


Climate change risk management in tree improvement programs: selection and movement of genotypes

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Abstract Tree improvement programs usually consist of multiple breeding populations that target different climatic or ecological regions. Parent breeding material normally originates from and is deployed within the same breeding region, assuming optimal local adaptation of populations. Given the climate trends observed over the last several decades in western Canada, this assumption is unlikely to still be valid. This problem needs to be addressed either by delineating new deployment areas for improved planting stock or by selecting genotypes suitable for changed climatic environments. In a case study for white spruce, we analyzed height data from 135,000 trees grown in 44 genetic tests established and evaluated over a period of 35 years by industry and government agencies in Alberta. We show how the risk of planting maladapted trees can be minimized by moving planting stock to new areas, or by eliminating genotypes from breeding programs that are sensitive to anticipated future climate

environments. Transfers that outperformed local sources consistently originated from locations with higher temperatures, suggesting north or northwest transfers. However, adaptation to cold appears to be a prevalent driver for genetic population differentiation in spruce, thus limiting how far material may be moved in current reforestation efforts to address future climate change.

Keywords Reforestation · Climate change · White spruce · Seed transfer · Breeding programs

Introduction

The choice of planting stock for reforestation is typically guided by both the suitability of a species for a planting site and the genetic adaptation of the seed source to the climatic environment. Populations of wide ranging forest tree species are usually genetically differentiated in response to various environmental conditions within the range where they naturally occur (Kawecki and Ebert 2004; Savolainen et al. 2007). A mismatch between the planting environments and the environmental conditions to which reforestation stock is adapted could cause early mortality in plantations, loss of productivity, and vulnerability to insects and diseases (Gray et al. 2011; Peng et al. 2011). To avoid such problems, reforestation programs and tree improvement efforts rely on a system of transfer guidelines and seed zones, where planting and breeding material typically originate from and are deployed within the same general area.

A key assumption for this deployment strategy, that local sources are best adapted to the environment in which they occur may no longer be valid given an observed trend towards warmer and drier climate conditions over the last several decades. Alberta has experienced a 0.8 °C increase in annual

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temperature and approximately 10 % reduction in precipitation in the past 25 years (Mbogga et al. 2009). As a consequence, drought-induced aspen dieback has been observed in Alberta's southern boreal forests (Hogg et al. 2002, 2008; Michaelian et al. 2011). Future projections suggest that the trend towards warmer and drier climatic conditions will continue in the coming decades, potentially causing more frequent or severe droughts across the province's managed boreal forests (Fettig et al. 2013; Field et al. 2007; Wang et al. 2014). For most boreal tree populations, including white spruce (*Picea glauca* (Moench) Voss), drought-induced stress

is expected to have negative impacts on growth and mortality (Barber et al. 2000; Peng et al. 2011).

Reforestation programs for white spruce in Alberta use planting stock from both tree improvement programs and natural stand collections. Alberta's tree improvement program for white spruce is divided into nine breeding regions, each spanning approximately 2° of latitude in the boreal region and 400 m of elevation in the Rocky Mountain Foothills (Fig. 1a). Each breeding region has independent seed orchards and genetic tests for selection of superior provenances, families, and clones (SRD 2009). To avoid potential maladaptation

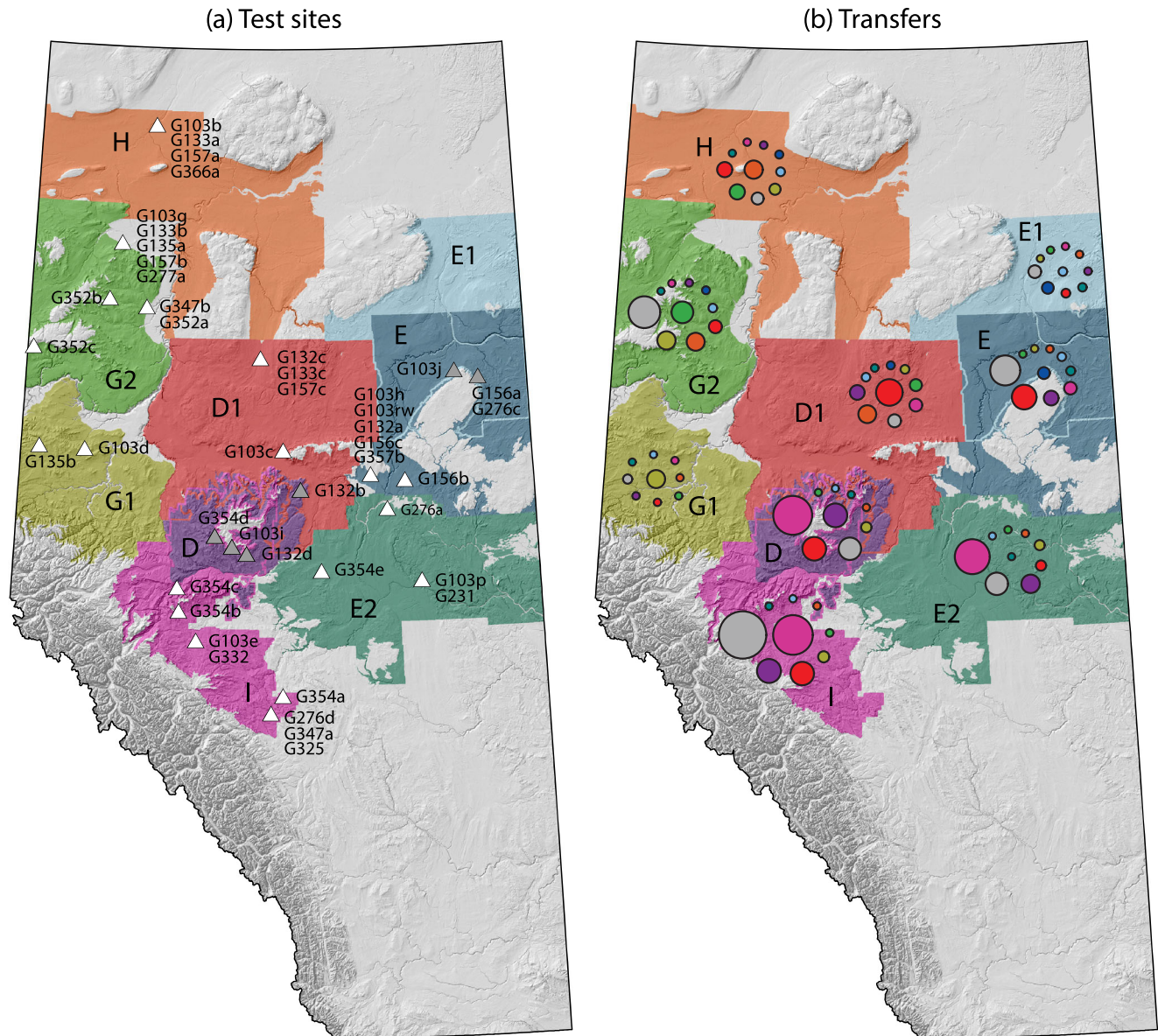


Fig. 1 Test sites (a) and transfers (b) among Alberta's white spruce breeding regions. For regions that overlap (D, D1, I and E, E1), the overlap boundaries are defined by the region outline of the same color. Test sites that fall within each region are presented as *triangles* with test sites that occur in an overlap between adjacent breeding regions colored *gray*. For each site, the trial series tested are identified with the trial series

test number (e.g., G103b). For the map of transfers, the size of the circles proportionally reflects the number of unique collections originating from within each colored breeding region respectively and transferred into another region for testing. The *circle* in the center represents the local breeding region collection

of planting stock used in reforestation programs, government regulations do not usually allow for improved planting stock from seed orchards to be transferred across regional boundaries (SRD 2009). However, even though breeding populations are assembled by selecting superior parent trees primarily from within the region, sources from outside the breeding region are extensively tested as well (Fig. 1b).

This reciprocal transfer of seed sources among breeding regions provides an opportunity to investigate how differently adapted populations respond in growth and survival when exposed to different climate conditions, and by implication, to climate change. Previous studies of one of these trial series (G103) have demonstrated genetic differentiation into three regions: northern, central, and high elevation (Rweyongeza et al. 2007b). Those differentiations primarily reflect adaptations to climate (Rweyongeza 2011), although some populations appear to inhabit suboptimal climate conditions with respect to growth potential (Rweyongeza et al. 2010). Climate-based seed transfer guidelines for observed and projected climate change have also been developed for white spruce in Alberta (Gray and Hamann 2012). However, they are based on the assumption that populations are currently optimally adapted to local climate conditions, and the recommendations did not consider actual growth response of different populations to climate change.

In the present study, we contribute a comprehensive evaluation of long-term genetic testing efforts of both government and industry programs in Alberta. We analyzed growth of 1170 white spruce families planted in 44 genetic tests both

within and outside their native breeding regions. The primary objective of this study is to quantify growth of improved planting stock when transferred among breeding regions. The results are interpreted in the context of the climatic differences between the source and target environments to infer how populations are adapted to climate, and which transfers may be safe under current climate conditions and anticipated climate change. Additionally, we aim to infer how different populations (represented by breeding regions) might in general respond to anticipated climate change. As a potential mitigation strategy, we investigate if we can minimize the risk of planting maladapted trees, eliminating from breeding and deployment populations those genotypes that appear less tolerant to anticipated trends to warmer and drier conditions. The results can be applied in tree improvement programs through roguing of seed orchards and exclusion of vulnerable genotypes from breeding populations.

Methods

Genetic field trials and measurements

Our analysis included data from ten white spruce progeny trial series (representing all nine breeding regions), where the female parents of the tested genotypes are known. These progeny trial series contain a total of 966 half-sib families in 28 trials at 20 sites (Table 1, Fig. 1). In total, about 110,000 trees in progeny trials were evaluated in this analysis. Next, we

Table 1 Summary of white spruce progeny and provenance trials by trial series, year planted, number of test sites and collections, and the age at time of evaluation for the progeny and provenance test series

Trial series	Year planted	Number of sites	Number of collections	Age at evaluation
Progeny test series				
G132	1986	4	150	16
G133	1988	3	131	24
G135	1988	2	73	21
G156	1994	3	70	18
G157	1994	3	61	18
G231	1986	1	18	30
G347	2000	2	88	10
G352	2001	3	137	10
G354	2001	5	301	14
G357	2002	2	79	7
Provenance test series				
G103	1981	11	86	32
G276	1993	4	23	17
G277	1993	1	40	17
G325	1997	1	49	15
G332	1999	1	73	12
G366	2005	2	53	7

Collections refer to open pollinated families and populations in progeny and provenance tests, respectively

included data from six provenance trial series that rely on bulk seed collections with multiple parent trees from a single forest stand. These provenance trial series test progeny from a total of 267 different populations planted across 20 trials at 14 sites (Table 1, Fig. 1). In total, approximately 25,000 trees in provenance trials were evaluated in this second analysis. We evaluated the latest available height measurements taken on all progeny and these varied between 7 and 32 years (Table 1). Measurements were expressed as percent height deviation from the local population, which we define as all collections that originate from within the breeding region where they were tested. All subsequent analysis and inferences are therefore based on relative deviations of the non-local sources from the local reference population.

Climatic data

Climatic characterization of the white spruce breeding regions was derived from spatially interpolated climate data for the 1961–1990 climate normal period generated using the software package ClimateWNA v4.62 (Hamann et al. 2013) freely available at <http://tinyurl.com/ClimateWNA>. This software relies on gridded climate surfaces generated with the Parameter Regression of Independent Slopes Model (PRISM) (Daly et al. 2008). The software also makes automatic lapse rate adjustments to temperature estimates if the elevation of the sample location of interest does not match the elevation of the gridded PRISM data (Hamann and Wang 2005). The variables we selected as potentially biologically relevant for population adaptation to climate included mean annual temperature (MAT), mean coldest month temperature (MCMT), mean warmest month temperature (MWMT), continentality (TD), mean annual precipitation (MAP), growing season precipitation (MSP), climate moisture deficit (CMD), frost-free period (FFP), number of frost-free days (NFFD), and growing degree days above 5 °C (DD5).

Estimating provenance and family performance

Over the 40 years since the earliest of the trials was installed, the experimental design has not always been identical. Generally, older trials (>15 years) rely on a randomized complete block design with row plots, while more recent trials were installed with an alpha design (Williams et al. 2002) with single-tree plots. To estimate the height of populations relative to local sources when transferred among breeding regions, we executed a two-step analysis. First, we obtained the best linear unbiased estimates (BLUEs) of provenance or family performance in each trial, taking advantage of their individual experimental designs. This analysis relied on a linear mixed model with blocks and incomplete blocks (if applicable) specified as random effects, and provenance or families as fixed effects. In the

second step, the BLUEs of breeding region means of source populations and target regions were calculated based on the BLUEs of individual families at individual test sites (obtained from the first step), according to the following model:

$$Y_{ijkl} = \mu + G(\text{RO})_{ji} + \text{RO}_j + S(\text{RT})_{lk} + \text{RT}_l + (\text{RO} \times \text{RT})_{jl} + e_{ijkl} \quad (1)$$

where Y_{ijkl} is the height measurement made for i^{th} genotypes (G) originating within the j^{th} region of origin (RO), and tested on the k^{th} site (S) within the l^{th} region of testing (RT). Genotype (G) stands for either a provenance or a half-sib family. (RO \times RT) represents the interaction between the region of origin and the region of testing, μ is the overall experimental mean and e the experimental error (residual). Note that both RO and RT refers to breeding regions, one being the breeding region where the genotype originated (RO), the other the breeding region where the genotype was tested (RT). RO and RT as well as their interaction were considered fixed effects. Random effects were provenances or families from within the breeding region of origin $G(\text{RO})$, and sites within breeding regions where the sites were located $S(\text{RT})$. Models for both steps were implemented with the *ASReml* package (Gilmour et al. 2009) for the R programming environment (R Development Core Team 2015). The BLUEs of relative height and their associated standard errors were obtained using the average information REML algorithm implemented with R function `predict.asreml` of the *ASReml* package (Gilmour et al. 1995).

For the purpose of roguing seed orchards or for selection of preferred genotypes for individual breeding populations, we fitted a third mixed model to estimate provenance or family performance, eliminating the breeding region of origin as a model effect,

$$Y_{ijk} = \mu + G_i + S(\text{RT})_{kj} + \text{RT}_k + (G \times \text{RT})_{ik} + e_{ijk} \quad (2)$$

where Y_{ijk} is the height measurement made for i^{th} genotypes (G) tested on the j^{th} site (S) within the k^{th} breeding region of testing (RT). Genotype (G) stands for either a provenance or a half-sib family and ($G \times \text{RT}$) represents the interaction between the genotype and the region of testing; μ is the overall experimental mean and e the experimental error (residual). Test sites within breeding regions were random effects and target breeding region and provenance or family were fixed effects. The BLUEs of the genotype \times breeding region interaction from this model represent the relative performance of individual provenances or families (G) within breeding regions (RT).

Genotype \times environment analysis

The breeding-region level genotype \times environment interaction term (RO \times RT) from model (1), representing the average

height of sources from their breeding region of origin (RO) when transferred to the breeding regions where they were tested (RT), was further investigated through hierarchical agglomerative clustering to visualize which individual combinations of breeding regions produced the strongest genotype \times environment interactions. This unconstrained analysis uses Ward's minimum variance criterion (Szekely and Rizzo 2005) using a Euclidean distance matrix calculated from the BLUEs for the (RO \times RT) interaction term. The analysis was implemented with the *dist* and *hclust* functions of the R base package (R Development Core Team 2015). To investigate the variance explained by each recursive split of the dataset through the cluster analysis, we used permutational multivariate analysis of variance using the R function *adonis* of the *vegan* package (Oksanen et al. 2013) for the R programming environment (R Development Core Team 2015).

To further investigate what portion of the total breeding-region level genotype \times environment interaction is due to climate, we used a constrained version of the above cluster analysis approach, where groups of sites were defined by climate variables. Multivariate regression tree analysis makes no assumptions about the mathematical nature of the relationship between predictor variables (climate) and response variables (tree height at multiple sites). For our application, it means that the reaction norms of genotypes over multivariate environmental gradients may take any form (Hamann et al. 2011). This multivariate

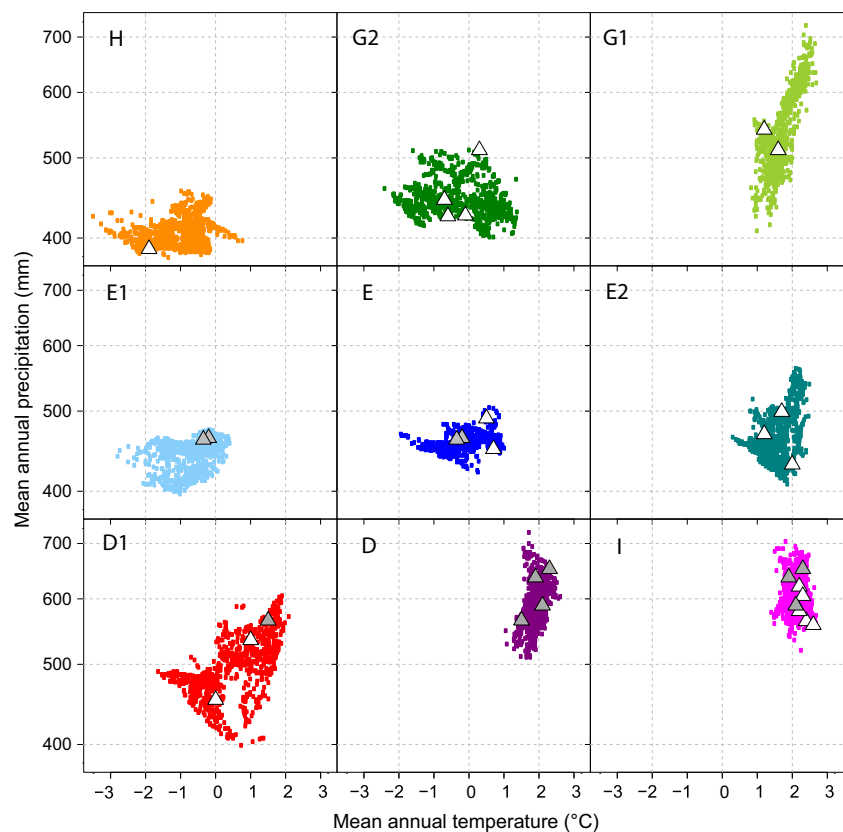
regression tree (MRT) analysis was performed with the R package *mvpart* (De'Ath 2002; De'ath 2014). The procedure iteratively tests all climate variables as criteria to split the height measurements into two groups, so that the within-group variance of height is minimized (De'Ath 2002). After the first split, the procedure repeats recursively for each sub-group until little additional variance can be explained by the partitioning criterion (climate variables). The package also reports the variance explained by each node, so that a follow-up multivariate analysis of variance was not required. Due to limited testing of genotypes originating from breeding region E, the genotype \times environment interaction values for material originating from this region were removed from the constrained multivariate regression tree analysis.

Results

Climatology of the white spruce breeding regions and experimental trial sites

The climatology of Alberta's white spruce breeding regions, as shown in Fig. 1, is characterized by a relatively high level of within-region climate variation (Fig. 2), primarily due to latitudinal and elevation gradients within regions. A plot of climate values at a random sample of locations within each breeding region (Fig. 2. colored dots) and test sites

Fig. 2 Summary of the mean annual temperature (MAT, °C) over the mean annual precipitation (MAP, mm) for each of Alberta's white spruce breeding regions. Colored points represent the range of climate at 1-km resolution for each region. The climate of test sites are shown as triangles, with test sites in overlap regions colored gray



representing each breeding region (Fig. 2, triangles) reveals that the climatic representation of potential planting sites by test sites is variable. The most remote regions (H and E1) are poorly covered by test sites, while the remaining breeding regions have variable coverage regarding the numbers of test sites, but generally have a fair representation of the breeding region climate space. Means for additional climate variables are shown in Table 2.

There are two macroclimatic regions, sub-boreal and boreal climates, where white spruce is planted in Alberta. Sub-boreal climates define the Rocky Mountain Foothills breeding regions G1 (light green), D (purple), and I (pink) which experience the greatest amount of precipitation (up to 700 mm at the high elevations), combined with the highest mean annual temperatures (1–3 °C). The boreal breeding region with the closest climate to that of the foothills is central Alberta's D1 region (red), which experiences similar precipitation, but lower mean annual temperatures than the foothills (1.5–2 °C). Like the foothills ecosystems, precipitation in this region is influenced by the jet stream-driven storm track that travels east through central Alberta from the Rocky Mountains. The remaining boreal breeding regions each experience lower precipitation (400–500 mm) and cooler temperature gradients (–3–1 °C) compared to the Rocky Mountain Foothills breeding regions.

In addition to the annual temperature gradients, Alberta's breeding regions can be further characterized by differences in winter severity. Sub-boreal breeding regions (D, G1, and I) offer milder climates with lower continentality (TD, Table 2) and warmer winter temperatures (MCMT, Table 2). In contrast, climates in northern boreal breeding regions (H, E, and E1) experience colder winter temperatures, with the central boreal breeding regions (G2, D1, and E2) bridging the gap. Hence, there is a diagonal gradient across Alberta from southwest to northeast towards more continental climate conditions.

Transfer of material among breeding regions

Typically in breeding programs, the majority of breeding material is sourced from within the breeding region itself. In this analysis, with the exception of breeding regions E, E1, and E2, this holds true with the greatest proportion of material tested within a breeding region originating locally (Fig. 1b).

Limited local testing in breeding regions E, E1, and E2 is due to these regions being relatively young compared to the other breeding regions in the province. Recently established provenance and progeny tests in these regions better reflect local testing; however, tree ages in these tests were too young to include in the present analyses. Overall, the number of transfers (cross-testing) among breeding regions ranged from 0 to 220 provenances or families.

The best linear unbiased estimates (BLUEs) representing the relative performance of parent material when planted locally or transferred to an alternative breeding region are presented in Table 3 and Fig. 3. In Table 3, values along the diagonal representing local transfers that are set to zero, and values under seed transfer indicate how seedlings that were transferred into this breeding region performed relative to the local source, with positive and negative values indicating better or worse performance in percentage relative to the local stock. For transfers represented by three or more provenance collections or families, we visualize the data in Fig. 3, where positive and negative performance under transfer is identified with green and red arrows, respectively. The width of each arrow indicates the magnitude of performance difference. As a measure of reliability of the estimate, the number of provenances or families tested from a breeding region is also provided at the base of the arrow. For example, 28 provenances or families originating from breeding region G1 performed, on average, 29 % below the local stock when tested in breeding region H, and therefore considered a strong negative performance estimate and represented by a thick red arrow.

Table 2 Climatic summary for experiment trial sites within Alberta's white spruce breeding regions for mean annual temperature (MAT, °C), mean coldest month temperature (MCMT, °C), mean warmest month temperature (MWMT, °C), continentality (TD), mean annual precipitation (MAP, mm), mean summer precipitation (MSP, mm), climate moisture deficit (CMD), forest-free period (FFP, days), the number of frost-free days (NFFD, days), and degree days above 5 °C (DD5)

Region	MAT	MCMT	MWMT	TD	MAP	MSP	CMD	FFP	NFFD	DD5
Northern breeding regions										
H	–1.7	–22.9	16.1	39.0	389	238	223	99	141	1183
E	0	–20.0	16.0	36.0	456	305	182	97	147	1227
E1	–0.3	–20.9	16.1	37.0	448	296	189	98	147	1238
Central breeding regions										
G2	–0.2	–19.3	15.2	34.6	447	276	188	100	145	1143
D1	0.6	–17.9	15.5	33.4	495	332	151	101	148	1200
E2	1.8	–15.7	16.4	32.1	454	327	198	111	157	1369
Rocky Mountain Foothills breeding regions										
G1	1.8	–13.4	14.8	28.2	561	354	120	106	153	1167
D	2.1	–11.9	14.7	26.6	602	422	62	109	154	1144
I	2.2	–11.6	14.5	26.1	601	422	65	103	150	1119

Table 3 Best linear unbiased estimates of relative height of trees when transferred among Alberta's white spruce breeding regions

Test site regions	Performance of transferred sources relative to local								
	D	D1	E	E1	E2	G1	G2	H	I
D	0 (2.1)	-2.8 (2.1)	No data	-17.7 (9.2)	-8.7 (7.2)	2.2 (2.8)	-6.2 (9.0)	-5.3 (5.6)	0.5 (2.0)
D1	1.2 (2.2)	0 (2.1)	4.4 (4.3)	1.8 (3.9)	7.3 (5.7)	-7.0 (3.5)	-11.2 (2.9)	-5.3 (2.7)	1.1 (2.3)
E	-4.2 (3.2)	-2.7 (3.1)	0 (3.2)	-0.1 (3.5)	3.0 (3.7)	-9.5 (5.3)	-4.8 (6.1)	-6.9 (4.4)	-4.5 (3.3)
E1	-5.2 (5.2)	-4.8 (3.7)	-1.8 (3.5)	0 (4.1)	3.7 (4.4)	-5.2 (9.2)	-4.2 (7.1)	-6.2 (5.1)	-2.9 (8.0)
E2	3.2 (4.0)	3.0 (4.2)	No data	20.9 (9.8)	0 (7.9)	6.5 (4.4)	-11.5 (7.6)	-3.1 (5.6)	2.3 (3.9)
G1	-2.6 (7.2)	-2.5 (7.2)	No data	-11.7 (10.3)	-2.1 (10.5)	0 (5.3)	-4.7 (7.1)	-5.1 (8.1)	-2.9 (8.0)
G2	-1.9 (4.8)	1.9 (3.0)	4.6 (4.5)	5.1 (4.0)	-2.0 (7.5)	-2.5 (3.1)	0 (2.9)	-4.3 (3.1)	-1.3 (5.7)
H	-7.9 (6.7)	1.9 (4.6)	9.7 (5.7)	8.1 (5.3)	-3.9 (10.2)	-29.0 (4.8)	-5.0 (4.7)	0 (4.6)	-6.3 (7.5)
I	-0.7 (2.0)	-4.0 (2.1)	No data	-13.8 (5.9)	-7.8 (5.0)	1.4 (2.4)	-5.0 (4.5)	-12.8 (3.8)	0 (2.0)

Values indicate the percent below or above the average performance of local material from the breeding region. Values in parentheses are standard errors of the estimates. Values in gray indicate fewer than three unique sources were used in the performance estimation

A prevalent result of the transfer analysis is that in general, transfers towards the west are strongly positive (Fig. 3, thick green arrows towards H, G2, and D1; Table 3), where transfers towards the east were strongly negative (Fig. 3, thick red arrows towards D1, E, and E1). Further long-distance latitudinal transfers either to the north or the south were associated with sub-optimal performance of transferred sources relative to local material (Fig. 3, north transfers towards H and south transfers towards I). Shorter geographic distance transfers had varying results. Sources originating from the Rocky Mountain Foothills appear to be optimally adapted to the sub-boreal breeding regions as they consistently outperformed boreal sources (Fig. 3). Conversely sub-boreal sources performed poorly in boreal breeding regions, with the exception of test sites in breeding regions G2 and D1 where the large number of sub-boreal provenance and families tested performed similarly to local seed (<2 %, Table 3). In general, transfers among adjacent breeding regions resulted in relatively neutral performance (Fig. 3, thin short arrows). Among adjacent breeding region, transfers towards the south are slightly negative and transfers towards the north tend to be slightly positive although there are exceptions (Fig. 3).

Genotype × environment interactions

The unconstrained hierarchical clustering analysis revealed the largest proportion of variance is explained by the difference in seedling performance at sites in the most northern breeding regions (H, E, and E1) and all remaining regions (Fig. 4, 31 % of the total variation explained). The constrained multivariate regression tree analysis found the same result and attributed this proportion of variation explained to the difference in frost-free period (FFP) among these regions (Fig. 4). Both the constrained and unconstrained analyses further split the southern breeding regions into identical groupings

representing breeding regions located in the Rocky Mountain Foothills (D, G1, and I) and central Alberta (D1, G2, E2), explaining 25 % of the total variation from the difference in the breeding region's mean coldest month temperature (MCMT) (Fig. 4). The three resulting breeding region groups appear diagonally oriented across Alberta (Fig. 1), representing a gradient of winter conditions where milder conditions (Fig. 4, greater frost-free period and warmer winter temperatures) found in south-western Alberta's Rocky Mountain Foothills extend to less favorable winter climates (Fig. 4, less frost-free period) in the far north and north-eastern corners of the province. Population performance, indicated by bar plots at the terminal nodes of the constrained analysis, further confirms that winter events (frost and cold temperatures) are strong drivers of genotype × environment interaction in these breeding regions, as local sources perform best in the gradient extremes (Fig. 4, unconstrained analysis source breeding region bars fall above the average in northern Alberta and Rocky Mountain Foothills groups), and all sources perform well in the central breeding regions (Fig. 4, all source breeding region bars fall above average in regions D1, E2 and G2).

Discussion

“Local is best” generally a valid assumption

Given observed population performance in the experimental trials evaluated, the assumption of local being best adapted to their home environments' appears reasonable for most breeding regions. If local populations were unsuitable for the test sites, we would expect to see the majority of the arrows in Fig. 3, representing the relative performance of transferred material, to be green. Instead, we found that the majority of

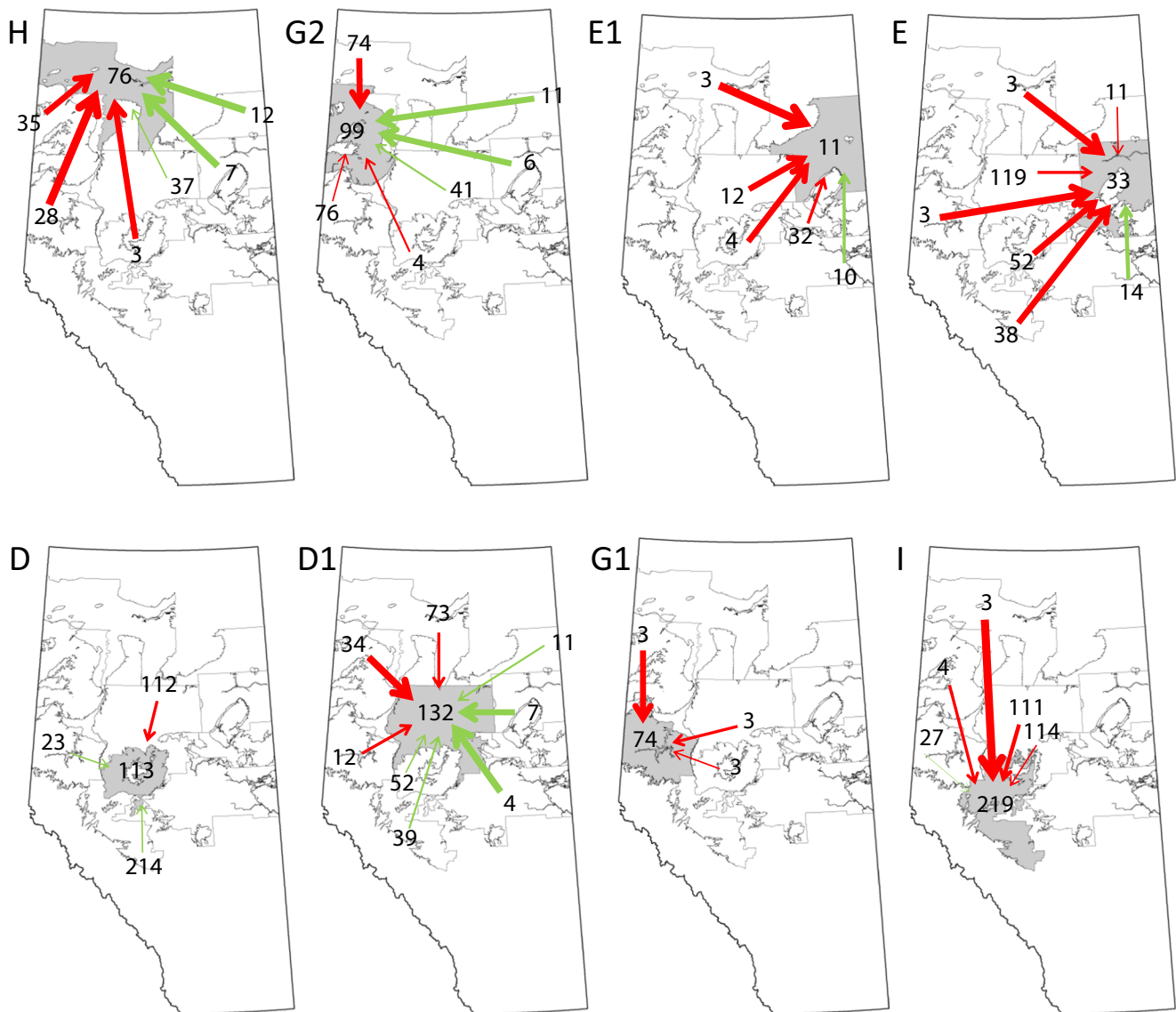


Fig. 3 Relative performance of progeny from parents when tested within the local and alternate regions, with *red* and *green* arrows representing below and above average performance compared to the local populations, respectively, based on percentage from the mean region performance for height. The *width* of the arrows represents the magnitude of performance

seed transfers underperformed compared to local sources, represented by red arrows (Fig. 3). While these results suggest that in general, seed transfer guidelines should continue to limit the deployment of seed material to within local breeding regions, our results only reflect performance over each trial's respective evaluation period which ranges between 7 and 32 years (Table 1). Over the last 25 years, Alberta has experienced an approximate 0.8 °C annual temperature increase coupled with a 10 % reduction in annual precipitation (Mbogga et al. 2009); thus, the magnitude of climate change experienced among trials during the evaluation period varied. Furthermore, a comparison of bioclimate envelope model outputs over a recent 25 year period (1961–1990 compared to

provided in Table 3. The number of unique collections transferred and used to calculate performance is located at the start of each arrow while the *number* located in the middle of the breeding region represents the number of local unique collections

1997–2006) estimates that climatically optimal white spruce populations have already shifted approximately 207 km north and 91 m in elevation within the boreal ecosystem in western North America (Gray and Hamann 2013). While this difference in optimal and realized climate currently experienced by white spruce provenances and families may be contained within the majority of breeding regions, the magnitude of shift projected to occur for these populations in boreal ecosystems under future climate conditions is expected to drastically increase to approximately 419 km north and 184 m in elevation by the 2050s, and 817 km north and 359 m in elevation by the 2080s (Gray and Hamann 2013), in most cases likely spanning beyond breeding region borders.

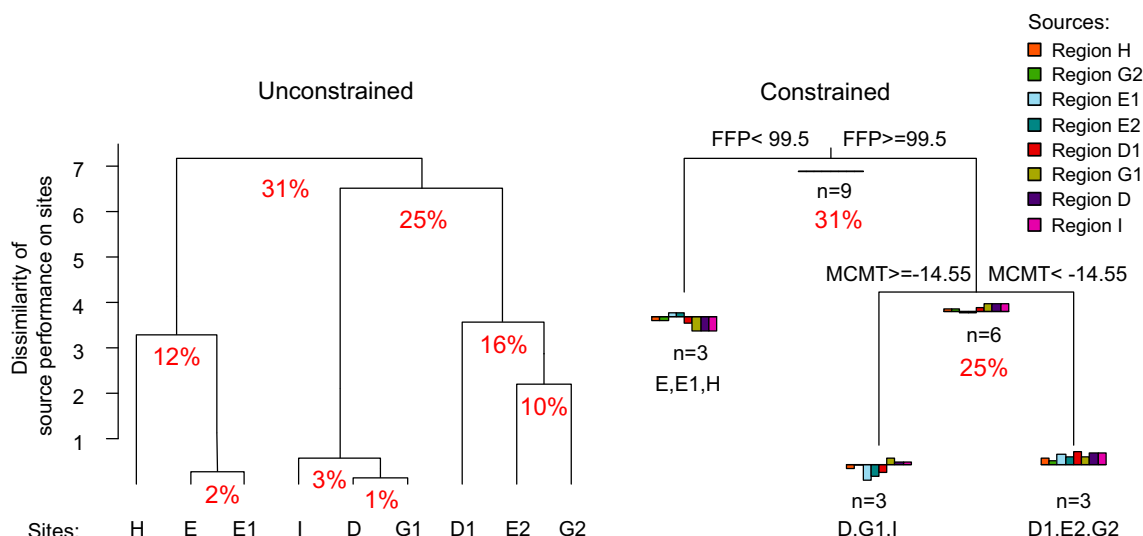


Fig. 4 Genotype \times environment interaction effects of relative performance expressed as a dendrogram from a hierarchical clustering analysis of breeding regions (unconstrained). The variance explained by each cluster split, corresponding to the similarity between breeding regions, is provided in red. Further, a multivariate regression tree

analysis where breeding regions groupings are constrained by frost-free period (FFP, days) and mean coldest month temperature (MCMT, $^{\circ}$ C) produces identical results. Bar plots at the terminal ends of the regional groups illustrate how material from source breeding regions performed in each of the defined groups

Transfers among breeding regions can be beneficial

Tree breeding regions are usually delineated to produce seed for specific deployment regions so that genotype \times environment interactions are minimized and productivity optimized. We find that despite local provenances and families performing well in their home breeding region, opportunities exist for transferring seed across breeding region boundaries that are either neutral or beneficial. Within the group of Rocky Mountain Foothills breeding regions (D, G1, and I), the proportion of variance explained by the difference in seedling performance across these regions is minimal (Fig. 4a, 3 and 1 % of the total variation explained), indicating little genotype \times environment effect among these regions. Transferred provenances and families performed equivalent to local sources within this group of breeding regions, ranging between 0.5 and 2.9 % below and above local sources, respectively (Table 3). In this case, where there is little genotype \times environment effect among breeding regions, superior genotypes from across the group of Rocky Mountain Foothills breeding regions could potentially be more widely used within these regions to achieve better genetic gains.

Among the group of northern breeding regions (E, E1, and H), the performance of transferred material varied with northwestern transfers observed to be more favorable than transfers southeast (Fig. 3). While these breeding regions have similar growing season climates (Table 2, MWMT and MSP) as well as frost-free periods compared to the remaining breeding regions, winter temperatures and annual temperatures are approximately 2 $^{\circ}$ C colder in breeding region H than regions E and E1 (Table 2). In breeding region H, transfer results indicate the local white spruce genotypes tested in this region may be

suffering from adaptational lag, which has been observed in this region in trembling aspen (*Populus tremuloides* Michx) when tested in reciprocal transplant experiments in the northern boreal region (Gray et al. 2011). Higher genotype \times environment effects among breeding regions E, E1, and H (Fig. 4a, 12 % proportion of the total variation explained) indicate that populations within the group of northern breeding regions are adapted to different climatic environments. However, superior families from across the northern breeding regions could be transferred into breeding region H, where they generally outperform the local sources (Table 3). Between breeding regions E and E1, a low variance component due to genotype \times environment effects and equivalent performance of local and transferred families suggests movement across these regional borders is possible with little risk of maladaptation (Table 3, Fig. 4a, 2 % of total variation explained).

In contrast to northern and foothills breeding region groups, genotype \times environment interactions within the central breeding regions (D1, G2, and E2) are relatively high (Fig. 4a, 16 and 10 % of total variation explained), indicating that provenances and families are adapted to local environmental conditions. Similar to the northern breeding regions, northwestern transfers were observed to be favorable compared to transfers southeast (Fig. 3 and Table 3). While the majority of climate conditions among these regions are similar, winter temperatures follow a gradient decreasing by 2 $^{\circ}$ C from east (E2) to west (G2) (Table 2, MCMT). Transfer results suggest that local provenances and families can be successfully moved northwest into colder climates within the group of central breeding regions, but transfers into warmer environments resulted in poor performance.

Minimum temperatures drive local adaptation

In two previous papers based on a single provenance trial series (G103, also included in this study), Rweyongeza et al. (2007a) reported that white spruce in Alberta is genetically differentiated into three major regional groups; northern boreal, southern boreal (central Alberta), and Rocky Mountain Foothills, within which population differentiation for growth potential is clinal along a temperature gradient. In the northern boreal, Rweyongeza et al. (2010) infer adaptation to cold winter temperatures and high continentality. They also suggest that photoperiod sensitivity may have resulted in populations that have low growth potential when transferred south into relatively warmer environments. Likewise, in the Rocky Mountain Foothills region, adaptation to cool temperatures and short growing season at high elevation was associated with low growth potential when transferred to lower elevations.

Our analysis of a much larger dataset largely confirms Rweyongeza et al.'s (2007a, 2010) work. Although using a completely different methodological approach and relying primarily on progeny trial data rather than provenance experiments, we identified cold temperatures to be the primary driver of local adaptation in white spruce with 56 % of the total variation in height growth explained by the frost-free period and mean coldest month temperature (Fig. 4b). Temperature and the closely related variables latitude and photoperiod have also been determined as drivers of local adaptation in other regions within the range of the species (Li et al. 1997; Beaulieu et al. 2004; Andalo et al. 2005). In this study, the inability of precipitation related variables to explain genetic differentiation among populations should not be mistakenly interpreted as not being important for tree growth. In fact, precipitation is likely a limiting factor for tree growth and survival throughout the region, especially at the southern fringe of the boreal forest (Peng et al. 2011). Rather, we could not find any evidence that populations exposed to water limitations are genetically adapted to better cope with dry conditions. Although genetic differences in response to drought have been documented experimentally (Bigras 2005), the majority of climate-driven population differentiation appears to be related to adaptations to cope with cold temperatures.

Implications for climate change

We have shown that north and north-west transfers to colder climate conditions can be beneficial, as also observed for white spruce populations in Ontario and Quebec (Li et al. 1997). However, the apparent prevalence of population adaptation to cold temperatures should serve as a note of caution for assisted migration prescriptions that may move planting stock northward too fast or too far in case climate change does not materialize as rapidly as predicted. Movement of

genotypes to much colder climates may result in poor seedling survival and suboptimal growth due to frost damage. Rather, we recommend moderate scale transfers among breeding regions that are supported by both appropriate climate differences and population performance from field trials. For example, a transfer from central breeding region D1 northwest into region G2 represents a 1.5 °C difference in mean coldest month temperature (Table 2, MCMT). This transfer also results in slightly better performance of introduced D1 material compared to the local G2 sources (Table 3, 1.9 % above local sources). Genotypes adapted to warmer region D1 temperatures would be safe to transfer under current climates and additionally be suitable under warming of mean annual temperature by 0.8 °C over the rotation period of the stand.

Given the uncertainty of future climate projections, methodological limitations inherent to provenance and progeny testing, and the need for planting stock to survive current climate conditions, assisted migration prescriptions should likely avoid very large transfer distances. While results from experimental seed transfers in provenance and progeny trials may be among the most valuable information to develop climate change adaptation strategies, the data is not without problems. Genotypes tested in field trials may not have experienced rare climate events such as unseasonal or extreme cold temperatures in the boreal north. Thus, good growth observed in populations transferred to colder climates may not necessarily reflect their long-term fitness. Another technical limitation of genetic field test is that competition in older trials may exaggerate genetic differentiation of genotypes. We therefore recommend that transfers should be generally be moderate (~300 km north) and should be restricted to geographically adjacent breeding regions, even if growth data seem to support long-distance transfers. Such restrictions could gradually be relaxed to allow for longer distance transfers as the climate continues to warm.

While seed transfer prescriptions to address climate change can be developed by modeling growth response of genotypes to different climate conditions (e.g., Andalo et al. 2005; Wang et al. 2010), tree breeding and seed management program and corresponding legislation are often organized around geographically delineated management areas. It is therefore of practical value to express transfer prescriptions in terms of seed zones or breeding regions that are widely used in many jurisdictions (e.g., O'Neill et al. 2008; Beaulieu 1996). Our analysis of transfer effects and interpretation of genotype \times environment interactions suggests that several general transfer permissions could safely be incorporated into the ministry's seed use guidelines based on the data from Tables 2 and 3, and Fig. 3. Once allowable transfers among breeding regions are established, individual companies can select families for such transfers that grow particularly well under those transfers based on data from Table S1, which provides growth estimates for transfers of individual families

to different breeding regions. Figure 5 shows that there is a considerable range of within-population performance of individual families for transfers that result in positive regional performances (Fig. 3, green arrows). Only the top-performing families should be chosen for assisted migration prescriptions. As an alternative climate adaptation strategy to seed transfer among breeding regions, Table S1 may also be used to remove genotypes from local breeding populations, if their climate sensitivity is indicated by performing poorly when transferred to warmer breeding regions.

While we could not document adaptation to drought in this analysis, drought-stress is often highlighted as a critical concern for forest management under observed and projected climate change. Recent studies have found drought-induced mortality to be the primary cause of aspen dieback across North America (Worrall et al. 2013) and along the southern edge of the Canadian boreal forest (Hogg et al. 2002, 2008; Michaelian et al. 2011). White spruce may not be as exposed as aspen in the transition zone from the boreal forests to grasslands, but Barber et al. (2000) and Lloyd and Fastie (2002) found drought to be an important factor limiting growth of boreal white spruce populations. If the southern fringe of white spruce represents its fundamental niche limit with respect to water availability, and the potential to procure seed adapted projected xeric conditions is limited, then projections of loss of suitable habitat for white spruce in Alberta under

climate change scenarios are likely to occur as modeled by Gray and Hamann (2013).

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Data accessibility Data from genetic field trials were provided by private companies and government agencies (see Acknowledgements), and so are not owned by the authors and thus not available in the archive.

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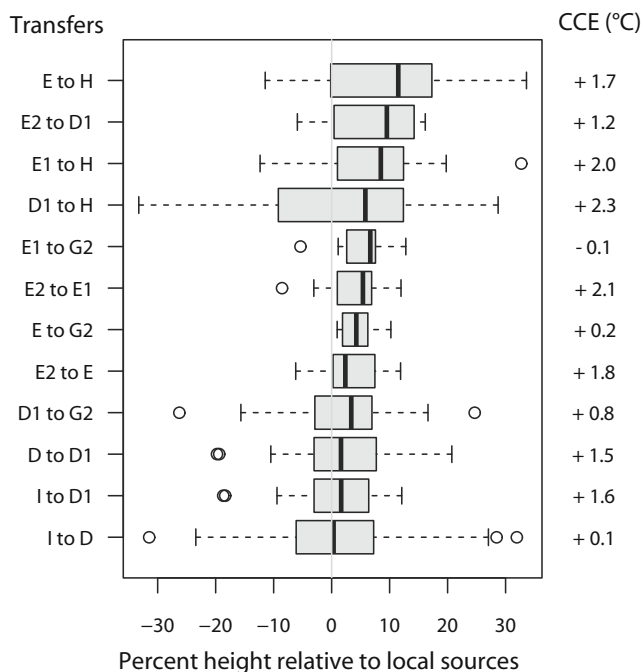


Fig. 5 Performance of individual families in response to transfer among breeding regions. Only transfers with a positive performance relative to local sources are shown. The climate change equivalent (CCE) for mean annual temperature is also shown, meaning that if climate warms by this amount, the transferred families would match their 1961–1990 reference climate of their origin

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