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Evaluating the effectiveness of climate-based seed transfer and assisted migration: a case study of lodgepole pine (Pinus contorta var. latifolia Dougl.) and interior spruce (Picea engelmanii x glauca (Moench) Voss and their hybrids) in western Canada

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Abstract

Key message Forest assisted migration applied in combination with a climate-based seed transfer system to two North American tree species: lodgepole pine (Pinus contorta var. latifolia Dougl.) and interior spruce (Picea engelmanii x glauca (Moench) Voss and their hybrids), resulted in increased height growth and a substantially expanded seed deployment area, compared to a geographic-based seed transfer system in British Columbia, Canada.

Context Forest assisted migration and climate-based seed transfer (CBST) are two recent innovations that have received significant attention as climate change adaptation strategies, but claims regarding their merits have not been well evaluated.

Aims We aim to test the claim that CBST, combined with assisted migration, can provide closer matching of seed source and plantation climate, greater height growth, and wider seedlot deployment area than a conventional geographic-based seed transfer system (GBST).

Methods Using transfer functions developed from two comprehensive, wide-ranging provenance trials of lodgepole pine and interior spruce, with populations from across western Canada, we estimated relative tree height growth at rotation and seed deployment area for a large set of simulated seed transfers in a CBST system with and without assisted migration and in a GBST system.

Results When assisted migration and CBST were used in combination, volume growth was 13% (lodgepole pine) or 6% (interior spruce) greater at rotation age and deployment area was 2.2 times (lodgepole pine) or 7.3 times (interior spruce) greater than was expected in a GBST system. Height growth increases were primarily associated

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with assisted migration, whereas increases in seed deployment area were primarily associated with the use of CBST rather than GBST.

Conclusion Converting from GBST to CBST in conjunction with assisted migration should substantially improve adaptation of lodgepole pine and interior spruce in British Columbia. This approach will also significantly offset the impacts of climate change on growth rates, increase deployment area, reduce seed collection costs, and provide greater flexibility to seed users.

Keywords Lodgepole pine, Interior spruce, Climate change, Transfer function, Provenance trial, Assisted migration, Climate-based seed transfer, Seed transfer systems

1 Introduction

Superior performance of local populations relative to non-local populations (i.e., local adaptation) has been reported for over a century and is most common in tree species with large populations and a wide geographic range (Leites and Benito-Garzon 2023; Wadgymar et al. 2022), notwithstanding some notable exceptions (Hereford 2009; Leimu and Fischer 2008; Candido-Ribeiro and Aitken 2024). Recognizing the importance of local seed sources to plantation health and productivity, recommendations to restrict seed movement appeared as early as 1873 in Sweden where the Board of State Forests advised foresters to use domestic provenances (Langlet 1971). Over the next century, recommendations evolved into seed transfer systems in most jurisdictions having a significant forestry sector to help ensure that reforestation and restoration plantations were established with seed sources adapted to the climate of the plantation location (Zobel and Talbert 1984; Ying and Yanchuk 2006; Johnson et al. 2010). Today, most seed transfer systems divide a jurisdiction into contiguous, or nearly contiguous, zones within which environmental variation or genotype-by-environment interaction is presumed to be minimal (Breed et al. 2018). Zones may be divided into elevational bands (subzones) and seed sources must remain within their zone or subzone of origin-hence the term "fixed zone" systems. Examples are found in Alberta, Canada (AAF 2016), and in Hungary (Cevallos et al. 2020).

Historically, seed zone size and delineation have relied on provenance test results, local expert knowledge, and coarse scale maps of vegetation, habitat types, or physiography (Johnson et al. 2004). However, with the advent of geographic information systems, increased accessibility of climate data (Wang et al. 2012, 2016; Fick and Hijmans 2017), and safe seed transfer distances estimated from provenance test data (O'Neill et al. 2014), it is now possible to identify more accurately a unique seed deployment zone for each seed source location (or unique seed procurement zone for each plantation location), resulting in a new class of seed transfer—a "focal point" seed transfer system (Parker and Niejenhuis 1996). While focal point systems are more effective at controlling maladaptation than fixed zone systems (Ukrainetz et al. 2011), the infinite number of zones makes seed supply and inventory planning difficult. To address this issue, a third form of seed transfer—a "focal zone" system—was proposed in British Columbia, Canada (O'Neill et al. 2017). In this system, a jurisdiction is divided into many small zones, and seed movement is permitted between climatically similar zones.

To address climate change-induced forest health and productivity declines associated with the expanding mismatch between the climates to which tree populations are adapted and the climates that they are experiencing (Aitken et al. 2008), it has been proposed that forest plantations be established with seed sources whose historic climates match the plantation climate shortly after establishment (i.e., forest assisted migration) (Pedlar et al. 2012; O'Neill et al. 2017; Xu and Prescott 2024). Incorporation of assisted migration into a focal zone system is easily achieved by planting seed sources whose historic climate matches the plantation climate expected shortly after plantation establishment. This is accomplished by calculating the climate distance between all pairs of seed zones, where the rows in this matrix represent the seed zones of the plantations and the columns represent the seed zones of the seed sources. A "migration distance" is added to the climate of the plantation seed zones prior to assessing the climate distance between pairs of seed zones. In the focal zone system implemented in British Columbia (O'Neill et al. 2017), migration distance is the historic (1931–1960) climate of the seed zone of the seed source subtracted from the climate of the seed zone of the plantation expected 15 years (for coastal seed zones) or 20 years (for interior seed zones) after plantation establishment.

As delineation of fixed zone systems is often based on geographic criteria, these systems are also referred to as "geographic-" based seed transfer systems (GBST), whereas focal point and focal zone systems are referred to as "climate-" based seed transfer systems (CBST) because migration distances and transferability between points (focal point systems) or between zones (focal zone systems) are usually climatically defined. It should be noted, that while CBST is sometimes used synonymously with assisted migration, it is possible to implement CBST without assisted migration by matching current seed source climates with current plantation location climates. We use CBST to refer to a focal-zone climate-based seed transfer system, and CBST-AM to refer to CBST with assisted migration.

Regardless of seed transfer system type, there is an important trade-off of plantation productivity with seed deployment area—the average area to which a given seed source can be used (Ukrainetz et al. 2011). Systems that are too permissive (i.e., allow seed to be moved long climate distances) can compromise the productivity of planted forests (Zobel and Talbert 1984); systems that are too stringent (allow seed to be moved only very short climate distances) can result in excessive wild stand seed collection efforts or unwarranted numbers of breeding and seed production programs, contributing to reduced operational flexibility and higher reforestation costs (Crowe and Parker 2005).

Data from provenance trials can be used to generate transfer functions relating traits of adaptive importance to seed transfer distance. Height or relative height (*HTp*, the height of a population as a percent of the height of a climatically local population) is often used as the dependent variable in these analyses because for tree species, height is considered an accurate measure of fitness and adaptation (Ying & Yanchuk 2006), owing to its positive correlation with fecundity (Andrus et al 2020), longevity, and competitiveness (Mitchell and Goudie 1980). (We also refer to *HTp* by the more informative term "genetic suitability"). Further, most other fitness-related traits cannot be measured on many thousands of trees with the accuracy and efficiency of height. Using seed zone mean climates, the expected HTp of trees associated with all pairs of seed zone climate mean-to-seed zone climate mean transfers can be estimated, and transfers having a *HTp* that exceeds a threshold *HTp* (t*HTp*, also called the threshold genetic suitability) can be identified to ensure that acceptable tree heights are achieved in all plantations.

As many fixed zone GBST systems were developed prior to the advent of climate models and geographic information systems, and without strong provenance data, it is important to examine the effectiveness of current GBST systems and thus to compare GBST and CBST systems. Here, we evaluated CBST at various genetic suitability thresholds (tHTp), with and without assisted migration, and compared them with GBST. We used simulated random transfers of natural stand seed sources of two of the most widespread and abundant tree species in western North America: interior lodgepole pine (*Pinus* *contorta* var. *latifolia* Dougl.) and interior spruce (*Picea* engelmanii x glauca (Moench) Voss and their hybrids) using British Columbia's current CBST system, its former fixed zone GBST system, and no seed transfer system, to assess the adaptation and deployment area in each system.

In light of these observations, and of the many possible comparisons these simulations provided, we focused on 3 hypotheses concerning height growth: (1) height growth is greater with assisted migration (i.e., CBST-AM) than without (i.e., CBST); (2) height growth is greater in CBST than in GBST; and (3) height growth is greater in CBST-AM than in GBST. We also consider the same 3 hypotheses as they pertain to the deployment area.

2 Material and methods

2.1 Data resources

2.1.1 Provenance trials

We obtained height growth data from three multi-site provenance trials. The lodgepole pine Illingworth provenance trial (EP 656.06), one of the most comprehensive and widely published provenance trials in the world, was established in 1974 with 140 range-wide populations tested at 60 test sites in interior British Columbia. These data were supplemented with data from the lodgepole pine Yukon provenance trial (EP657.07) containing the same populations as the Illingworth trial and tested at two sites in the Yukon. Within each site, 60 populations were tested in a 3×3 tree square plot at 2.5 m spacing in each of two randomized complete blocks (Ying et al. 1985). Tree heights used in the lodgepole pine analysis were collected from the 135 populations that were alive at the 41 Illingworth and Yukon test sites that were measured at age 32.

The Interior Spruce Climate Change/Genecology Trial (the "interior spruce provenance trial," EP 670.71.12) consists of 127 spruce populations from western Canada and the USA, 99 of which were natural stand populations. All populations were tested on 18 sites in British Columbia, Alberta, and the Yukon. Populations and test sites were strategically selected to sample nearly the full climate range of the species' distribution, with three test sites located beyond each species' natural distribution. At each site, an incomplete block design was applied with populations grouped into one of 16 sets in each of eight replications. Each family was tested in a four-tree row-plot in each replication. The trial was planted with 1-year-old seedlings in 2005. The height of the 99 natural stand populations measured after six field seasons (7 years from seed) at 17 extant sites was used in this analysis. Geographic and climatic distributions of the provenances and the frequency distribution of the transfers in these provenance trials are shown in Fig. 1.



Fig. 1 Geographic locations and climate of lodgepole pine (A) and interior spruce (B) used in this analysis. Site refers to the provenance test. Prov refers to provenances. MAT refers to mean annual temperature and log MAP refers to logarithm of the mean annual precipitation of sites and provenances in lodgepole pine (C) and interior spruce (D) provenance trials. Frequency distribution is calculated on seed transfer distance of MAT (E) and MAP (F) associated provenance trials of lodgepole pine and interior spruce

We use the term "population" to refer to a group of interbreeding individuals, and 'provenance' to refer to the location from which a population originated.

2.1.2 Climate data

We queried ClimateBC V7.10 (https://climatebc.ca/), and ClimateNA V7.10 (http://climatena.ca/) (Wang et al. 2012, 2016) to obtain 1961–1990 normal period mean values of 25 annual climate variables (accessed on June 17th, 2022) for each test site and provenance within and outside British Columbia, respectively.

Values of annual climate variables for the 30-year normal periods centered on 1975, 2025, 2055, and 2085 were also obtained from ClimateBC for a 1.6-km grid of British Columbia and used to interpolate or extrapolate to 2045, 2065, and 2105 (we refer to 30-year periods by their mid-period year). Climates of 2025, 2055, and 2085 were obtained from ClimateBC's ensemble of 13 general circulation models and shared socioeconomic pathway 245 in the CMIP 6 (Coupled Model Intercomparison Project Phase 6) climate change scenario, under which an additional radiative forcing of 4.5 W/m² by the year 2100 is predicted (Eyring et al. 2016).

Incorporating assisted migration into a seed transfer system will be most effective when the climate variables used to guide seed source migration and build seed transfer models are pairwise independent, or nearly so, and have changed considerably with Anthropogenic climate change. Using these criteria, we selected seven of the 25 annual climate variables-the same variables as were used in British Columbia's CBST system (O'Neill et al. 2017), which we used together with latitude to build transfer functions. These include mean annual temperature (MAT), mean coldest month temperature (MCMT), continentality (TD, temperature difference between coldest and warmest month mean temperature), mean annual precipitation (MAP), mean summer precipitation (MSP), growing degree days greater than 5 °C (DD5) and precipitation as snow (PAS)-variables often related to population differentiation in North American conifers (Table 1) (for simplicity, we refer to latitude and the seven climate variables collectively as "climate" variables). Preliminary analysis of 1961–1990 climate values of a 1.6-km grid of British Columbia showed skewed distributions of five of the climate variables; consequently, the BoxCox procedure (Box and Cox 1964) was used in PROC TRANSREG

Table 1	Annual	climate	variables	used t	o develop:	transfer
function	s in this	analysis				

Variable abbreviation	Climate variable	Unit
MAP	Mean annual precipitation	mm
DD5	Degree-days above 5 $^{\circ}$ C	℃ days
MAT	Mean annual temperature	°C
MCMT	Mean coldest month temperature	°C
MSP	Mean summer precipitation	mm
PAS	Precipitation as snow	mm
TD	Temperature difference (continentality; Mean warmest month temperature-MCMT)	°C

of SAS version 9.4 (2023) to find the optimum power transformation for each climate variable to achieve normality. The transformed variables are trTD=TD $^{0.25}$; trMAP=MAP $^{-0.75}$; trMSP=MSP $^{-0.75}$; trDD5=DD5 $^{0.5}$; and trPAS=PAS $^{-0.25}$.

2.1.3 Geographic data

Digital shape files were obtained for British Columbia's 24 wild stand (Class B) seed zones (Seed Planning Zones), British Columbia's 208 Biogeoclimatic Ecosystem Classification (BEC ver. 10) subzone variants (British Columbia Data Catalogue https://catalogue.data.gov.bc.ca/dataset/seed-planning-zones) (last accessed in June 2023). BEC subzone variants are hereafter referred to as 'seed zones'.

2.2 Data analysis

As an overview of the analyses, we simulated seed transfers within British Columbia that would be acceptable at eight genetic suitability thresholds in British Columbia's CBST system with and without assisted migration (i.e., 16 scenarios) and in British Columbia's GBST system and without any restrictions (no seed transfer system) (Table 2). For each of the 18 scenarios, the median genetic suitability of acceptable simulated point-topoint transfers (med*HTp*) and deployment area were calculated.

To calculate the genetic suitability of the acceptable simulated point-to-point transfers in the CBST scenarios (see Fig. 2), we used population × site height means from the provenance data to fit transfer functions relating population relative height (HTp) to climatic seed transfer distance. Lists of genetic suitability values for seed zone-to-seed zone transfers (calculated using seed zone mean climates) were created. A large set of simulated point-to-point transfers within British Columbia was created and the lists were used to identify those simulated transfers

Table 2 Seed transfer system scenarios evaluated in this report

Scenario	System	Assisted migration	Genetic suitability threshold (%)
1	CBST	No	99.0
2	CBST	No	98.0
3	CBST	No	97.0
4	CBST	No	96.0
5	CBST	No	95.0
6	CBST	No	94.0
7	CBST	No	93.0
8	CBST	No	92.0
9	CBST	Yes	99.0
10	CBST	Yes	98.0
11	CBST	Yes	97.0
12	CBST	Yes	96.0
13	CBST	Yes	95.0
14	CBST	Yes	94.0
15	CBST	Yes	93.0
16	CBST	Yes	92.0
17	GBST	No	N/A
18	No system	No	N/A

 $[\]it CBST$ climate-based seed transfer, $\it GBST$ geographic-based seed transfer, $\it N/A$ not applicable

deemed acceptable in CBST and CBST-AM at each of the 8 genetic suitability thresholds. Those transfers that met the geographic constraints of British Columbia's GBST system were also identified. Climate transfer distances of acceptable simulated transfers in each scenario were used to estimate Euclidean transfer distances, which were substituted into the fitted transfer functions to calculate medHTp, the median HTp of the acceptable simulated transfer scenarios.

2.2.1 Transfer functions

Site and population climate variables were transformed (see Climate data section above) and the transformed values rescaled to standard normal deviates based on the mean and standard deviation of 1975 climate values of a 1.6-km grid of points in British Columbia. Distances between provenances and test sites for the eight "climate" variables (latitude plus seven climate variables) were then condensed into a univariate Euclidean distance (ED) index. As EDs are necessarily positive, a half-normal function was used to fit individual transfer functions (Eq. 1) relating population mean height (*Y*) to ED for each site using the nonlinear NLIN procedure in SAS:

$$Y = A \times exp^{\frac{-0.5 \times ED^2}{\sigma^2}}$$
(1)



The following procedures were followed for each tree species:

- 1. Provenance data, together with test site and provenance climate data, were used to fit a transfer function.
- 2. Using seed zone climate means, two lists of genetic suitability (HTp) values were created for all seed zone-to-seed zone transfers within British Columbia: one list that does not use assisted migration and one list that uses assisted migration.

Then for each simulation scenario the following analyses were conducted at each of the 8 genetic suitability threshold levels (tHTp):

- 3. Forty thousand random point-to-point transfers within British Columbia were simulated.
- 4. The genetic suitably lists from (1) above were used to identify those random point-to-point transfers that are acceptable (inter-seed zone HTp > tHTp).
- 5. The climates of the seed sources and the plantations of the acceptable simulated transfers were used to calculate the Euclidean transfer distance of each transfer. The Euclidean transfer distance was substituted into the transfer function and used to calculate HTp of each simulated transfer, The median HTp of acceptable transfers (medHTp) was calculated for each scenario.

Fig. 2 Outline of climate-based seed transfer analysis to calculate impacts of seed transfer on genetic suitability

where *A* and σ^2 are model parameters that describe the scalar (maximum fitted response value) and rate of decline of the response value, respectively at each site.

In the next step, data were pooled, extending the climate transfer range to lend stability to the function (Carter 1996), and a single half-normal function fitted for each species. Several factors can result in local adaptation not being detected in individual provenance trials, including insufficient extreme climate events, high levels of damaging biotic agents, substantial environmental variation, insufficient replication or sample size, measurement error, planting error, or data error. In these cases, transfer function curves could be biased or unrealistically flat. Consequently, to avoid underestimating local adaptation by generating pooled transfer functions that are flatter than what might be expected from ideal design, testing, and measurement, we removed the least informative sites (i.e., sites with poor-fitting transfer functions, R^2 < 0.25) prior to pooling data. To account for site productivity differences, prior to pooling, population mean heights, Y, were divided by A (i.e., by the modeled height of a local population) for each site and multiplied by 100 to calculate HTp, population height values expressed as a percent of the estimated height of a local population at each site. HTp was used as the dependent variable in the pooled transfer function (Carter 1996).

To facilitate the interpretation of impacts to height associated with a given climate transfer distance, we forced the pooled transfer function to pass through the point (0,100) by setting *A* to 100. Also, to allow transferability to differ among climates, σ^2 in Eq. 1 was replaced with an exponentiated linear combination of one of the eight site climate variables:

$$\sigma^2 = e^{(b_o + b_1 \times Cli.s)} \tag{2}$$

where b_0 and b_1 are fitted constants and *Cli.s* is a slope-modifying site climate variable.

2.2.2 Genetic suitability lists

Euclidean climate distances between all pairs of seed zones were calculated using seed zone mean climates and substituted into the pooled transfer functions to calculate HTp for each inter-seed zone transfer for each species. Values in this list constitute the genetic suitability

for inter-seed zone transfers conducted without assisted migration (CBST).

To mitigate climate change impacts on plantations, the historic climates of seed sources should match the plantation climate shortly after establishment, which implies that seed used in reforestation should be selected from climates slightly warmer than the plantation location (Pedlar et al. 2012; O'Neill et al. 2017). Following procedures similar to those recommended by Ukrainetz et al. (2011) and O'Neill et al. (2017), we used an establishment date of 2025 and an 80-year plantation lifespan to represent the harvest cycle of many boreal and sub-boreal forestry regions. Climate migration distances were calculated for each seed zone by subtracting the climate to which the seed is expected to be best adapted (i.e., its historic climate, 1945) from its target climate-the climate expected at ¼ of the plantation lifespan (20 years after establishment, 2045). Migration distances for each seed zone were then added to the corresponding seed zone's historic plantation climate before calculating climate distances between all pairs of seed zone climate means. Climate distances of each inter-seed zone transfer were then substituted into the pooled transfer functions to calculate *HTp* for each inter-seed zone transfer for each species, with *HTp* representing the genetic suitability of transfers conducted with assisted migration (CBST-AM).

Acceptable simulated CBST and CBST-AM transfers were identified as those with inter-seed zone HTp > tHTp.

2.2.3 Seed transfer scenarios and assessment

To assess the effect of assisted migration and the genetic suitability threshold on expected growth and deployment area, for each species we generated 16 seed transfer scenarios in a CBST system: eight genetic suitability thresholds (tHTp) between 92.0% and 99.0%, with and without assisted migration (Table 2). Also, for each species, two additional scenarios were run-one in a GBST system and one in the absence of a seed transfer system (Table 2). Each of the 18 scenarios was simulated independently with 40,000 random point-to-point transfers within British Columbia. Impacts were quantified on 2 dates (2025-establishment and 2105-harvest) by using climates on these two dates for plantation point climates. Each scenario was run 4 times. The number of simulated random transfers was increased beyond 40,000 for a small number of scenarios to ensure that the number of acceptable transfers exceeded 1000.

For each simulated point-to-point transfer, the distance between the climate of the seed source and the climate of the plantation was used to calculate *HTp*. Acceptable GBST transfers were identified as those that remained within their seed zone of origin, and for which the absolute transfer distances for elevation, latitude, and longitude were less than 200 m, 1.5°, and 2.5° for lodgepole pine, and 300 m, 1.5°, and 3.5° for interior spruce. British Columbia's former wild stand seed transfer system used asymmetric geographic transfer limits (e.g., 300 m upward, 100 m downward) (Nicholls 2018), while most other jurisdictions with fixed zone seed transfer systems require seed to remain within the elevational band from which it originated, or they use symmetric geographic transfer limits. For example, the deployment of natural stand seedlots in Alberta, Canada, and Washington state, USA, is restricted to the same seed zone and elevation band as it originated (AAF 2016; Randall and Berang 2002). Therefore, to increase the inference of our results, we emulated other jurisdictions by using symmetric transfer limits equal in range to that of British Columbia's former GBST system.

Adaptation was quantified as the median HTp for all acceptable transfers within each scenario (medHTp). Deployment area was also calculated for each scenario as the sum of the area (km²) of all seed zones to which each simulated seed source was eligible to be deployed.

Four runs of each scenario enabled 1-sided, 2-sample, unequal variance t-tests to be calculated to test our three hypotheses on both species. The effect of assisted migration (Hypothesis 1) was tested by comparing med-HTp in CBST with assisted migration (CBST-AM) and CBST without assisted migration (CBST) (scenario 11 vs 3, Table 2). The effect of the seed transfer system was tested by comparing medHTp in CBST and in GBST (Hypothesis 2). In this analysis, CBST was run without assisted migration to isolate the impacts of the seed transfer system from those of assisted migration. Finally, the combined effect of CBST and assisted migration versus GBST was evaluated in a test of medHTp in CBST-AM versus GBST (scenario 11 vs 17, Table 2) (Hypothesis 3). All tests involving CBST used scenarios where tHTpwas 97.0%-the average genetic suitability value across all species in British Columbia-and used responses in 2105, the date when impacts are most evident. The three t-tests were repeated to assess the impacts of the deployment area.

To assess the trade-off between adaptation and deployment area, we regressed the deployment area on med-*HTp* in 2105 for CBST-AM and examined the slope of the fitted regression. And lastly, as some jurisdictions have no seed transfer system, we also calculated med*HTp* for the situation where seed transfer is unconstrained to provide a baseline for assessing the impacts of seed transfer systems in general.

Technical terms used in the data analysis are explained in the Glossary of terms.

Luo et al. Annals of Forest Science (2025) 82:7

3 Results

3.1 Transfer functions

Pooled transfer functions were relatively strong and nearly equivalent for both species (RMSE = 14.0 and 13.9 for lodgepole pine and interior spruce, respectively), but were considerably steeper for lodgepole pine than for interior spruce (Fig. 3 and Table 3). MCMT and TD were identified as the site climate variables that accounted for the most variation in tree height for lodgepole pine and interior spruce, respectively, with steeper curves associated with harsher site climates. Plots of the predicted and observed values of medHTp did not show any evidence of heteroscedasticity (Fig. 4).

3.2 Seed transfer simulations

At harvest age (i.e., in 2105), assisted migration had a large, positive, and significant effect on height of lodgepole pine (medHTp=92.5% (CBST-AM) and 84.9% (CBST), *p*=0.0000) and a small, positive, and significant effect on height of interior spruce (medHTp=94.7% (CBST-AM) and 92.4% (CBST), *p*=0.0000) (Hypothesis 1) (Table 4). The seed transfer system had a small and significant effect on the height of lodgepole pine (med-HTp=84.9% (CBST) and 86.0% (GBST), *p*=0.0004) and interior spruce (medHTp=92.4% (CBST) and 91.7% (GBST), *p*=0.0103) (Hypothesis 2). However, when assisted migration was used in conjunction with CBST, height was substantially greater than in GBST

8



Euclidean transfer distance

Fig. 3 Transfer functions relating genetic suitability (*HTp*, population height relative to local population height) to the multivariate (Euclidean) climate transfer distance and site climate for four test site climates. Test site climate variables are mean coldest month temperatures (MCMT) for lodgepole pine and temperature difference (the difference between coldest and warmest month mean temperature, TD) for interior spruce

Species	Site climate variable	b _o	<i>b</i> ₁	df	No. sites	RMSE
Lodgepole pine	MCMT	3.3807	0.0351	1835	42	14.0
Interior spruce	TD	5.1272	-0.0512	623	5	13.9

 Table 3
 Summary of the pooled height transfer function analysis for lodgepole pine and interior spruce

Pooled height transfer function relates genetic suitability (i.e., *HTp*, population height relative to local population height) to Euclidean climate transfer distance and site climate in a half normal function (Eqs. 1 and 2). b_0 and b_1 are parameter estimates. df is residual degrees of freedom. No. sites refer to the number of retained test sites. RMSE is the root mean square error of the transfer function



Fig. 4 Predicted versus observed values of HTp for the fitted pooled transfer functions for lodgepole pine (a) and interior spruce (b)

for lodgepole pine (medHTp = 92.5% (CBST-AM) and 86.0% (GBST), p = 0.0000) and for interior spruce (medHTp = 94.7% (CBST-AM) and 86.0% (GBST), p = 0.0000) (Hypothesis 3) (Tables 4).

At age of harvest, assisted migration reduced deployment area of lodgepole pine (area = 28,215 km² (CBST-AM) and 57,204 km² (CBST), p = 0.0000) but increased it in interior spruce (area = 136,601 km² (CBST-AM) and 155,375 km² (CBST), p = 0.0000) (Hypothesis 1) (Fig. 5, Table 4). However, the seed transfer system had a large effect on the deployment area for lodgepole pine (area = $57,204 \text{ km}^2$ (CBST) and 12,725 km² (GBST), p = 0.0000) and interior spruce $(area = 155,374 \text{ km}^2 \text{ (CBST)} \text{ and } 18,660 \text{ km}^2 \text{ (GBST)},$ p = 0.0000) (Hypothesis 2). When assisted migration was used in conjunction with CBST, deployment area was substantially greater than in GBST for lodgepole pine (Area = 28,215 km² (CBST-AM) and 12,725 km^2 (GBST), p = 0.0000) and for interior spruce (Area = 136,601 km² (CBST-AM) and 18,660 km² (GBST), p = 0.0000) (Hypothesis 3).

Increases in genetic suitability (med*HTp*) in 2105 associated with the use of more restrictive genetic suitability thresholds resulted in considerably greater declines in deployment area for spruce ($-81,822 \text{ km}^2$ /unit of med-*HTp*) than for lodgepole pine ($-16,424 \text{ km}^2$ /unit of med-*HTp*) when using CBST-AM (Fig. 5 and Table 5).

Were seed transfers to be unrestricted in British Columbia, seed could be deployed to the full extent of the province (946,069 km²), however, average genetic suitability would be only 70.1% (*versus* 86.0% in GBST) for lodgepole pine and 86.9% (*versus* 91.7% in GBST) for interior spruce (Table 5). Therefore, GBST can be expected to increase height growth at rotation by 15.9% in lodgepole pine and 4.8% in interior spruce, relative to no seed transfer system.

4 Discussion

4.1 Assisted migration increases growth while CBST increases deployment area

Geographic-based seed transfer systems (GBST) widely used in forestry have remained largely unchanged in their design and application since they were first implemented in Europe in 1927 (Eneroth 1927), and in British Columbia in 1940 (Ying and Yanchuk 2006). However, new high-resolution climate models, geographic information systems, and new analysis techniques have set the stage for two recent innovations to seed source selection-focal zone, climate-based seed transfer systems, and assisted migration-that may provide significant opportunities to mitigate climate change impacts to adaptation while increasing seed deployment area. Using wide-ranging provenance trials, we find that assisted migration can provide substantial improvement in growth in the face of a changing climate, while a focal zone, climate-based seed transfer system (CBST), compared with a GBST system, can vastly increase seed deployment area for two important conifer tree species in western Canada. When used in combination, a focal zone, climate-based seed transfer system (CBST) together with assisted migration (scenario 11, Table 2), had a moderate and positive impact on the height growth of lodgepole pine (6.5%) and interior spruce (3.0%) at harvest, and a very large and positive impact

Table 4 Results of tests of three hypotheses associated with impacts of simulations of seed transfer system scenar

	t-test scenario	а		Ь					
Hypotheses	a>b		SD		SD	med <i>HTp</i> difference (%)	Volume difference (%)	Deployment ratio	<i>p</i> -value
Lodgepole pine									
1. Height growth is greater in CBST-AM than in CBST	11>3	92.5 (%)	0.13 (%)	84.9 (%)	0.25 (%)	7.6	15.3		0.0000
2. Height growth is greater in CBST than in GBST	3>17	84.9 (%)	0.25 (%)	86.0 (%)	0.26 (%)	- 1.1	-2.3		0.0004
3. Height growth is greater in CBST-AM than in GBST	11>17	92.5 (%)	0.13 (%)	86.0 (%)	0.26 (%)	6.5	13.0		0.0000
1. Deployment area is greater in CBST-AM than in CBST	11>3	28,215 (km²)	1314 (km²)	57,204 (km ²)	788 (km²)			0.5	0.0000
2. Deployment area is greater in CBST than in GBST	3>17	57,204 (km ²)	788 (km²)	12,725 (km²)	769 (km²)			4.5	0.0000
3. Deployment area is greater in CBST-AM than in GBST	11>17	28,215 (km²)	1314 (km²)	12,725 (km ²)	769 (km²)			2.2	0.0000
Interior spruce									
1. Height growth is greater in CBST-AM than in CBST	11>3	94.7 (%)	0.04 (%)	92.4 (%)	0.05 (%)	2.3	4.7		0.0000
2. Height growth is greater in CBST than in GBST	3>17	92.4 (%)	0.05 (%)	91.7 (%)	0.31 (%)	0.7	1.4		0.0103
3. Height growth is greater in CBST-AM than in GBST	11>17	94.7 (%)	0.04 (%)	91.7 (%)	0.31 (%)	3.0	6.0		0.0001
1. Deployment area is greater in CBST-AM than in CBST	11>3	136,601 (km²)	2610 (km²)	155,374 (km²)	1840 (km²)			0.9	0.0000
2. Deployment area is greater in CBST than in GBST	3>17	155,374 (km ²)	1840 (km²)	18,660 (km ²)	903 (km²)			8.3	0.0000
3. Deployment area is greater in CBST-AM than in GBST	11>17	136,601 (km²)	2610 (km ²)	18,660 (km²)	903 (km²)			7.3	0.0000

 \bar{x} and SD are the average and standard deviation of median genetic suitability (med*HTp*, population height values as a percent of the estimated height of a local population) and deployment area for seed transfer system scenarios for lodgepole pine and interior spruce at harvest. All tests are 1-sided, 2-sample, equal variance *t*-tests based on *n* = 4 independent, large-scale runs of each simulation. Hypotheses involving height pertain to med*HTp* in 2105. CBST-AM and CBST refer to climate-based seed transfer systems with and without assisted migration, respectively. med*HTp* difference is the difference expressed in the hypothesis. Volume difference is twice the med*HTp* difference (see Sect. 4.1). Deployment ratio is the deployment area of scenario *a* divided by the deployment area of scenario *b*

on deployment area of lodgepole pine (2.2 times greater) and interior spruce (7.3 times greater) relative to GBST (scenario 17, Tables 2 and 5). Given that changes to volume for lodgepole pine and interior spruce are approximately double those of height, according to British Columbia's Table Interpolation Program for Stand Yields (Xie and Yanchuk 2003), volume gains (i.e., 13.0% and 6.0%, respectively) (Table 4) and greatly increased seed

deployability should justify the small cost of converting to a CBST-AM system.

These findings speak to the ability of a focal zone climate-based seed transfer system to accommodate transfer between climates that recur in disparate locations, and the stronger relationship of population differentiation with climate than with geography. The superiority of the CBST system used here over a GBST system also likely reveals the ability of British Columbia's ecosystem



Fig. 5 Genetic suitability—deployment area trade-off for lodgepole pine (a and b) and interior spruce (c and d). Values are for eight levels of transferability from a threshold genetic suitability of 99.0% (most restrictive) to 92.0% (least restrictive) at ¼ of the plantation lifespan (i.e., in 2045) when using a climate-based seed transfer (CBST) system, with and without assisted migration, and a geographic-based seed transfer system (GBST). Numbers beside dots indicate the genetic suitability threshold. Results are provided at two points in the lifespan of a plantation: at establishment (2025, **a** and **c**) and harvest (2105, **b** and **d**). Genetic suitability values and deployment areas are the average of a minimum of 1000 randomly selected point-to-point simulated seed transfers that meet the genetic suitability threshold for CBST or the seed transfer limits for British Columbia's former GBST system. Average (i.e., realized) genetic suitability was calculated from the climate transfer distances associated with the seed climate of 1961–1990 and plantation location climates at establishment and harvest

classification system—based largely on vegetation—to reflect climate variation (Delong et al. 2010), and its ecosystems to serve as effective seed zones in a focal zone seed transfer system. The efficiency of CBST (i.e., greater growth rate and deployment area than GBST) also arises from the use of considerably more zones than are commonly used in GBST: British Columbia's ecosystem classification system used in its CBST system contains 208 ecosystems, while its former GBST system contained 24 zones. The use of more zones and overlapping deployment areas for seedlots from different seed zones can complicate administration. Nonetheless, the expanded deployment area reduces wildstand seed collection efforts and the number of breeding and seed production programs needed and provides better matching of seed source and plantation climate, which should vastly outweigh the slightly increased administration effort. Although local adaptation is not detected for some traits, even for tree species with wide geographic ranges (Candido-Ribeiro and Aitken 2024), local adaptation of height growth, as shown by the strong relationship between genetic suitability and transfer distance, suggests that assisted migration should mitigate growth impacts associated with climate change.

	SD		0.30	0.18	0.25	0.36	0.37	0.44	0.41	0.40	0.18	0.26	0.13	0.23	0.27	0.19	0.10	0.16	0.26	0.11		0.07	0.04	0.05	0.05	0.04	0.04	0.02	0.02	0.16	0.03	0.04	0.04
	Mean		34.3	34.9	34.9	34.7	34.6	33.8	33.8	33.3	94.7	93.9	92.5	91.7	90.1	38.8	38.7	38.3	36.0	70.1		91.8	92.3	92.4	91.7	91.7	91.5	91.3	91.1	1.76	96.1	94.7	744
	n 4 n		1.7 8	1.7 8	8.	1.5 8	5.1	3.5 8	8.7 8	8.1 8	9.1	8.8	5.7	œ.	9.9	3.5 8	8.7 8	8.2 8	5.0 8	1.0		7.9	2.2	6.3	.7 9	.7 9	-7: 0	с. С	-1	9 9	5.1 9	9.1	0
	n 3 Ri		6	6	7	7 84	4	5 83	4 83	2 83	5	3 93	5 92	4 91	800	88	5 86	2 86	2 86	2		3 91	32	4 92	7 91	16 21	5 91	3 91	1 91	2	2	7	4
	2 Rui		83.	84.	.42	84.	84.	83.	83.	83.	94.	94.	92.	91.	89.	88	88.	88	86.	70.		.19	92.	92.	91.	91.	91.	91.	91.	97.	.96	94.	94,
	Run		84.4	85.0	85.0	84.4	84.5	83.5	83.8	83.1	94.7	93.8	92.4	91.6	90.2	88.7	88.6	88.2	86.3	70.0		91.9	92.3	92.3	91.7	91.6	91.4	91.3	91.1	97.2	96.1	94.7	643
ed <i>HTp</i> 2105	Run 1		84.4	85.2	85.2	85.2	85.1	84.4	84.4	83.9	94.9	93.9	92.6	92.0	90.4	89.0	88.7	88.5	85.7	70.0		91.9	92.3	92.4	91.8	91.7	91.5	91.3	91.1	97.2	96.1	94.7	04.4
ε	ß		0.33	0.16	0.20	0.31	0.22	0.32	0.14	0.25	0.10	0.20	0.04	0.29	0.19	0.12	0.08	0.19	0.13	0.0		0.02	0.01	0.02	0.04	0.05	0.03	0.04	0.03	0.04	0.03	0.04	0.03
	Mean		94.6	94.8	94.5	94.1	93.6	92.9	92.5	91.9	96.8	96.5	96.0	95.4	95.0	94.3	94.0	93.6	96.4	74.2		97.6	97.4	97.1	96.4	96.1	95.7	95.3	95.1	98.6	98.1	97.4	070
	Run 4		94.5	94.7	94.4	93.9	93.5	93.0	92.3	91.7	96.8	96.3	96.0	95.4	94.9	94.2	94.0	93.4	96.4	74.2		97.6	97.4	97.0	96.4	96.1	95.7	95.3	95.0	98.6	98.1	97.4	0.7.0
	Run 3		94.8	94.8	94.3	94.1	93.6	92.6	92.4	91.9	96.8	96.7	96.0	95.5	94.9	94.3	93.9	93.6	96.2	74.3		97.6	97.4	97.1	96.5	96.2	95.8	95.4	95.1	98.7	98.1	97.5	1.16
	lun 2		94.2	94.7	94.4	3.9 9	3.5	92.8	92.4	91.8	96.8	96.7	96.0	95.0	94.9	94.3	94.0	3.6	96.4	4.1		97.6	97.4	97.1	96.4	96.1	95.7	95.4	95.1	98.7	98.1	97.4	97.1
ITp 2025	-		01	01	0.	0,	01	0.	0.	01	0.	0.	0.	0.	0.	0.	0.	0.	0.			0,	0,	01	0,	0.	0,	0,	0.	0.	0.	0.	
hedh	Run 1		94.8	95.0	94.8	94.5	94.0	93.4	92.6	92.3	96.6	96.4	95.9	95.7	95.3	94.5	94.1	93.9	96.5	74.2		97.6	97.4	97.1	96.4	96.1	95.7	95.3	95.1	98.6	98.1	97.5	97.0
	SD		995	1159	788	1103	1096	2158	2051	1993	725	464	1314	769	2486	2406	2592	412	769	0		332	1127	1840	2474	2904	4352	4524	2961	752	1513	2610	1241
	Mean		28,182	40,548	57,204	75,535	94,331	120,724	145,617	170,318	9374	17,016	28,215	46,587	66,774	89,955	105,561	120,964	12,725	946,069		54,153	102,177	155,374	231,496	286,217	343,076	403,829	441,591	25,289	80,045	136,601	193.762
	lun 4		7,462	9,572	6,774	5,504	3,612	22,594	43,119	67,752	804	6,925	8,248	6,380	6,924	37,753	08,686	20,408	1,844	46,069		4,496	02,834	57,723	33,289	89,823	47,246	170	44,658	14,988	'9,425	37,650	94,027
(2)	un 3		9,293 2	0,685 3	5,322 5	5,270 7	4,234 9	19,503 1	44,832 1	70,357 1	344 9	7,627 1	5,349 2	7,723 4	5,419 6	3,101 8	796 1	21,154 1	3,689 1	46,069 <u>5</u>		3,953 5	01,161 1	55,689 1	30,386 2	36,876 2	41,359 3	33,453 2	42,114 4	4,456 2	3,761 7	32,700 1	91.936
area (km	n 2 R		231 29	803 4(719 56	355 71	568 94	2,494 1	6,822 14	2,616 1.	99	011 10	,047 2(,053 4.	906 6(529 93	2,508 10	0,927 1.	861 13	5,069 94		367 53	1,288 1(4,747 15	8,538 23	2,906 28	7,759 34	7,658 4(7,541 44	,489 2	767 78	7,873 13	4.562 19
oloyment	1 Ru		40 27,	31 39,	02 57,	13 74,	11 93,	305 12.	694 14	549 17.	4 83	02 17,	17 29,	91 46,	45 69,	38 90,	256 10	367 120	05 12,	069 94		97 54,	423 10	338 154	769 22	265 28	941 33	036 39.	049 43	23 25,	25 79,	183 13	522 19.
Dep	Run		28,7	42,1	58,0	77,0	95,9	118	147,	170,	966	16,5	29,2	46,1	63,8	88,4	106,	121,	12,5	946		53,7	103,	153,	233,	285,	345,	408,	442	26,2	82,2	138,	194
	tHTp		99.0	98.0	97.0	96.0	95.0	94.0	93.0	92.0	99.0	98.0	97.0	96.0	95.0	94.0	93.0	92.0	N/A	0		99.0	98.0	97.0	96.0	95.0	94.0	93.0	92.0	99.0	98.0	97.0	96.0
	WH L		No	No	No	No	No	No	No	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	No		No	No	No	No	No	No	No	No	Yes	Yes	Yes	Yes
	System	ole pine	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	GBST	No system	spruce	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST	CBST
	Sce- nario	Lodgep		2	m	4	-2	9	7	00	6	10	11	12	13	14	15	16	17	18	Interior		2	m	4	-2	9	7	00	6	10	11	12

(2025) 82:7

	med <i>HTp</i> 2025	
Table 5 (continued)	Deployment area (km²)	

				Deploym	ient area ((km²)				medHTp 2(125				теритр:	2105					
13	CBST	Yes	95.0	250,860	250,849	248,073	250,995	250,194	1415	96.6	96.7	9.96	96.6	96.6	0.03	93.9	93.8	93.9	93.8	93.8	0.07
14	CBST	Yes	94.0	300,887	301,116	299,178	303,498	301,170	1777	96.3	96.3	96.2	96.2	96.3	0.03	93.4	93.3	93.5	93.4	93.4	0.05
15	CBST	Yes	93.0	356,157	354,835	353,395	358,644	355,758	2230	95.8	95.9	95.8	95.8	95.8	0.02	92.9	92.8	92.9	92.9	92.9	0.03
16	CBST	Yes	92.0	407,701	406,377	403,668	411,081	407,207	3080	95.4	95.5	95.4	95.4	95.4	0.05	92.5	92.4	92.5	92.4	92.4	0.03
17	GBST	No	N/A	17,934	18,861	19,855	17,990	18,660	903	97.8	97.9	98.0	97.8	97.9	0.08	91.6	91.6	91.4	92.1	91.7	0.31
18	No	No	0	946,069	946,069	946,069	946,069	946,069	0	90.5	90.4	90.4	90.4	90.4	0.05	86.8	86.9	87.0	87.0	86.9	0.08
	system																				

HTp is the population height as a percent of the estimated height of a local population. medHTp is the median HTp of simulated random transfers at establishment (2025) and harvest (2105). SD refers to the standard deviation of medHTp. AM refers to assisted migration. tHTp refers to the genetic suitability threshold. CBST refers to climate-based seed transfer. GBST refers to assisted migration.

The ability of assisted migration to mitigate climate change impacts on height was evident at establishment, increased toward harvest, and was more pronounced in lodgepole pine than in interior spruce (Fig. 5, Table 5). These findings can be understood by considering transfer function steepness (Fig. 3) and the trajectory of climate change (Fig. 6). In our simulations, medHTp-our measure of adaptation-directly reflects the climate distance between seed sources and plantations of all acceptable transfers in a seed transfer system. Also evident in Fig. 6 is the evolutionary lag when assisted migration is not invoked, with the mean climate of the eligible seed sources being colder than that of the plantation location, and the extent to which assisted migration reduces the lag. We selected SSP 245, a climate change scenario corresponding to intermediate greenhouse gas emissions, to demonstrate the potential assisted migration to address climate change. However, the same procedure of assessing assisted migration can be easily repeated for other climate change scenarios, under which greater or lesser maladaptation is expected. Finally, the accelerating steepness of the transfer functions from their peak (Fig. 3) translates into exponentially increasing benefits of assisted migration over time, as observed in Figs. 5 and 6, and suggests that long-lived species or regions with long harvest ages may benefit the most from assisted migration. Likewise, if future emissions trajectories exceed the SSP 245 scenario employed in this analysis, the actual benefit of assisted migration is likely greater than is shown by our analyses.

4.2 Designing a focal zone seed transfer system

The eligibility of a given transfer in a focal zone seed transfer system is determined by the climate distance between the mean climate of a seed source seed zone and the mean climate of the plantation seed zone. As the climates of both the seed source and plantation seed zones consist of a distribution of climates about their means, some transfers may exceed the climate distance associated with the genetic suitability threshold. For example, using a genetic suitability threshold of 97.0% for lodgepole pine in a CBST system without assisted migration would result in an observed (medHTp) genetic suitability of 94.5% in 2025 (Fig. 5, Table 4), indicating that a significant proportion of transfers do not reach the genetic suitability threshold. This situation occurs when the climate distance between the seed source and plantation mean climates approaches the threshold, or the climate range of the seed source or plantation seed zones is large, as the average distance between points of two distributions is the square root of the distance between the distribution means plus the sum of the variances of the two distributions.

Consequently, to ensure that observed genetic suitability values (medHTp) are not substantially smaller than the genetic suitability threshold (t*HTp*), that is, to avoid unintendedly long transfers and associated risk of maladaptation, policy makers would be prudent to select a genetic suitability threshold cognizant that some transfers will exceed the threshold, particularly when the climate range within seed zones is considerably larger than the acceptable inter-seed zone climate range. This situation may be avoided by using ecosystems, or other classification systems, containing smaller zones that possess narrower climate space than those used in fixed zone seed transfer systems. Ideally, classification systems that minimize within zone climate range and maximize among zone climate space (Ukrainetz et al. 2011) and those with a uniform distribution of climate range among zones will be most effective at minimizing transfer distances and maximizing adaptation.

4.3 Setting the genetic suitability threshold

Our quantification of genetic suitability and deployment area at various genetic suitability thresholds provides a starting point for selecting an optimum threshold with which to restrict seed transfer. The relationship appears to be steeper at harvest than at establishment, steeper with assisted migration than without, and steeper for lodgepole pine than for interior spruce. Nonetheless, the optimum threshold in any situation will depend on the value each jurisdiction ascribes to adaptation versus deployment area. In the example provided in this analysis, using CBST-AM at a genetic suitability threshold of 97.0%, interior spruce can be deployed to a very large area (136,601 km²), but has a relatively small height gain (3.0%) (volume gain 6.0%) over GBST. Policymakers may choose instead to favor volume gain by using a more restrictive genetic suitability threshold (e.g., 99.0%), which would increase height gain to 5.5% (volume gain 11.0%) (Table 5). In this scenario, the deployment area (25,289 km²) would be much smaller but would still exceed that of GBST. The application of economic weights to these traits would enable the optimization of this assessment.

Also of note is the lack of linearity of the adaptationdeployment area relationship, particularly at high genetic suitability thresholds where medHTp declines at increased tHTp (Fig. 5). In these situations, only a handful of eligible seed procurement seed zones remain for a given plantation seed zone, and because seed zone climate means are not uniformly distributed in climate space, the further restriction can result in large changes in the average climate of the few remaining seed procurement seed zones. The lack of linearity in the adaptationdeployment area relationship is also greater for lodgepole



Fig. 6 Mean annual temperature and precipitation of randomly selected interior spruce seed sources in British Columbia (black dots) that are acceptable for planting in a randomly selected seed zone (Biogeoclimatic Ecosystem Classification subzone variant: ESSFmc—moist, cold Engelmann Spruce Subalpine fir) (red dots) according to a climate-based seed transfer system (CBST) under genetic suitability threshold 98.0% (**a** and **c**) and 95.0% (**b** and **d**) without (**a** and **b**) and with (**c** and **d**) assisted migration. Note that the average climate distance between the seed source climate and the climate of the plantation (*HTp*) is greater when the genetic suitability threshold is lower and is greater as the plantation climate warms

pine because its steeper transfer functions result in fewer eligible seed source seed zones at all genetic suitability thresholds.

Differences between the study's two tree species are also important. The adaptation-deployment area slope was steeper for lodgepole pine. Consequently, pursuing a higher medHTp (observed genetic suitability) for lodgepole pine will return a smaller deployment area compared to interior spruce, potentially leading to wider deployment of interior spruce. These findings highlight the need to consider the adaptation-deployment area relationship when setting genetic suitability thresholds.

4.4 The half-normal function

The results of these analyses are strongly influenced by the shape of transfer functions that translate climate

transfer distance into height growth impacts. Non-local optimality, the situation in which the fittest populations for a plantation are not found locally, and which can arise due to constrained gene flow (Slatkin 1987; Wu and Ying 2004), adaptation lag (Etterson et al. 2020; Frejaville et al. 2020), or random drift (Blanquart et al. 2012), is well documented, particularly in long-lived, sessile species such as forest trees, and offers the prospect of identifying climates hosting populations expected to outperform local populations. However, the climate of optimum non-local populations cannot be identified from the halfnormal transfer function used in our analyses and in British Columbia's CBST system, as the function peaks at the zero-transfer distance. Also, asymmetry sometimes observed in 2-tailed transfer functions (Savolainen et al. 2007; Wang et al. 2010; Leites et al. 2012a,), is obscured in the half-normal function, potentially biasing estimates of transfer impacts.

Mitigating these concerns is the argument that locating the climate of populations expected to be best adapted to a plantation location is more likely to be achieved by adding the migration distance to the plantation climate, than by locating the position of the vertex of a 2-tailed transfer function or universal response function. The migration distance is accurately and easily determined from the historic and near-future climate of the plantation, whereas the position of the vertex can vary substantially with both the dependent and independent variable (Berlin et al. 2016), tree age, climate transfer range, and distribution (Wang et al. 2010; Leites et al. 2012a, 2012b) and test site climate (Rehfeldt et al. 1999; O'Neill et al. 2008). The half-normal function, on the other hand, accommodates Euclidean climate transfer distances which provide stability across a range of climates when composed of multiple climate variables (O'Neill et al. 2014); it is relatively insensitive to situations where a "tail" is lacking on one side of a transfer function, a frequent situation in provenance tests and a common source of spurious results in genecology analyses (Wang et al. 2010; Leites et al. 2012a); it has a logical form (broad, flat vertex and asymptotic tail); and perhaps, most importantly, it obviates reliance on the function to estimate recent evolutionary lag.

4.5 Transfer distances are shorter in extreme environments

Transfer functions were steeper in more extreme plantation climates, resulting in shorter safe seed transfer distances on the periphery of species' distributions where extreme climates are located (Fig. 2). As tree population density is typically lower on the periphery of a species' distribution, net gene flow is likely to be toward the periphery. Known as "gene swamping" (Davis and Shaw 2001; Aitken et al. 2008), this phenomenon provides a plausible explanation for steeper transfer functions in extreme environments, as it may result in suitable seed sources for more central plantations being located across a wider geographic and climate range than plantations in peripheral locations where suitable seed sources may be found only in relatively proximal climates.

5 Conclusions and limitations

Results presented in this study provide strong evidence that assisted migration implemented in a climate-based focal zone seed transfer system will afford a closer match of seed and plantation climates and greater deployment area than will current GBST systems for lodgepole pine and interior spruce in western Canada. Implementation of CBST should therefore yield improved adaptation, reduced seed collection costs, and greater flexibility to users in a changing climate. Further, these analyses offer an approach to assess the adaptation-deployment tradeoff, helping to optimize competing needs for adaptation and wider seed deployability.

Notwithstanding the points mentioned above, our study has several limitations that constrain the inference of our findings. We examine two western North American conifer species tested exclusively in western North America. Our analyses use height growth in assessing local adaptation, however, other adaptation traits (e.g., diameter, survival, health, or drought resistance) or combinations of traits could reveal greater insight into local adaptation and the effectiveness of assisted migration. We used a single emissions scenario; other scenarios could provide different outcomes.

Further, our simulations of CBST systems with assisted migration will need periodic adjustment as continued climate warming will necessitate longer migration distances. Simulations such as we have performed require accurate transfer functions that rely on strong provenance test data. While many jurisdictions lack provenance tests required to perform these analyses, safe seed transfer distances needed to implement CBST can be inferred from existing fixed zone systems, or from tests of specialist species that have conservative (short) safe seed transfer distances. It is our hope that these findings will support improved decision-making, and together with research into other climate change adaptation strategies (e.g., composite and climate-adjusted provenancing (Breed et al. 2013; Prober et al. 2015) and close-to-nature silviculture (Brang et al 2014)) will lead to more resilient future forests, as forest managers and policy makers work to adapt to the climate crisis.

Glossary

НТр	is a population height value expressed as a percent of the estimated height of
	a local population at each site in a prov-
	enance trial. HTp values are the depend-
	ent values used to fit transfer functions.
Genetic suitability	is the HTp value of a simulated single
	point-to-point random transfer cal-
	culated by substituting the Euclidean
	climate distance for the transfer into a
	fitted transfer function.
Median genetic suitability (medH1p)	is the median HIP of all the simulated
	point-to-point random transfers associ-
	Aled with a specific seed transfer scenario.
	called 'observed' appetic suitabilities
Genetic suitability list	is the set of HTp values for all inter-seed
Genetic suitability list	zone transfers calculated by substituting
	the mean climates of the seed zone of
	the plantation and the seed source into
	the fitted transfer function for each spe-
	cies. Genetic suitability list values are also
	called 'expected' genetic suitabilities.
Genetic suitability threshold (tHTp)	is a HTp value that identifies acceptable
	seed zone-to-seed zone transfers. Trans-
	fers are acceptable where HTp > t HTp.
Migration distances	are climate values added to the climates
	of the seed zones of the plantations before
	genetic suitability lists are created. Add-
	ing migration distances to climates of the
	seed zones of the plantations is intended
	to ensure that planted populations are
	exposed to their historic climates shortly
	after establishment and is the mechanism
	by which assisted migration is imple-
	menteu în climate-paseu seeu trânsfêf.

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Authors' contributions

Conceptualization: DL; methodology: DL, GO; formal analysis and investigation: DL, GO; writing—original draft preparation: DL; writing—review and editing: GO, BT, NU, TW; funding acquisition: NU, GO; supervision: GO. All authors have read and approved the final manuscript.

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Data availability

Data access is authorized by the BC Ministry of Forest and is available upon request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors agreed to the content of this publication.

Competing interests

The authors declare no conflict of interest.

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