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Developing management strategies for tree improvement programs under climate change: Insights gained from long-term field trials with lodgepole pine

Laura K. Gray [a,*], Deogratias Rweyongeza [b], Andreas Hamann [a], Sally John [c], Barb R. Thomas [d]

[a] University of Alberta, Department of Renewable Resources, 751 General Services Building, Edmonton, Alberta T5H 4R1, Canada
[b] Alberta Agriculture and Forestry, Forest Management Branch, 9920-108 Street, Edmonton, Alberta T5K 2M4, Canada
[c] Isabella Point Forestry Ltd., 331 Roland Road, Salt Spring Island, British Columbia V8K 1V1, Canada
[d] University of Alberta, Department of Renewable Resources, 442 Earth Sciences Building, Edmonton, Alberta T6G 2E3, Canada

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ABSTRACT

The growing concern of the impact of climate change in forestry has prompted tree improvement programs and regulatory agencies to integrate climate change adaptation in the production and use of tree seed. In support of such adaptation strategies, we conducted a case study for lodgepole pine (*Pinus contorta* Dougl.) in Alberta, Canada. We compared the tree height for populations and families planted across 37 progeny and provenance trials when transferred among six physiogeographically and climatically distinct breeding regions. Based on these results we infer how lodgepole populations and families are adapted to current climate conditions and how they might respond to future changes in climate. Interestingly, in almost all regions we found that local populations grew better than introduced sources, suggesting that in the current climate the use of local populations is still an appropriate reforestation strategy with some exceptions. Notably, in cool and wet higher elevation environments (between 1050 and 1650 m), local populations were outgrown by populations originating from warmer lower elevation regions. Moreover, these higher elevation populations were always outgrown when transferred to other regions. A number of transfers among regions were identified that ensure productivity gains under recent climate conditions, and simultaneously represent a short term adaptation measure for warming of about +0.5 °C. Further, we provide a database for selection of families within breeding populations to enhance their resilience to climate change.

1. Introduction

Climate is widely acknowledged to be a key agent of natural selection in plant populations including forest trees (Villalba et al., 1994; Linhart and Grant, 1996; Matyas, 1996; Lo et al., 2010; McLane et al., 2011). Although many environmental factors contribute to genetic differentiation and evolution of locally adapted populations (e.g. Linhart and Grant, 1996), temperature and geographic and topographic variables that affect temperature appear to be the main drivers of natural selection in northern conifers such as white spruce (Li et al., 1997; Rweyongeza et al., 2010; Gray et al., 2016; Liepe et al., 2016), black spruce (Morgenstern, 1978; Beaulieu et al., 2004; Wei et al., 2004), Norway spruce (Oleksyn et al., 1998a; Kapeller et al., 2012; Schueler et al., 2013), lodgepole pine (Wu and Ying, 2004; Wang et al., 2006; Rweyongeza et al., 2007; Liepe et al., 2016), jack pine (van Niejenhuis and Parker, 1996; Thomson and Parker, 2008) and Scots pine (Beuker et al., 1998; Oleksyn et al., 1998b). These and many other studies show that temperature explains most of adaptive genetic variation in survival, shoot phenology, rate of growth, frost hardness, morphology and physiological process such as photosynthesis.

Lodgepole pine (*Pinus contorta* spp. *latifolia*), as a major commercial forestry species, has been particularly well studied with respect to adaptation to climate. In early studies, Rehfeldt (1988) and Rehfeldt and Wykoff (1981) found that the majority of population differentiation in lodgepole pine growth was explained by clinal patterns of variation that in general reflected elevation and the climatic variable frost-free period. In range-wide provenance studies, response functions of lodgepole pine populations have highlighted the sensitivity of height growth and survival to even small fluctuations in temperature of ±1 °C (Rehfeldt et al., 1999, 2001; Wang et al., 2006; O'Neill et al., 2008). Approaches other

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[*] Corresponding author.
E-mail address: lkgray@ualberta.ca (L.K. Gray).

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than provenance trials confirm the sensitivity of lodgepole pine to climate change. For example, using dendrochronology, Chhin et al. (2008a) found that heat and moisture stress in later summer reduced annual radial growth of lodgepole pine in Alberta. Further, predicted growth under climate change scenarios suggests negative impacts on the productivity of lodgepole pine in the Alberta Foothills (Chhin et al., 2008b). Given lodgepole pine is the second most important commercial tree species in Alberta, climate change adaptation measures are needed to lower the vulnerability of lodgepole pine in Alberta as well as protect species habitats and commercial investments.

Foresters and tree breeders manage genetic adaptation to climate in commercial forestry by using seed zones and tree breeding regions. Rather than developing breeding strategies that include traits for adaptation, a more logical way to guarantee adaptation for traits such as tolerance to climatic stress, resistance to insects and diseases, and reproductive fitness is to rely on delineation of breeding and deployment zones that are characterized by relatively homogenous environments (e.g. Linhart and Grant, 1996; Vander Mijnsbrugge et al., 2010). The use of such zones may be the easiest way to avoid what Zobel and Kellison (1978) called the rate of growth syndrome in tree breeding, which erroneously overemphasizes height growth at the expense of other traits that are important for population adaptation, yield and product quality.

Studies show that in the past few decades, climate has been changing faster than expected in many regions of Canada (Mbogga et al., 2009; Jiang et al., 2015). Jiang et al. (2015) shows that, from the year 1900–2011, the December – February temperature for northern Alberta, Canada, increased by an average of 0.5 °C/decade. Future projection suggests that between 2020s and 2080s, Alberta's changes in seasonal precipitation could range from a decline of 25% to an increase of 36% with the increases occurring in the period between December and May. In the same period, temperature would increase throughout Alberta with the highest increase occurring in the December – February period (maximum of 6.8 °C). Rapid changes in climate could significantly affect the regeneration success as well as the health and productivity of both natural and managed forests. For example, observed climate shifts in Alberta over the last decade have been linked to drought-related dieback of boreal trees (Hogg et al., 2002; Allen, 2009; Michaelian et al., 2011). Drought in particular would reduce regeneration success thereby increasing the cost of reforestation. Moreover, the loss of biomass production would affect the forest industry and economies of forestry-dependent communities.

In response to observed climate change over the last several decades, a number of adaptation strategies have been suggested to maintain forest health and productivity. They include: (i) planting new species, (ii) planting species mixtures instead of single-species stands, (iii) planting mixtures of many provenances instead of single seed sources, (iv) assisted species migration to new environments to prevent extinction, (v) assisted population migration/translocation beyond their current area of commercial planting, (vi) planting uneven-aged instead of even-aged stands and (vii) retaining higher levels of genetic diversity in reforestation seed (e.g. Ledig and Kitzmiller, 1992; Millar et al., 2007; Vander Mijnsbrugge et al., 2010; Williams and Dumroese, 2013). These strategies are designed to enable the use of seed from sources where populations better suited to the new climate can potentially be found, establish managed forestry with diverse structures that reduce the risk of total stand failure, and maintaining high genetic diversity to buffer forests against unforeseeable climatic stresses that would otherwise decimate genetically depleted even-aged single-species stands. Another long-term adaptation strategy could be to select and breed commercial species for optimum biomass production for the expected future climate. However, even with advances in genomics and marker assisted selection (see Neale and Kremer, 2011; Sork et al., 2013), operational breeding for climate change adaptation in northern conifers is still years away. Therefore, alternative sources of seed for immediate deployment to address climate change are needed.

In this study, we explore the opportunities for population translocation among the six lodgepole pine breeding regions in Alberta to address climate change challenges. Our focus is on sustaining biomass productivity where climate change projections suggest a possible decline, and to enhance productivity where climate change will improve growing condition but local populations are unlikely to utilize it due to their intrinsic low growth potential. The research objectives are: (1) to investigate if local material originating within each breeding region is best for existing seed production needs, (2) to identify the transferability of genetic material between breeding regions, (3) to determine if the current breeding region delineations adequately capture genetic population differentiation, and (4) to infer how lodgepole pine seed sources may be deployed under anticipated climate change based on their performance when transferred to warmer environments.

2. Methods

2.1. Genetic field trials

In this study, we used height growth data from 10 series of progeny trials across six breeding regions. These series contained in total approximately 140,000 trees including 1669 open-pollinated families within 29 trials established at 27 locations (Fig. 1a). In addition, we included data from 6 series of provenance trials with in total approximately 17,000 trees from 203 different populations within 8 trials on 8 locations (Fig. 1a). All trials are summarized in Table 1. Data used in this study are from measurement of trees established with bulk seedlots representing provenances or single-tree cone collections representing half-sib families. However, to simplify terminology and avoid repetitions, the term "population" will be used throughout this article to refer to both provenances and families, except where the distinction is necessary to describe statistical analyses.

2.2. Climatic data

Climatic characterization of the lodgepole pine 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). This software relies on gridded climate surfaces generated with the Parameter Regression of Independent Slopes Model (PRISM) (Daly et al., 2008). The software makes automatic lapse rate adjustments to temperature estimates for seed collection locations if the elevation of a location does not match the elevation of the gridded PRISM data (Hamann and Wang, 2005). Only climatic variables considered biologically relevant for describing genetic differentiation of plant populations were selected for the current study. They include Mean Annual Temperature (MAT), Mean Coldest Month Temperature (MCMT), Mean Warmest Month Temperature (MWMT), Continentality (TD = MWMT – MCMT), Mean Annual Precipitation (MAP), Growing Season Precipitation (MSP), Climate Moisture Deficit (CMD, calculated as the sum of the monthly difference between reference atmospheric evaporative demand and precipitation), Frost Free Period (FFP), Number of Frost Free Days (NFFD), Growing Degree Days above 5 °C (DD5). A detailed description of how the variables are calculated can be found in Wang et al. (2012).

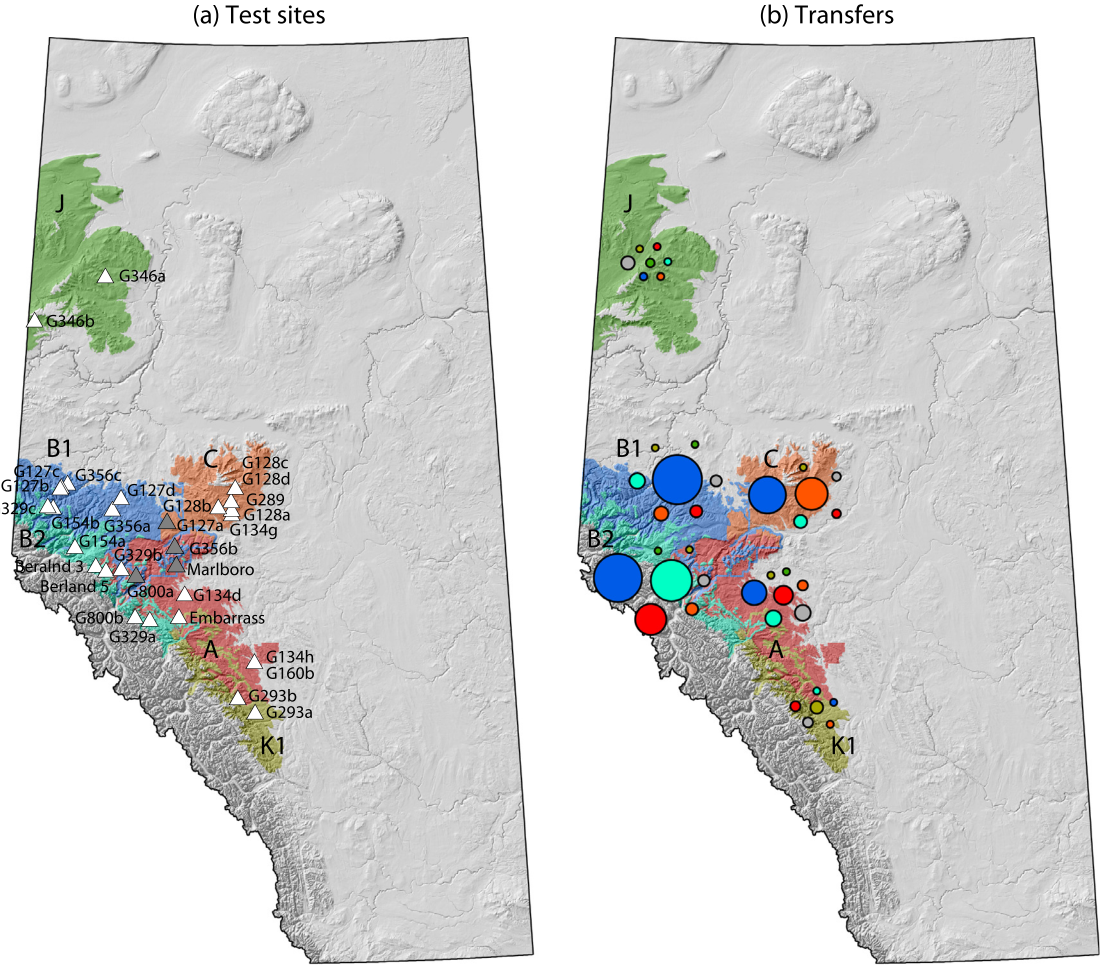


Fig. 1. Provenance and progeny trials (1a) and population and family transfers among Alberta's six lodgepole pine breeding regions (1b). Where the breeding regions overlaps, the overlap boundary is defined by the region outline of the same color. In (1a), a white triangle identifies trials located within the target breeding region, whereas a gray triangle identifies trials located in an overlap area of two adjacent breeding regions. The size and color of the circles represent the number of populations tested in each breeding region with the center circle representing local sources. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary of lodgepole pine progeny and provenance trials by trial series, year planted, number of test sites and collections, and evaluation age for the progeny and provenance test series.

Trial series	Year planted	Number of sites	Number of populations/families	Evaluation age	Mean height & standard deviation (cm)
Progeny test series					
G127	1981	4	404	27	900 (107)
G128	1982	4	232	30	1052 (61)
G154	1991	2	466	20	399 (39)
G160	1994	2	52	15	507 (62)
G293	1996	2	114	14	395 (34)
G329	1998	3	166	15	367 (72)
G346	2000	3	117	9	252 (45)
G356	2002	3	250	14	420 (45)
G358	2003	4	32	10	164 (48)
G800	1978	2	160	22	542 (60)
Provenance test series					
G134	1985	3	21	25	789 (222)
G289	1992	1	167	20	731 (79)
Berland 3	1981	1	14	15	421 (9)
Berland 5	1980	1	14	16	318 (13)
Embarrass	1980	1	14	16	491 (32)
Marlboro	1979	1	17	16	537 (53)

2.3. Assessing population growth under seed transfer

To estimate the height of populations relative to local sources when transferred among breeding regions, we executed a two-step analysis. First, we obtained best linear unbiased estimates (BLUEs) of provenance or family performance in each trial (e.g. G346a, Fig. 1a), taking advantage of their individual experimental designs. Older trial series established prior to 2002, utilized a "sets in reps" design with row plots, and more recent trials were installed using an alpha design (Williams et al., 2002) with single-tree plots. In these models, provenance and family effects were treated as fixed effects, whereas replication and block-within-replication (where applicable) effects were treated as random effects. The BLUEs for families or provenances from individual site analysis were subsequently converted to percentages of the mean site height, and in a subsequent step as percentage of mean breeding region height. The use of BLUEs as percentages enabled us to use all available data irrespective of tree age differences across trial series. All linear mixed model analyses were implemented in the ASReml package (Gilmour et al., 2009) for the R programming environment (R Development Core Team, 2014). All BLUEs and their associated standard errors were obtained by using the average information REML algorithm (Gilmour et al., 1995) implemented with the *predict.asreml* function of the ASReml package for R.

In the second step, the effect of transferring populations within breeding regions was estimated using the following linear mixed-model which utilized BLUEs expressed as percentage from the individual-site analysis described above:

$$Y_{ijkl} = \mu + RT_i + S_j(RT_i) + RO_k + P_l(RO_k) + RO_kRT_i + \varepsilon_{ijkl} \qquad (1)$$

where Y_{ijkl} is the height for the lth population (provenance of family) from the kth breeding region tested at jth test site in ith breeding region of testing, and μ represents the general mean. Fixed effects were defined asRO_k which represents the effect of the kth breeding region of seed origin; RT_i which represents the effect of the ith breeding region of the test site; and RO_kRT_i which represents the interaction between the breeding region of seed origin and breeding region of the test site. Alternatively $S_j(RT_i)$ representing the effect of the jth test site within the ith breeding region of the test site; $P_l(RO_k)$ representing the effect of the lth population (provenance or family) within the kth breeding region of seed origin; and ε_{ijkl}= $S_j(RT_i) \times P_l(RO_k)$ representing the residual error, were all defined as random effects. To simplify interpretations of model outputs, estimates for all local sources were set to zero so performance of transferred populations are expressed as percentages relative to using sources that originated within the same breeding region.

The following linear mixed model was fitted to estimate the effect of transfer among breeding regions on individual provenances or families:

$$Y_{ijl} = \mu + RT_i + S_j(RT_i) + P_l + P_lRT_i + \varepsilon_{ijl} \qquad (2)$$

where Y_{ijl} is the height of the lth population planted at jth test site in ith breeding region, and μ represents the general mean. In this model, P_l representing the effect of the lth population (provenance or family), andP_lRT_i representing the interaction between the lth population (provenance or family) and ith breeding region of the test site were defined as fixed effects. Random effects were defined as RT_i which represents the effect of the ith breeding region of the test site; $S_j(RT_i)$ which represents the effect of the jth test site within the ith breeding region of the test site; and the residual error,ε_{ijl}. In this model the effect of the origin breeding region is removed, and BLUEs of the population × breeding region interaction shows the extent with which growth and/or ranking of individual populations changes by the breeding region in which the test site is located. Again to simplify interpretations of model outputs, the average of the BLUEs for local sources were set to zero, so that all transfers to different breeding regions are expressed as percentages relative to using sources that originated within the same breeding region.

2.4. Genotype × environment effect

To quantify the genotype × environment interaction, pairwise correlations between population performances within breeding regions was calculated using the resulting breeding-region level (RO_kRT_i) interaction term from model 1. Here source breeding regions represented lodgepole pine populations and the pairwise correlations were calculated between population performances within test site breeding regions using the *cor* function of the R base package (R Development Core Team, 2014) with the *pairwise.complete.obs* option.As a second step to investigate the maximum variance that could be explained by the genotype × environment interaction among breeding regions, the resulting breeding-region level (RO_kRT_i) interaction term from model (1) was analyzed with a unconstrained hierarchical agglomerative clustering technique implemented with the *dist* and *hclust* functions of the R base package (R Development Core Team, 2014). For this analysis Ward's minimum variance criterion (Szekely and Rizzo, 2005) and a Euclidean distance matrix calculated from the BLUEs for the interaction term were utilized. At each recursive split from the cluster analysis, the variance explained by the observed groupings was extracted from a permutational multivariate analysis of variance using the R function *adonis* of the vegan package (Oksanen et al., 2007) for the R programming environment (R Development Core Team, 2014).

3. Results

3.1. Climatology of Alberta's lodgepole pine breeding regions and test sites

The climatic characterization of populations and test sites within each breeding region (Fig. 2) reveals that the majority of the climate range observed within Alberta's lodgepole pine breeding regions (Fig. 2, colored dots) is well represented at regional test sites (Fig. 2, triangles). Further resources, however, could be invested to capture greater climatic variation within breeding regions J and K1, as only two test sites are currently located within each of these regions and both regions offer opportunities to test genotype performance in drier environments.

Alberta's lodgepole pine breeding regions (Fig. 1a & b) present very distinct climate envelopes in reference to the two macroclimate zones within the province where they geographically occur, namely, the boreal highlands (region J), and sub-boreal foothills (regions A, B1, B2, C, and K1) defined by the Rocky Mountain Foothills. In the boreal highlands, breeding region J (Fig. 2, dark green) represent a relatively cool and dry climate with cold winter temperature (Table 2, MCMT) characteristic of high latitude boreal forests. In contrast, the remaining breeding sub-boreal lodgepole pine breeding regions represent environments with 2–3 °C warmer annual temperatures and approximately 50% more precipitation compared to breeding region J (Table 2). Within the Rocky Mountain Foothills, the breeding regions at the highest altitudes, B2 and K1 (Fig. 2, cyan and light green respectively) have noticeably fewer growing degree days (Table 2, DD5) indicative of shorter growing seasons within these regions.

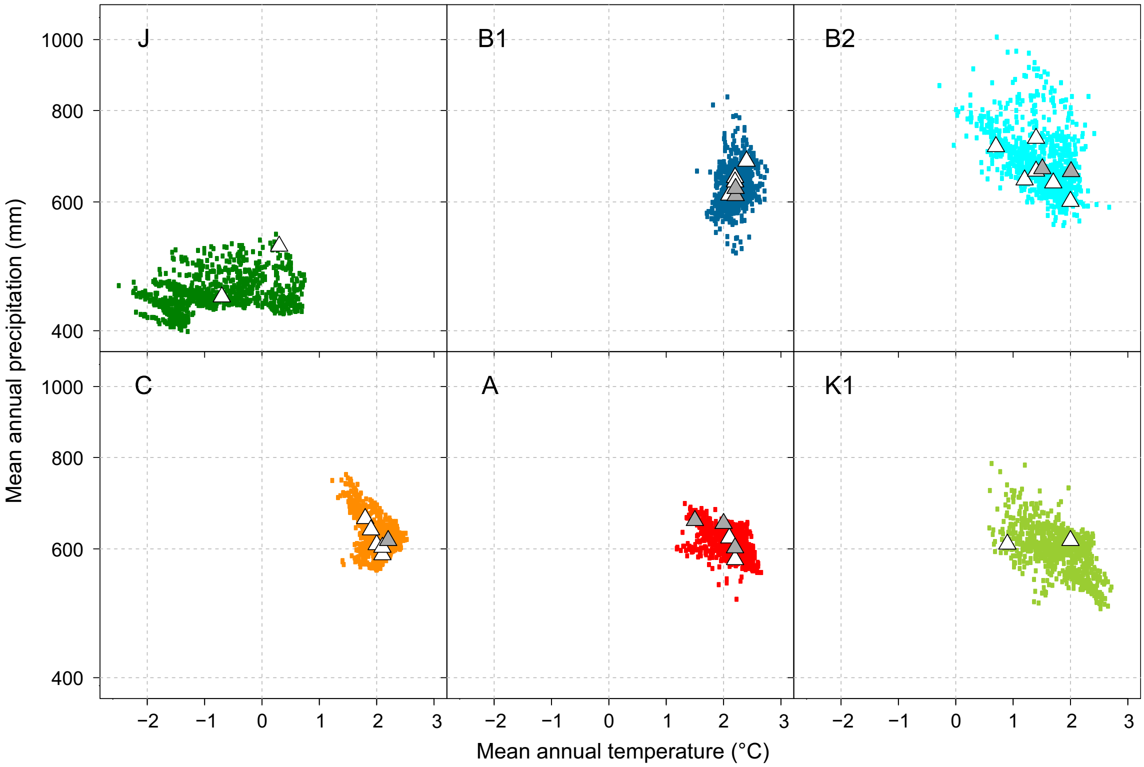


Fig. 2. Summary of the mean annual temperature (MAT, °C) over the mean annual precipitation (MAP, mm) for each of Alberta's lodgepole pine breeding regions (A, B1, B2, C, J, and K1). Colored points represent the range of climate at 1 km resolution for each region. The climate of test sites are shown as triangles, with test sites that occur in an overlap between adjacent breeding regions are colored gray as in Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Climatic description of Alberta lodgepole pine breeding regions based on average climatic profiles of provenance and progeny trials located in the breeding regions. The climate variables include: mean annual temperature (MAT, °C), mean coldest month temperature (MCMT, °C), mean warmest month temperature (MWMT, °C), contentinality (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). The range of elevation (meters) for trial locations is also provided.

Region	MAT	MCMT	MWMT	TD	MAP	MSP	CMD	FFP	NFFD	DD5	Elevation range
Sub-boreal foothills											
A	2	−11.4	13.9	25.3	613	424	57	94	144	1032	972–1322
B1	2.2	−11.2	14.3	25.5	627	423	52	104	151	1087	867–1185
B2	1.5	−10.5	13	23.5	667	426	31	93	140	888	1230–1582
C	2.1	−10.7	14.3	25.1	624	437	46	111	153	1090	928–1139
K1	1.4	−12.3	13.3	25.6	608	416	58	79	129	946	1215–1464
Boreal highlands											
J	−0.9	−19.5	14.6	34.2	464	281	143	97	142	1029	630–931

3.2. Seed transfer among breeding regions

The majority of populations tested in each breeding region were from within the breeding region and are therefore considered local sources (Fig. 1b). The number of populations transferred among breeding regions for testing varies with the age of the trials. Trials established after the year 2002 have more and longer transfers than earlier trials (Fig. 1b, Table 1). Sources originating from within breeding region B1 (Fig. 1b, blue) which represents an average climate among the sub-boreal foothills regions (Table 2), are the most widely tested sources. Conversely, transfers occurring between the boreal highlands (region J) and sub-boreal macroclimate zones, representing the largest climatic shifts, are limited (Fig. 1b, Fig. 2). Transfers of material up-slope are strongly represented with sources originating from both breeding regions B1 (Fig. 1b, blue) and A (Fig. 1b, red), making up the majority of material tested in the high elevation lodgepole pine breeding region B2 (Fig. 1b, cyan). Reverse transfers of region B2 material down slope are present, however to a lesser magnitude.

Table 3 presents the best linear unbiased estimates (BLUEs) for heights of transferred populations, where the performance of the local sources in their own breeding regions are set to zero and therefore omitted from the table. These values are also visually presented in Fig. 3 with blue and red arrows denoting positive and negative values, respectively. BLUEs are expressed in percentage relative to the average growth of all populations and families sampled from within the breeding region which represents the local source. For example, when tested in breeding region B2, the 62 populations originating in breeding region C were on average 2.9% taller than the 384 local populations. (Fig. 3, Table 3). This is illustrated by a thin blue arrow from region C to region B2 (Fig. 3). In a reverse transfer, the 74 region B2 populations tested in region C were on average 11.9% shorter than the 284 local populations (Table 3). This is illustrated by a thick red arrow from

Table 3

Best linear unbiased estimates (BLUEs) indicating the relative performance, based on height, of transferred populations and families relative to performance of populations and families from within Alberta's lodgepole pine breeding regions (A, B1, B2, C, J, and K1). Values represent the height percentage above or below the local population with standard errors in parentheses.

Test site breeding region	Performance of transferred sources relative to local breeding region sources (BLUEs)					
	A	B1	B2	C	J	K1
A		−0.1 ± 0.7	−4.3 ± 0.8	1.2 ± 1.1	0.4 ± 3.8	−3.0 ± 3.2
B1	−1.6 ± 0.8		−8.0 ± 0.7	0.5 ± 0.7	−3.7 ± 3.9[ϕ]	−7.1 ± 3.8[ϕ]
B2	2.5 ± 0.6	1.6 ± 0.6		2.9 ± 0.8	−1.8 ± 5.0[ϕ]	3.2 ± 4.9[ϕ]
C	−9.3 ± 1.3	−3.1 ± 0.7	−11.9 ± 1.0		No data	−6.7 ± 5.1[ϕ]
J	−7.2 ± 3.0	−3.6 ± 2.0	−9.9 ± 2.9	−0.6 ± 2.5		−8.4 ± 4.0[ϕ]
K1	0.2 ± 1.6	−7.3 ± 2.9	−11.3 ± 3.0	−0.6 ± 2.7	No data	

[ϕ] Values estimated from fewer than three populations or families.

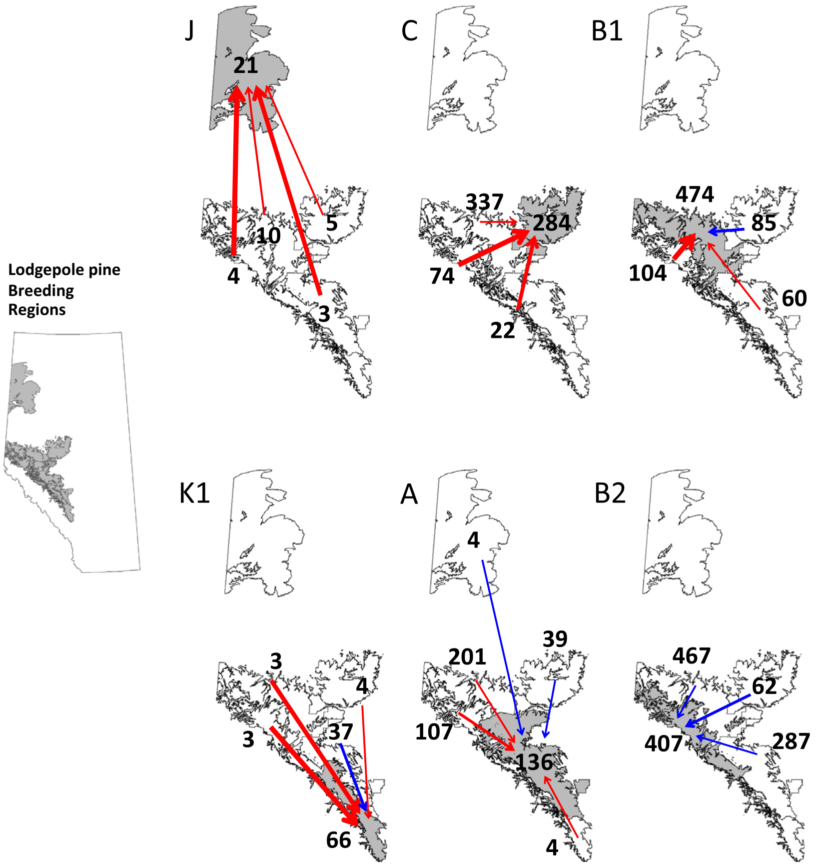


Fig. 3. Comparative growth of provenances and families when transferred to other breeding regions. Red and blue arrows represent growth below and above the mean of local breeding region populations. The width of the arrows represents the magnitudes of performance differences, also provided in Table 3. The number at the beginning of the arrow indicates the number of transferred provenances and families used to estimate the mean of introduced populations from a specified breeding region. The number in the center indicates the number of local provenances and families used to estimate the mean of the local reference population for that breeding region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

B2 to C (Fig. 3). Although estimates based on less than three populations are considered less reliable, they provide an indication of what could be expected from reciprocal population transfers between respective breeding regions. We therefore include these less reliable estimates in Table 3 for reference, but they are not represented by arrows in Fig. 3.

In general, provenances and families originating from within the breeding region were found to be optimally adapted to the local region environments. However, equivalent or optimal performance of transferred material was observed when sub-boreal foothills material was transferred up-slope in the Foothills regions. In breeding region B2 sources transferred from lower elevations in regions A, B1 and C were on average between 1 and 3% taller than the local B2 populations (Table 3). Each of these transfers represents a shift towards approximately 0.5 °C colder temperatures, as well as a variable increase in available precipitation (MAP and CMD, Table 2). Region C populations were approximately equivalent to local populations when transferred into breeding regions A and B1 (Table 3, ⩽1.2%), all of which have similar elevation ranges (Table 2). Although transfers between the high elevation breeding regions B2 and K1 are very limited (⩽3 populations), north transfers at high elevation resulted in 3.2% taller trees compared to local B2 populations, where south transfers resulted in 11.3% shorter trees compared to K1 populations (Table 3).

While transfers up-slope were found to be advantageous, transfers down-slope resulted in sub-optimal performance. High elevation populations from region B2 were found to be on average between 4 and 12% shorter than local populations across all breeding regions (Table 3). Similarly, sources from A and B1 were on average between 3 and 9.5% below local populations when transferred down-slope into region C with relatively small standard errors (SE ⩽ 1.3%, Table 3).

Long-distance latitudinal transfers north from the sub-boreal foothills breeding regions into the boreal highlands were found to be disadvantageous as the majority of transferred populations were on average between 3 and 10% shorter than local region J populations (Table 3). While region J populations were found to perform equivalent to local sources when transferred south into region A (Table 3, 04%), this estimate was based on a small number of sources as indicated by the relatively large standard error (SE = 3.8%, Table 3), reducing the confidence in this estimate.

3.3. Genotype × environment interactions

As previously stated, the number of populations and families transferred from regions J and K1 to other breeding regions (A, B1, B2 and C) and vice versa was very small, resulting in high standard errors of BLUEs for these transfers in Table 3. Therefore, to avoid misleading results due to inadequate data, regions J and K1 were excluded from the unconstrained hierarchical clustering analysis. Overall 96% of the total variance explained by G × E interactions can be attributed to the difference in population growth in regions C (67%) and B2 (29%) (Fig. 4). The differences between regions A and B1 accounted for only a negligible fraction (4%) of the genotype × environment interaction (Fig. 4). Pairwise correlations for region C with A, B1 and K1 were found to be moderate (r = 0.38–0.76), whereas the correlations for region B2 with A and B1 indicate little or no correlation between population performance in these regions (Fig. 4). However, a highly positive correlation was found between regions A and B1 (r = 0.92) further suggesting that growth response for populations was similar among these regions. Performance in region J was also found to be moderate to highly correlated with performance in A, B1 and C (r = 0.69–0.95) even though this region is located further north in the Boreal Highlands; however very few populations were cross-tested among breeding regions limiting the inferences from region J results.

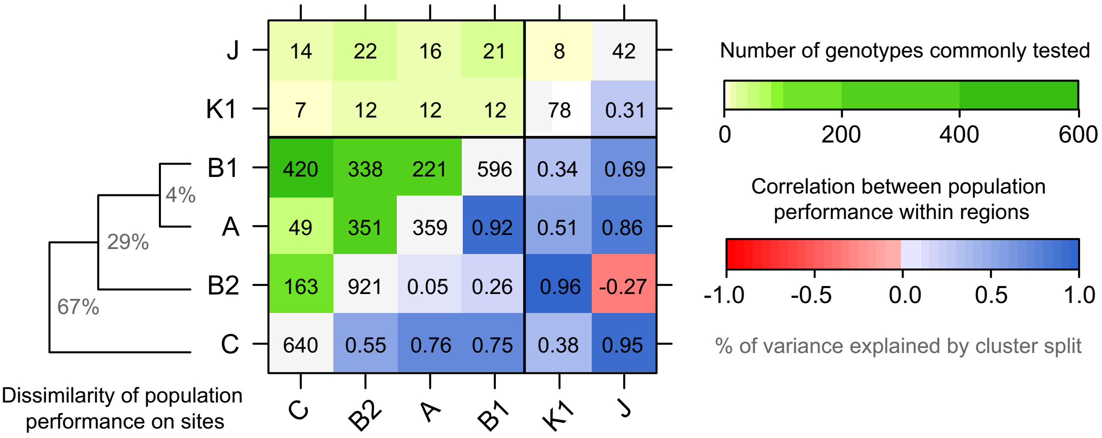
4. Discussion

4.1. Local populations perform best, but some transfer opportunities exist

With the exception of the highest elevation lodgepole pine breeding region B2, Alberta populations were found to be optimally adapted to environments within their local breeding region. Thus, the current assumption guiding seed transfer policy, "local seed is best for reforestation" appears valid for most of the lodgepole pine breeding programs in the province (SRD, 2009). In breeding region B2, however, consistent sub-optimal growth from local genotypes could indicate an adaptational-lag due to observed climate change is occurring among region B2 populations (Aitken, 1999; Aitken et al., 2008; Gray et al., 2011). However, since we do not observe similar sub-optimal growth of local sources across all breeding regions, adaptational-lag due to climate change for region B2 populations alone appears to be an unlikely explanation.

Considering the strong linkage between climate and genetic differentiation, we expect B2 provenances and families to be genetically adapted to exhibit a greater emphasis on frost hardiness, in terms of both frost tolerance and growth at cold temperatures, at the expense of initiating shoot (needle) primordia to maximize height growth (Loehle, 1998). Lodgepople pine populations originating from low latitude and elevation (warmer climates) have been observed initiating shoot primordia at higher rates compared to populations from cooler climates (Cannell and Willett, 1975). Consequently, over the growing season populations from cooler climates could have accumulated fewer stem units than populations from warmer climates, accounting for their overall lower height growth. For these marginal populations adapted to colder climates, restricting growth to small amounts each year prior to dormancy induction is likely an adaption to prevent possible damage from early frost events or climate-induced mortality (McLane et al., 2011). The results also conform to adaptive patterns of other regional studies by Rehfeldt (1988) and Rehfeldt and Wykoff (1981), who found that frost-free period explained the majority of genetic differentiation along elevational gradients.

The costs of adaptation to inhabiting climatically marginal environments may also manifest in other forms of defence mechanisms attained at the expense of evolution for growth potential (Loehle and LeBlanc, 1996; Loehle, 1998; Chuine et al., 2006). Thus,



	C	B2	A	B1	K1	J
J	14	22	16	21	8	42
K1	7	12	12	12	78	0.31
B1	420	338	221	596	0.34	0.69
A	49	351	359	0.92	0.51	0.86
B2	163	921	0.05	0.26	0.96	-0.27
C	640	0.55	0.76	0.75	0.38	0.95

Fig. 4. Genotype × environment interaction effects of relative performance expressed as a dendrogram from a hierarchical clustering analysis of breeding regions as well as the pairwise correlation between population performances at test sites within each region (red to blue). The variance explained by each cluster split, corresponding to the similarity between breeding regions, is shown in gray. Further, the number of populations tested between regions is provided as a measure of confidence in the correlations (yellow to green). Breeding regions K1 and J were removed from the hierarchical cluster analysis due to low connectivity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

climatic-mediated natural selection may have favored growth potential in regions B1 and C and in lower elevation parts of regions A and K1 while favouring selection for defence mechanisms in region B2. Therefore, when planted in parts of region B2 where climate does not limit survival or seriously inhibit biological processes contributing to initiation of shoot primordia, populations from lower elevation regions with warmer climate, like regions B1 nad C may have a good opportunity to outgrow local ones, while potentially making themselves more vulnerable to early frost events. Alternatively, the trade-off between frost hardiness and maximizing height growth would result in sub-optimal height of provenances and families originating from higher altitudes, when transferred down-slope, which we observed for all transfers of both K1 and B2 populations (Table 3).

While our results suggest transferring sub-boreal lodgepole pine provenances and families' up-slope could be advantageous, it should be noted that in all cases height improvements were at best approximately 3% higher than local populations (Table 3). Although the use of populations originating from lower altitudes may currently only offer minimal improvement to planted stands, climatic conditions associated with lower foothills ecosystems are projected to track up-slope within the sub-boreal foothills regions towards the 2020s and 2050s (Gray and Hamann, 2011), suggesting that the optimality of lower altitude sources in higher elevation environments will likely continue in the future.

4.2. Some breeding region delineations could be revised

Alberta's lodgepole pine breeding regions were initially delineated based on general genetic and ecological information as well as administrative boundaries (SRD, 2009). Over time, regional boundaries have been modified on the basis of further progeny and provenance testing and in an effort to capture a wider climatic extent to explore the broader adaptability of populations within the species range (SRD, 2009). With minor exceptions, the current regions are 400-m elevation bands largely distinguished by their locations in the south (A and K1) and north (B1, B2 and C) of the foothills and Rocky Mountains region, and hill systems in the northern boreal forest (J). While geographic, climatic and elevation distinctions are evident among breeding regions J, B2 and K1 (Table 2), distinction between regions A, B1 and C are not as clearly defined. The operational elevation of regions B1 and C is 800–1200 m, which overlaps significantly with that of region A (1050–1350 m). Additionally, regions B1 and C are within the same latitudinal zone, which coincides with the northern portion of region A (Fig. 1). Climatically, the only visible differences between A, B1 and C is the slightly lower frost-free period (FFP) and number of frost-free days (NFFP) in region A (Table 2), which could be attributed to its slightly higher elevation limit (1350 m) compared to the upper elevation limits of regions B1 and C (1200 m).

Regions A and B1 are described as an area dominated by a mixture of coniferous and deciduous species, whereas region C has areas dominated by coniferous-deciduous species mixture and those dominated by pure coniferous stands. In addition, region C is characterized as an area of lodgepole pine and jack pine (*Pinus banksiana* Lamb) hybridization which has found to be extensive in Alberta (Wheeler and Guries, 1987; Ye et al., 2002; Cullingham et al., 2012). Geographically, region C is closer to the western edge of jack pine natural range making it a more likely breeding region for hybrids than region B1. This may have been one of the initial reasons for separating regions B1 and C despite their clear geographic proximity and climatic similarities.

G × E interaction can be caused by different factors including climate, soils, the way trials were managed or ontogenetic effects due to tree age differences between trials. For tree improvement programs, G × E interaction caused by climate is of greatest interest due to its spatial predictability and the ability to manage it through seed and breeding region zoning. Moderate correlations of region C with A ($r = 0.76$) and B1 ($r = 0.75$) suggest that even though these regions have similar climate (Table 2), ranking of families and populations differed on region C compared to breeding regions A and B1. Further 67% of the total variation in population performance was able to be explained by region C suggesting population performance is distinct within this region and the observed G × E interaction may not be due to climate alone (Fig. 4). Conversely only 4% of the total variation in relative population performance distinguishing the G × E effect between breeding regions A and B1 (Fig. 4), indicating that provenances and genotypes performed similarly in both of these breeding regions. Given correlations greater than 0.80 ± 0.20 indicate G × E interaction to have no practical significance (Robertson, 1959), the highly positive correlation between regions A and B1 ($r = 0.92$) suggest that there is little distinction between these regions. In the case where the G × E effect is small and the positive correlation between population performances between regions is high, breeding regions could be combined in an effort to expand breeding programs without losing genetic population differentiation. In the case where the proprietary investment of independent forestry companies would prevent the amalgamation of regions A and B1, policy should be revised to allow superior performing provenances and families from within these regions to be used over a wider deployment area which crosses administrative boundaries.

Given large climatic differences and very limited cross-testing, moderate to high correlation ($r = 0.69$–0.95) between region J in the north and other foothill regions in the south may not be reliable indicators of transferability of seed between region J and other breeding regions. Earlier analysis of lodgepole pine provenance trials in Alberta showed that correlations for three sites located in the foothills (52°37′–54°24′N and 990–1006 m) with a site located at 49°23′ and 1350 m above sea level were 0.52–0.80 (Rweyongeza et al., 2010). These correlations suggest that, although the analysis of the G × E interaction between region J and other regions was based on very few populations and families, the observed correlation was within the expected range. Nevertheless, a more concerted cross-testing is needed to clearly determine the extent of the G × E interaction before attempting operational seed transfers between region J and other breeding regions.

4.3. Implications for climate change adaptation

The effects of past population transfers among breeding regions can allow inferences for performance under climate change when the growth effects are interpreted in light of regional climate differences (Table 2). Temperature differences among Alberta's lodgepole pine breeding regions are not very large (typically around 0.5 °C), with the exception of breeding region J, which is about 2.5 °C colder than all other breeding regions. Transfer results to breeding region J are uniformly negative, and therefore a climate change adaptation prescription to compensate for an approximately 2.5 °C increase would certainly entail high risks of sub-optimal growth in the near future. Breeding region J is also considerably drier, so climatically matching seed sources may be difficult to find under climate change. Conversely, transfers that entail a moderate shift in temperature, equivalent to approximately 0.5 °C warming, had a uniformly positive effect (Fig. 5). In fact, all but one transfer (Fig. 5, C to B1) showed that superior growth of introduced populations relative to local sources were associated with a transfer to a colder environment. Transfer of sources from warmer to colder environments also represents a safe climate change adaptation strategy. Once anticipated climate change occurs at a magnitude equivalent to the transfer,

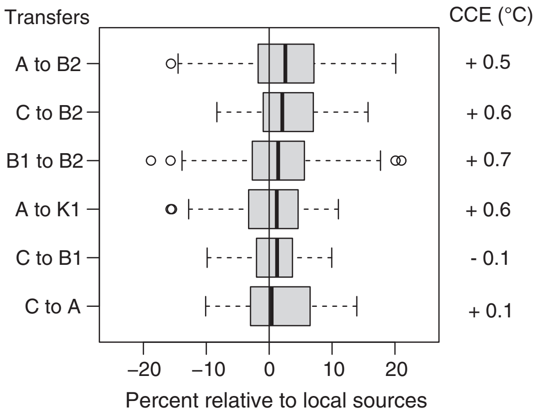


Fig. 5. Performance of individual families in response to transfer among breeding regions. Only transfers with a positive performance relative to local sources are shown. The climate change equivalent (CCE) for mean annual temperature is also shown, meaning that if climate warms by this amount, the transferred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

populations should be again in equilibrium with their environment, assuming they were originally optimally adapted to their local climatic environment. We can therefore safely recommend the transfers shown in Fig. 5, which both ensure proven productivity gains under recent climate conditions, plus a short term adaptation measure for warming of about +0.5 °C. This change may have already occurred during the evaluated growing period, and may therefore simply represent a population shift to compensate for past warming.

Provenance and progeny tests analyzed in this study do not provide an opportunity to support seed transfer recommendations to address potential drought issues under climate change. Region J is the only breeding region that has a substantially drier environment (Table 2, MAP, MSP and CMD), and none of the transfers to this region outperform the local sources. Considering drought-induced sub-optimal growth has been observed in other boreal tree species (Barber et al., 2000; Hogg and Bernier, 2005; Worrall et al., 2013), the Boreal Highlands breeding region J should place emphasis on identifying drought tolerant genotypes, currently not in the breeding program, for future reforestation. Within the sub-boreal foothills, there is a strong similarity in heat and precipitation (MAP, DD5 and CMD) among breeding regions A, B1 and C (Table 2). Thus, seed transfer between regions A, B1 and C may not offer significant compensation in terms of assisted population migration as an adaptation to drought caused by a changing climate. Conversely, regions A, B1 and C are potential sources of drought tolerant populations for regions B2. Transfer of seed from A, B1 and C to some sections of B2 is transfer of seed from a lower to a higher elevation, which if done appropriately could increase productivity in B2 while potentially introducing drought-hardy populations and genes. However, it should be noted that for species such as lodgepole pine that exists as pure species and as hybrids in segments of its natural range, any transfer of seed from regions where hybrids are known to exist should be approached with caution (i.e. Fig 5, B1 to B2 and C to B2).

This study does not explicitly project growth under various climate change scenarios, but field results can be interpreted in conjunction with a climate envelope molding study that provides this context (Gray and Hamann, 2011). In this study, approximately 80% of the Lower Foothills sub-region is projected to remain climatically suitable for lodgepople pine until the end of the century. The best matching seed source for the 2020s and 2050s originates from the Natural Subregion LF 1.3, which closely corresponds to breeding region C (Gray and Hamann, 2011, Tables S8 and S9). Interestingly, provenances and families originating from breeding region C performed either better or approximately equivalent to local sources in all sub-boreal foothills breeding regions (Table 3, Fig. 3). Although in this study we could only observe genotype response to small increases in temperature, results from Gray and Hamann (2011) suggest superior genotypes from region C could be more widely deployed in the sub-boreal foothills breeding regions until the 2050s.

In addition to general prescriptions of seed transfers among breeding regions to address climate change, we should note that a large portion of the genetic variation resides within breeding populations as illustrated by boxplots in Fig. 5. If we consider the recommendation to transfer genotypes to colder environments to increase productivity relative to local sources according to Fig. 5, only the top-performing populations represented in the right tails of the boxplots should be chosen for assisted migration prescriptions. To support such population selections, we provide a database of the best linear unbiased estimates (BLUEs) representing height estimates relative to local populations for all individual provenances and families tested in every breeding region (Supporting Information Table S1). Additionally the database may be used to remove genotypes from local breeding populations, if their sensitivity to projected climate change is indicated by performing poorly when transferred to warmer breeding regions.

5. Conclusions

This paper represents a comprehensive regional case study building on 30 years of tree improvement activities by government agencies and private companies. More than 1800 families and provenances were tested in 37 genetic field trials across six breeding regions, to assess genotype × environment interactions, and we show how this information allows the development of a regional climate change adaptation strategy. The results indicate that local populations perform well, but that some transfer opportunities exist. With the exception of the highest elevation populations, the general assumption guiding seed transfer policy, “local seed is best for reforestation” appears largely valid for most of the lodgepole pine breeding programs in Alberta. We also found that some breeding regions could be amalgamated based on the observation of high positive correlation of population performance and very low genotype by environment interactions. Alternatively, policy change may allow superior performing families to be deployed across similar breeding regions without merging their breeding populations. The study only allows for limited recommendations of seed transfer under climate change, as temperature differences among most breeding regions were small, allowing for inferences corresponding to about 0.5 °C warming. Nevertheless, the observed growth effects were consistently positive and we can make transfer recommendations accordingly. The proposed transfers ensure productivity gains under recent climate conditions, plus a short term adaptation measure to compensate for warming of about +0.5 °C. A large portion of the genetic variation resides within breeding populations, and therefore an alternate adaptation strategy could be the selection of families within breeding regions to enhance resilience to climate change. To support such family selections, we provide a database of performance for all individual provenances and families tested in every breeding region.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.06.041.

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