here (e and f). Black pixels indicate climate conditions that are identical to those of the test site

3.5 | Yellow birch

Transfer function results for individual yellow birch test sites are provided in Table S5 and Figure S5a–e. *R*-square values were low, ranging from 0.09 to 0.19 across climate variables and test sites (Table 1). Regressions involving GSELENGTH had the highest average *r*-square

value (0.19) and generated statistically significant transfer functions at five out of seven test sites (71%). Precipitation-related variables (ANNP and CMI) were not significant at any of the test sites; thus, CSTD values were calculated only for the temperature-related variables. CSTD values were again large; for example, on average, seed sources could be moved to planting sites that were up to 7.8°C of

MAT cooler or had up to a 70-day shorter growing season than their maternal climate before exhibiting height forfeitures greater than 10% (Table 1).

3.6 | General patterns

The datasets assembled here allowed us to examine the extent to which local populations grow best at a given planting site. To this end, we calculated the optimal transfer distance for each test site by solving the first derivative of the best-fit quadratic function (Tables S1–S5). With this approach, an optimal transfer distance of zero would be expected if local populations do indeed grow best. The strongest patterns were associated with the temperature-related variables MAT and GLENGTH. In both cases, optimal height growth was achieved with modest northward movements of seed sources—on average 1.6°C (with a 95% confidence interval of $\pm 0.5^\circ\text{C}$) for MAT and 19.0 (± 4.3) days for GLENGTH. This pattern was relatively consistent across test sites, with optimal height growth associated with northward transfers for 82% and 90% of test sites for MAT and GLENGTH, respectively. Relationships involving precipitation-based variables were less consistent. For example, optimal height growth was associated with seed sources that received, on average, 89.3 (± 74.5) mm more ANNP than test sites; however, this pattern of achieving optimal growth through wet-to-dry transfers only held for 60% of test sites.

We also examined the extent to which CSTD values varied in relation to test site climate. We carried out this analysis, which was exploratory in nature, by running simple linear regressions between the calculated CSTD values at each test site (for both cooler/dryer and warmer/wetter transfers) and the value of the corresponding climate variable at each test site. Critical seed transfer distance values varied significantly in relation to climate for many species and climate variables (see Table S6 and Figure S6a–e for full results). Here we illustrate our findings using results for black spruce for MAT and ANNP under the 10% height growth forfeiture cut-off (Figure 4). For warm-to-cold transfers, sites at the cool end of the MAT range could tolerate greater transfer distances than those at the warm end of the spectrum (Figure 4a, blue regression line); the opposite was true for cold-to-warm transfers (Figure 4a, red regression line). Similar patterns emerged for ANNP, with sites at the dry end of the spectrum able to tolerate larger wet-to-dry transfers than wet sites (Figure 4b, blue regression line) and vice versa (Figure 4b, red regression line).

The regression equations in Table S6 can be used to calculate more accurate CSTD values for a given location; however, we note several caveats to this application. First, as is clear from Figure 4, employing these equations can result in very large transfer distances. For example, northward seed movements of nearly 10°C for planting at far northern locations (as predicted by Figure 4a) would likely incur significant risk of frost damage to resulting plantations. Obtaining further evidence to support the feasibility of such plantings is advisable before such movements are undertaken. Second, regression results associated with range edges—both southern and northern—should be

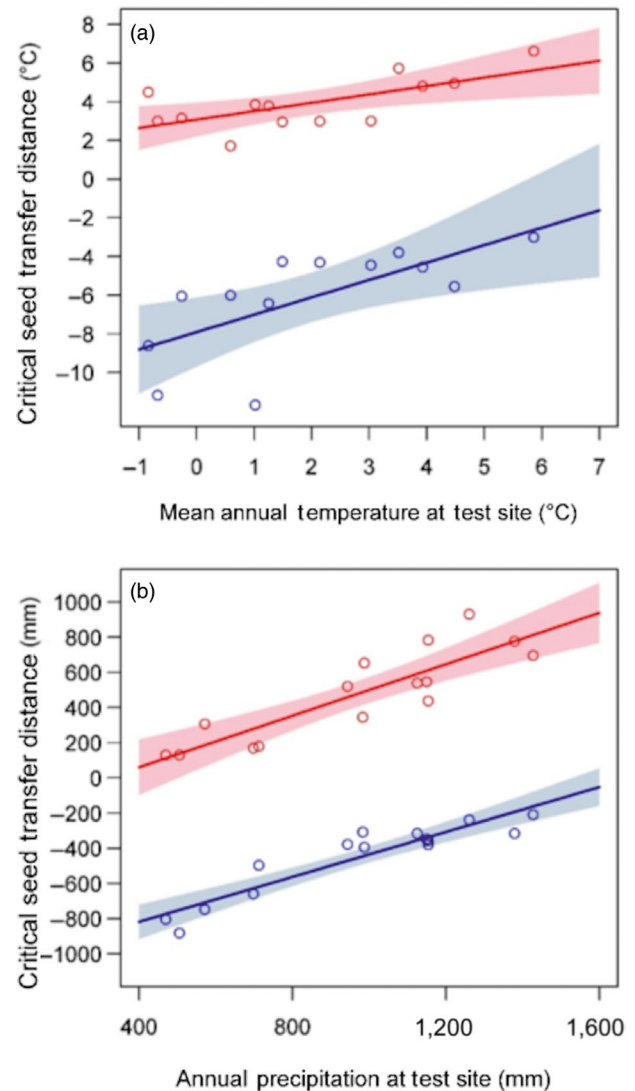


FIGURE 4 Relationship between critical seed transfer distance and test site climate for (a) mean annual temperature and (b) annual precipitation. Blue lines and symbols indicate seed transfers to cooler/dryer planting sites while red lines and symbols indicate transfers to warmer/wetter sites

interpreted cautiously as there is typically a degree of extrapolation involved in such situations. For example, our finding that relatively short northward seed transfers are preferable at planting sites near the southern range limit for black spruce (Figure 4a) inevitably reflects the fact that such transfers rarely exist and are thus largely absent from our provenance data. For these reasons, the use of average CSTD values (Tables S1–S5) may be more prudent than those derived from the climate-based regression equations (Table S6).

3.7 | Climate change application

We demonstrate the use of CSTDs under climate change using the black spruce transfer function summaries in Table 1. For this example,

which demonstrates a focal point seed zone approach (*sensu* Parker & van Niejenhuis, 1996), we employ a hypothetical planting site near Sudbury Ontario (Figure 3) and its projected climate for the 2041–2050 period under a moderate emissions scenario. To identify potential seed sources for current planting under climate change, we add the average CSTD values from Table 1 (for both the 90% and 95% height cut-offs) to the future climate value at the site of interest and locate the resulting ranges on the map of climate for the 1961–1990 period. For MAT with a 90% height expectation, potential seed source locations ranged from Sudbury in the north to Tennessee and North Carolina in the south (Figure 3b); a slightly narrower geographical range was defined using the 95% height cut-off (Figure 3b). For ANNP, the geographical range of potential seed sources was even broader, covering much of eastern North America for both height growth cut-offs (Figure 3d). Similarity between the ANNP-based procurement zones under current (Figure 3c) and future (Figure 3d) climate indicates the modest changes in precipitation that are projected for this region under RCP4.5 by the middle of the current century. Finally, procurement areas for each climate variable were superimposed to identify pixels that fall within the climatic transfer limits of all five climate variables considered here (Figure 3e,f). Not surprisingly, this composite procurement area was smaller than that associated with any single climate variable in the study, though still considerably larger than most seed zones in North America. Given that trees are adapted to various aspects of climate, multi-variable procurement areas are likely more appropriate than those based on a single climate variable. Note that this example is not intended to identify specific seed source locations, but rather to demonstrate the use of CSTDs under climate change; indeed, many areas identified as potential seed sources in Figure 3 are outside the current range of black spruce, making seed collection from these regions problematic.

4 | DISCUSSION

4.1 | Critical seed transfer distances

The CSTDs identified here were very broad (Figure 3), with poleward CSTDs ranging from 6 to 9°C (5–8°C) for MAT and 400–1,200 mm (300–1,100 mm) for ANNP at a height forfeiture tolerance of 10 (5)%. Potential deployment area was somewhat reduced when CSTDs for all five climate variables were superimposed, though resulting seed procurement zones still spanned hundreds of kilometres. Critical seed transfer distances were relatively stable across species, though white pine consistently exhibited larger CSTD values for cooler/drier transfers than the other species—potentially reflecting weak levels of adaptive variation across the range of this species (Yang et al., 2015). We also presented regression results that allow site-specific CSTD values to be calculated at any location for which climate data are available. While these results indicated that somewhat shorter transfer distances may be appropriate at some locations (e.g. northward seed transfers to planting sites near the southern range

limit), most locations still involved considerable transfer distances. These findings, along with the significant uncertainty in future climate projections, suggest that seed transfer systems in eastern North America may not require fine spatial resolution to maintain a productive forest regeneration system; coarse zones, on the scale of hundreds of kilometres, may suffice for tracking seed movements given the climate sensitivities shown here. We note that, where climate gradients change abruptly (e.g. in mountainous and/or coastal situations), much finer spatial resolution may be required.

In order for the within-range-assisted migration of seed sources to be an effective climate change adaptation tool, a species must exhibit strong patterns of adaptive variation across its geographical range. If this is the case, transfer functions should reveal clear relationships between performance (e.g. height growth) and climatic transfer distance—with optimal performance associated with seed sources that originate at, or near, test site climates. We found modest evidence to support the existence of local adaptation, with near-local populations often growing well at test sites. For example, optimal height growth at test sites was associated with modest warm-to-cold (i.e. northward) seed transfers of 1.6°C on average—a disparity that may reflect climate change-related temperature shifts that have occurred since the start of the industrial revolution (Yang et al., 2015). However, many test sites exhibited non-significant transfer functions and, among those that were significant, most had relatively low *r*-square values and defined broad climate relationships (with correspondingly large CSTD values). Numerous other studies have also reported weak population differentiation along climatic gradients (Pedlar & McKenney, 2017; Thomson & Parker, 2008; Thomson et al., 2009; Tiscar et al., 2018; Wang et al., 2006, 2010; Yang et al., 2015). These results raise legitimate concerns as to whether seed movements that are constrained within existing species' range limits are an effective response to climate change. Forest managers may need to consider more aggressive forms of assisted migration—such as assisted range expansion (Ste-Marie et al., 2011)—wherein species are moved beyond current range limits to address potential climate change impacts on forest health and productivity.

O'Neill et al. (2014, 2017), undertook a similar assessment of critical seed transfer distances for three major timber species in British Columbia—lodgepole pine, Douglas-fir (*Pseudotsuga menziesii*) and interior spruce (*Picea glauca*, *P. engelmannii* and their hybrids). Their results are challenging to compare directly with ours because they employed a multivariate Euclidean climate variable in their transfer functions (as opposed to the single climate variables used here), but they did appear to identify much narrower CSTD limits than those reported here (compare Figure 3 in O'Neill et al., 2014 with Figure 3 here). This difference may be due, in part, to steeper genetic and climatic gradients in the mountainous region where their study took place but it also reflects methodological differences between the studies. Specifically, when calculating final CSTD values, O'Neill et al. (2014) averaged CSTD values from the four test sites with the most constraining transfer limits. This decision reflects the operational context of their study and their

stated preference to minimize risk to future plantations by employing narrow transfer limits. Here, we report average CSTD values across all test sites, though test site-specific CSTD values—from which customized transfer limits can be calculated—are provided in the Supplementary Material for each species.

We provided CSTDs for two height forfeiture tolerance values (i.e. 5% and 10% relative to the expected height of the local seed source), similar to those reported in previous studies (O'Neill et al., 2014, 2017; Ukrainetz et al., 2011). Height is a widely used variable in provenance studies as it can be measured relatively easily at any age and is a strong reflection of fitness (Ying & Yanchuk, 2006). It should be noted, however, that forfeitures in height do not translate directly to forfeitures in other growth metrics, such as tree volume. For example, using height–diameter and volume equations for black spruce in Ontario (Honer et al., 1983; Peng et al., 2001), 10% and 5% reductions in height translate into volume reductions of approximately 30% and 15%, respectively. Given the importance of tree volume to forest industry, a height forfeiture tolerance of 10% may be too relaxed for many forestry applications. Note that CSTDs for height forfeiture tolerances other than those provided here can be calculated using equation 2 and the transfer function parameters provided in the Supplementary Material for each species.

4.2 | Climate variables

We employed five climate variables that summarize moisture and temperature gradients and have been used in previous tree growth studies. No variable consistently outperformed the others, though the temperature-related variables (MAT, XMINT and GLENGTH) provided slightly more explanatory power than the moisture-related variables (ANNP and CMI). Furthermore, the moisture-related variables tended to identify very broad CSTD limits that covered vast geographical regions (Figure 3c,d). Given this situation, and in the context of climate change where spatial projections of precipitation are less certain than those for temperature (Zhang et al., 2019), it may be appropriate to focus on temperature-related variables when developing climate-based seed transfer systems in eastern North America.

Extreme weather events can have widespread negative impacts on tree populations (Benito-Garzon et al., 2013; Gu et al., 2008; Hopkin et al., 2003). While we did not find strong relationships between height growth and extreme minimum temperature in the current work, we recognize that this is a complex topic, made more challenging by the inherent uncertainty associated with the location and timing of extreme events under climate change (Sillmann et al., 2017). Concern regarding such events is a valid reason to limit seed transfer distances, which can be accomplished by setting low growth forfeiture tolerances as discussed above (e.g. 5% height forfeiture or less) and/or limiting migration distances under climate change (via selection of modest RCP scenarios and/or targeting near-term future time periods).

Previous provenance studies have incorporated multiple climate variables into one or more synthetic explanatory variables using principal components analysis (Rweyongeza et al., 2010) or Euclidean distance metrics (O'Neill et al., 2014, 2017). These approaches have the advantage of condensing large amounts of climate information into a limited number of variables; however, the resulting variables can be a challenge to interpret and operationalize across regions and end users. Given our focus on providing baseline seed transfer information in a transparent manner, we opted for the single variable approach. If desired, land managers can combine CSTD values from multiple climate variables by mapping the transfer limits for each climate variable and identifying areas of overlap (Figure 3e,f).

4.3 | Caveats and future work

The current effort focused on height growth, but a related topic is how survival rates vary with transfer distance. Importantly, this addresses a slightly different question from that of height growth, with a focus on short-term survival during the vulnerable early years of plantation development as opposed to maintaining productivity over the course of a rotation. O'Neill et al. (2014) produced transfer functions using both height and survival as response variables for two conifer species in British Columbia. They reported generally similar results from the two response metrics, though relationships were weaker—and CSTDs larger—with the survival-based functions. Preliminary analyses of our provenance data, using a subset of species and test sites for which survival data were available, revealed a similar pattern. Thus, although survival is an important consideration when moving seeds, we would not expect survival-based CSTDs to differ substantially from the height-based results presented here.

Provenance studies, while providing valuable insights into climate–growth relationships, do not always provide a balanced and comprehensive sampling of the climatic gradients across the geographical range of a species (O'Neill et al., 2014, 2017; Wang et al., 2010). As a result, some of the transfer functions presented here required extrapolation beyond the range of sampled climate values to estimate CSTD values (see plots in Supplementary Material). This may have resulted in unrealistic CSTD values at certain test sites—a situation that could be remedied by constraining the test sites included in the final CSTD calculations. Note that, given the exploratory nature of the current work, weak constraints were placed on test site inclusion in the CSTD summaries (i.e. basic Gaussian shape and $p < 0.10$).

We explored the possibility of combining transfer functions across test sites, but significant site by climate interactions indicated that test site-level analyses were more appropriate. Note that, preliminary analyses of combined test site data identified even broader CSTDs than those reported here. Future work may examine the best approach for combining site-level transfer functions and/or aim to build on our exploratory work here that related site-level variation in CSTD values to climate.

Finally, the current effort focuses on seed movements under climate change, but an important related topic is the anticipated response of in situ populations to climate change. Though beyond the scope of the current work, other studies have employed portions of the datasets presented here to address this topic (Pedlar & McKenney, 2017; Thomson & Parker, 2008; Thomson et al., 2009; Yang et al., 2015).

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AUTHORS' CONTRIBUTIONS

J.H.P. assembled and analysed the data and wrote the initial draft of the manuscript; D.W.M. helped design the project and contributed both ideas and words to the manuscript; P.L. contributed provenance data, formative discussions on the topic and revisions to the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.dv41ns1x2> (Pedlar et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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