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Climatic drivers of genotype-environment interactions in lodgepole pine based on multi-environment trial data and a factor analytic model of additive covariance

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Abstract

The optimum deployment of select material from tree breeding programs is affected by the presence of genotype-environment (GxE) interactions and further complicated by future climate change. Here, we analyzed tree height data from 28 progeny test sites in a multi-environment trial (MET) dataset for two testing cycles of the lodgepole pine (*Pinus contorta* Douglas ex Loudon) breeding program in British Columbia to characterize one approach to investigating the climatic variables influencing GxE, and the potential impacts of climate change. Linear mixed model analysis was conducted using an approximate reduced animal model with a factor analytic (FA) variance model to estimate the complex additive (co)variance structure. Test sites were grouped according to patterns of GxE and climate modelling was employed to project historical and future deployment zones for each group. Based on these findings, it appears that breeding groups with historically wide deployment zones from northern environments will become less important as the climate warms, and therefore investment should be directed toward southern breeding groups which will be useful across a very wide geographic range in the near to mid-term future.

Keywords

Genotype-environment interactions, multi-environment trial, factor analytic, climate change, tree breeding, lodgepole pine.

31 Introduction

32 The variability in performance of tree genotypes when grown under different environmental conditions
33 (*i.e.* sites) is commonly referred to as genotype-environment interactions (GxE). Moreover, the
34 interactions can be detected statistically in common garden experiments that are replicated at multiple
35 locations, and can be caused by either heterogenous variances or rank changes among genotypes (Muir
36 et al. 1992). The effect of heterogenous variances occurs when genetic variance is significantly different
37 among test environments (for example, variance due to family or provenance effects), and is often
38 referred to as scale effects. GxE resulting from rank changes among genotypes growing in different
39 environments is important when considering intensive crop management, as it affects optimization of
40 performance over a given area throughout the life of the crop. There are two general approaches to
41 managing GxE (Raymond and Namkoong 1990). The first requires partitioning the deployment area into
42 homogeneous environments which display minimal GxE. This is only possible if patterns of GxE are
43 predictable, and requires selection of genotypes that are optimal for each environment. For example,
44 Johnson and Burdon (1990) correlated patterns of Type B genetic correlations to soil type and Gapare et
45 al. (2015) used regression tree models and environmental variables to explain patterns of GxE for
46 radiata pine. The second approach is to select genotypes that grow well over a wide range of
47 environments, regardless of specific environmental factors (Cullis et al. 2014).

48 Tree species often have wide geographic distributions and considerable genetic variation, and in order
49 to control GxE breeders partition the deployment area into small zones with similar environmental
50 characteristics, such as climate and soils. Thus, a conservative approach to managing GxE is to have
51 many small breeding zones that minimize the amount of environmental variation to which the
52 deployment population will be exposed, however, this is costly and inefficient (Ukrainetz et al. 2011;
53 Gray and Hamann 2011). Defining the boundaries among environments is difficult because genetic and

environmental variation are often clinal, and in order to detect patterns of GxE one must have accurate rankings of each genotype in each environment. The correlation of breeding values in different environments is the preferred method for characterizing GxE in forest tree breeding programs because it helps characterize the role of environment in generating the interactions (Burdon 1977). However, it can be biased and inefficient if working with a small number of common families and many environments (Cullis et al. 2014). Other approaches for characterizing GxE include stability analysis, type-B genetic correlation biplot analysis, reaction norm and factor analytic (Li et al. 2017).

Multi-environment trial (MET) datasets can be used to assess patterns of GxE for the breeding population, identify parent trees that are specialists or generalists (*i.e.*, have a higher amount of phenotypic plasticity), and inform the selection of genotypes for breeding and deployment populations (Smith et al. 2001; Breeck et al. 2010; Cullis et al. 2014). However, these datasets can be difficult to analyse when the number of test environments (sites) is large and connectivity is poor, because fitting an unstructured variance model becomes cumbersome and inefficient. Cullis et al. (2014) have developed an elegant approach to dealing with large MET datasets that involves using an approximate reduced animal model (ARAM) to improve computational efficiency, which is based on the reduced animal model of Quaas and Pollack (1980), and a factor analytic (FA) structure for modelling additive (co)variance (Smith et al. 2001). The ARAM partitions the additive component into parental effects and effects related to Mendelian segregation in the gametes. In the absence of significant inbreeding in the population, the ARAM is equivalent to the full animal model, but with significantly fewer equations to solve, which greatly improves computational efficiency. The FA model facilitates simultaneous analysis of all test environments and the efficient capture of complex variance structure in MET datasets with a high degree of imbalance. The FA component is a model that fits a linear combination of coefficients known as factor loadings and factor scores that are used to determine the breeding values for trees at each test site. Recently, Cullis et al. (2014) used this approach to analyze a large MET dataset for the

radiata pine breeding program in Australia and New Zealand, while several other studies employing forest tree MET datasets have also included similar models to account for various components of the data (Hardner et al. 2010; Costa e Silva et al. 2006; Zapata-Valenzuela 2012). A major challenge is organizing and summarizing the complex outputs generated from MET analyses. Cullis et al. (2010) provided guidance and several approaches to characterize patterns of GxE ensuing from MET analyses with FA models, which include clustering sites based on the dissimilarity matrix of additive effects and using a 'heatmap' to visualize patterns. Gapare et al. (2015) attempted to further characterize patterns of GxE from a MET analysis of radiata pine in New Zealand using hierarchical cluster analyses, multiple regression tree models and climate data, and determined that minimum temperature was an important driver of GxE in both progeny and provenance trials, and partitioned the target environment to optimize deployment of selected material.

In forestry, the underlying principle that governs seed use is that local populations are regarded as well adapted to their parochial environments and, although not always optimal, are safest to use for reforestation (Ying and Yanchuk 2006). In fact, several studies have used provenance test data to show that local populations generally grow best in the absence of rapid climate change (Wang et al. 2006; Wang et al. 2010). Moreover, in some locations, seed transfer guidelines restrict the movement of seed in order to minimize the risk of maladaptation resulting from negative interactions with biotic and abiotic factors in the environment. Although seed from local populations is a low-risk option, it is not always optimal. For instance, Wang et al. (2006) showed that some populations of lodgepole pine (*Pinus contorta* Douglas ex Loudon) had higher growth performance over a very broad range of environments and often outgrew local populations. Furthermore, Wang et al. (2010) estimated the increase in height growth when using the optimum population for reforestation. Some techniques used for creating seed transfer systems to restrict seed deployment include focal point systems (Parker 1992; Lesser and Parker 2006; Ukrainetz et al. 2011), fixed zone systems based on minimizing within-zone variation (O'Neill and

Aitken 2004), and using provenance test data to delineate a critical or safe transfer distance (Campbell 1986; Rehfeldt 1988). Most transfer systems are focused on restricting the movement of seed from natural populations, however, managing deployment of seed from breeding programs should attempt to balance gain with minimizing the risk of maladaptation.

Synthetic breeding populations have been selected to be optimal in a given environment and climate envelope. With rapid climate change and the significant rotation age of gymnosperms grown in the northern hemisphere, it is likely that deployment and breeding populations will become sub-optimal before harvest, resulting in less than full potential use of the land. Therefore, in the face of climate change, it will be important for breeders to construct and allocate deployment populations to environments where they will be well adapted. In the absence of human intervention, tree species with large geographic ranges and substantial genetic variation have the inherent qualities required to persist and adapt to changes in climate, but will suffer from reduced growth and fitness during the adaptation lag that occurs when climate change outpaces rates of adaptation. As such, human intervention is required to maximize the production of resources that flow from forests. Most research investigating the effects of climate change on tree species has been conducted on natural populations using common garden experiments (Andalo et al. 2005; Beaulieu and Rainville 2005; Matyas 1994; O'Neill et al. 2008; Rehfeldt et al. 1999; Wang et al. 2010). Generally, these studies indicate a small increase in productivity in the short term, but increased maladaptation in the absence of assisted gene flow (transfer of populations within the species range) over the long term. Implementing assisted gene flow through seed transfer regulations is one strategy to help optimize forest productivity when using natural populations for reforestation, but little is known about the response of synthetic breeding populations to climate change. Furthermore, the future deployment area of breeding and operational populations will change through time, and understanding these shifts will help guide investment.

The goal of this project was to model patterns of GxE for a tree breeding program by analyzing a MET dataset using the ARAM and a factor analytic model for additive (co)variance. The lodgepole pine breeding program in British Columbia, Canada, was used as the motivating example for this analysis. Using this technique we were able to better understand the climatic drivers of GxE across the breeding population and apply climate change projections to understand the future importance of the breeding populations.

Materials and methods

Test population

The motivating example for this project was the lodgepole pine breeding program in British Columbia, Canada. The province of British Columbia was divided into breeding zones based on knowledge of population variation, geography, ecology and climate in an attempt to manage GxE interactions in the breeding program. It was assumed that the characteristics of each zone resulted in a unique elite population for breeding and seed deployment. The elite population for each zone was selected based on results from open-pollinated (OP) progeny tests planted between 1984 and 2000 (OP tests). Five breeding zones were subsequently selected for advanced generation breeding programs and crosses were made among parents selected for the elite population in each zone. Second-generation progeny tests were established between 2002 and 2006 in the five breeding zones with advanced generation breeding programs (CP tests).

Experimental design of progeny tests

The goal of open-pollinated testing was to estimate the additive genetic (breeding values) for founder parents to inform roguing of early seed orchards and the base population. The strategy was to test

approximately 300 base parents using seed from open-pollinated collections on three test sites within each breeding zone using the following allocation (Table 1):

1. 125 to 150 parent trees from within the zone;
2. 100 parent trees from outside of the zone;
3. 50 parent trees from selected populations based on provenance testing.

The result was an open-pollinated progeny testing program with a significant number of common families tested between zones. The OP tests also included four to six operational control seed collections that were representative of wild seed being used for reforestation within each zone, and five open-pollinated families selected in stands adjacent to each test site. The OP tests were established using a randomized complete block design with families planted in four-tree row plots. In order to keep block sizes small and minimize within-block variation, sites for larger testing programs were established in two or three planting series, each with a unique complement of OP families and often deployed in successive years. Several smaller testing programs deviated from the strategy used for the main breeding zones and are included here for completeness.

Parent trees were selected based on the performance of progeny in first-cycle progeny tests for growth and wood quality in five breeding zones. Using assortative mating and a factorial mating design (two 5 x 5 factorials and the diagonals of three 5 x 5 factorials), two sub-populations were created for each breeding zone for growth and wood density. Each sub-population was composed of 65 full-sib families (controlled pollination (CP) families) for a total of 130 families available for testing within each zone (Table 1). The goal of second-generation testing was to allow recombination among elite parents and select the best individuals within families. CP sites were then established using a randomized complete block design with families planted in five-tree row plots. Families from each sub-population were

deployed randomly within each of 10 blocks per site along with operational control seed collections, families selected for other traits and operational orchard seed collections.

Multi-environment trial dataset

The MET dataset included growth data for progeny (non-parents) of 1,503 base parents and 646 controlled crosses tested across 42 progeny test sites from two generations of testing (Figure 1). Two sites (HELA and HELC) had poor connectedness with other testing series and were therefore removed from further consideration along with seven sites that tested less than 40 families (POMM, PERR, COTT, WIDP, REDP, WIOP and REOP) or lacked age 10 data (Table 1). WICP, WIFI and WIPG were established at a farm-field study site and were considered representative of a single test environment. These three tests (two OP sites and one CP site) were subsequently considered a single test site (WILL). Based on single-site analyses, three sites had no significant additive variation and were removed from further consideration (LORN, THRE and REDC). Furthermore, families (half- and full-sib families) from parents that were not used for advanced generation breeding were removed from further analysis. After removing sites with poor design or connectedness (as described above), and progeny of parents that were not selected for advanced generation breeding, the final MET dataset had 348 base parents tested on 28 sites with an average of 106 parents per site which ranged from 27 to 185. The average number of common parents between sites (connectedness) was 38, which ranged from 2 to 134.

Single-site analyses

Genetic parameters were estimated for each site using a linear mixed model analysis in ASReml-R (version 3). For each trial, y represents the $n \times 1$ vector of height data, where n is the number of planting positions on the site. If we assume that there is pedigree information for m trees, the model used to assess each trial was:

$$[1] \quad y = X\tau + Z_g u_a + Z_p u_p + e$$

190

191 where, τ is a vector of fixed effects with the associated design matrix X , u_p is a vector of random effects
 192 for the experimental design features with design matrix Z_p , u_a is an $m \times 1$ vector of random additive
 193 genetic effects, Z_g is the design matrix for u_a , and e is a vector of random residuals. The random effects
 194 for u_p , u_a and e are independent and multivariate Gaussian with zero means. The variance matrix for
 195 random effects (u_p) is $G_p = \bigoplus_{v=1}^b \sigma_{p_v}^2 I_{q_v}$, where v is the component of the matrix ($v=1$ to b), $\sigma_{p_v}^2$ is the
 196 variance of component v , u_{pv} are the random effects for component v , and q_v is the number of effects or
 197 size of u_{pv} . The variance of random genetic effects (u_a) is $\sigma_a^2 A$, where A is the numerator relationship
 198 matrix and the variance of random residual effects is $R = \sigma^2 I_n$.

199 The single-site analyses for estimating heritability were conducted using full information, which included
 200 all elite and non-elite base parents. In order to account for the effects of population variation in the
 201 data, genetic groups were added as fixed effects to single-site models for OP sites. Each base parent was
 202 assigned to a genetic group based on its original geographic location and elevation. Planting series was
 203 added to the model as a fixed effect for OP sites, blocks nested within planting series were treated as
 204 random effects (u_p), and the residual variance component is a combination of non-additive genetic and
 205 residual variation. The effects of population variation were absent in CP sites and the site mean
 206 (intercept) was the only fixed effect. The random design effects (u_p) included cross (SCA), blocks, and the
 207 interaction of cross and blocks. Adding cross to single-site models for CP sites partitions the non-additive
 208 genetic effects (dominance).

209 Narrow sense heritability for single-site analyses was calculated using the following equation:

$$[2] \quad h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_c^2 + \sigma_{bc}^2 + \sigma^2}$$

210

211 where, σ_c^2 is the variance component for full-sib crosses and σ_{bc}^2 is the variance component for the
212 interaction of block and cross. For OP sites, σ_c^2 and σ_{bc}^2 are dropped from the equation.

213 Significance of additive effects was assessed as the average one-tail probability value of the chi square
214 test with and without the random effect (additive effects: $Z_g\mu_a$) in the model (Verbeke and Molenberghs
215 2000):

[3]

$$p = \frac{p(\chi^2, f) + p(\chi^2, f-1)}{2}$$

216 where, $p(\chi^2, f)$ and $p(\chi^2, f-1)$ are the one-tail probability values for the chi square test with f degrees of
217 freedom equal to the number of random effects in the model and the chi square value, defined as

[4]

$$\chi^2 = 2 \times (L_f - L_{f-1})$$

218 where, L_f and L_{f-1} are the log likelihood with f and $f-1$ random effects in the model, respectively.

219 MET analysis

220 Next, we describe the analysis of a MET dataset with 28 test sites from the first (OP) and second-cycle
221 (CP) progeny testing programs for lodgepole pine in British Columbia, and follow the methods and
222 conventions outlined by Cullis et al. (2014) with modifications.

223 The reduced animal (RA) model proposed by Quaas and Pollack (1980) deconstructs the additive
224 variance into parental and Mendelian segregation components. The ARA model is a variation of the RA
225 model that ignores the variation attributed to Mendelian segregation and is equivalent to the RA model
226 and full animal model when inbreeding is negligible. Cullis et al (2014) describe the special case of no
227 data on parental individuals with the ARA model for OP and CP trials as:

$$[5] \quad y = X\tau + 1/2 (F_{np} + M_{np})u_{ap} + Z_p u_p + e_a^*$$

228 where, y is a vector of height data described by $y = (y_1^T, y_2^T, \dots, y_t^T)^T$ and t is the number of trials, $y_j = n_j$
 229 $\times 1$ vector of data for the j^{th} trial, n_j is the number of planting spots in that trial, and the total number of
 230 planting spots across all trials is $n = \sum_{j=1}^t n_j$. F_{np} and M_{np} are the $m_n \times t \times 1$ female and male indicator
 231 matrices assigning each non-parent to its parent, and m_n is the number of non-parents with pedigree
 232 information. The $m_p \times t$ vector of genetic effects for the parents (u_{ap}) is described by $u_{ap} =$
 233 $(u_{ap_1}^T, u_{ap_2}^T, \dots, u_{ap_t}^T)^T$, and the vector of non-genetic effects (experimental design features) is
 234 described by $u_p = (u_{p_1}^T, u_{p_2}^T, \dots, u_{p_t}^T)^T$ with design matrix Z_p . Since this model does not explicitly fit the
 235 non-additive residual genetic effects (u_e) or the Mendelian sampling effects (u_{m_n}) these terms are
 236 included in a composite residual effect (e_a^*) and is described as $e_{a_j}^2 = (e_{a_1}^{*T}, e_{a_2}^{*T}, \dots, e_{a_t}^{*T})^T$. The effects
 237 for u_{ap} , u_p and e_a^* are assumed to be mutually independent and multivariate Gaussian with zero mean.
 238 The variance of u_p for the ARA model is the same as above for the single-site analysis. The variance for
 239 u_{ap} is described as $(u_{ap}) = A_{pp} \otimes G_a$, where A_{pp} is the $n_p \times n_p$ upper-left component of the numerator
 240 relationship matrix describing the relationship among parents, and G_a is the $t \times t$ matrix of between-
 241 environment additive variance with diagonal elements $\sigma_{a_j}^2$. The variance of residuals (e_a^*) is =
 242 $\bigoplus_{j=1}^t \sigma_j^2 I_{n_j}$, where the residual variance for CP sites is $\sigma_{cp_j}^2 = 1/2 (1 - \bar{f})\sigma_{a_j}^2 + \sigma_{e_j}^2 + \sigma_j^2$, and for OP
 243 sites is $\sigma_{op_j}^2 = 1/2 (0.75 - 0.25\bar{f})\sigma_{a_j}^2 + \sigma_{e_j}^2 + \sigma_j^2$.

244 To overcome issues around poor connectivity in the MET dataset and difficulty fitting an unstructured
 245 model with a prohibitively large number of parameters, Cullis et al. (2014) propose using a factor
 246 analytic (FA) variance model for additive genetic effects. The FA model can be viewed as a multiplicative
 247 or regression model of the genetic effects:

$$[6] \quad u_{ap_{ij}} = \lambda_{ap_{1j}} f_{ap_{1i}} + \lambda_{ap_{2j}} f_{ap_{2i}} + \dots \lambda_{ap_{kj}} f_{ap_{ki}} + \delta_{ap_{ij}}$$

where, u_{ap} is a sum of k multiplicative terms and k is known as the order of the model, and we refer to the model as FA(k). Each term in the model is split into a factor loading ($\lambda_{ap_{kj}}$) and factor score ($f_{ap_{kj}}$). The factor loadings are genetic variance components that represent the between environment (test site) covariance structure which we hypothesize are driven by some environmental covariate, and factor scores are the genetic effects of individual trees, or in the case of the ARA model the parents. The final term in the model ($\delta_{ap_{ij}}$) is a genetic regression residual or lack of fit term. The FA model can be written in matrix notation as:

$$[7] \quad u_{ap} = (I_{np} \otimes \Lambda_a) f_{ap} + \delta_a$$

where, u_{ap} is a vector of genetic effects as described above, I_{np} is an identity matrix for non-parents, Λ_a is a $t \times k$ matrix of factor loadings, f_{ap} is an $m_p \times k$ vector of genetic scores, δ_a is an $m_p \times 1$ vector of genetic regression residuals, and m_p is the number of parents with pedigree information. We assume that f_{ap} and δ_a are mutually independent and distributed as multivariate Gaussian with zero mean. The variance of factor scores (f_{ap}) is $A \otimes I_k$ and the variance of genetic regression residuals (δ_a) is $A \otimes \Psi_a$. The variance of genetic effects (u_{ap}) is $\otimes (\Lambda_a \Lambda_a^T + \Psi_a)$, and $G_a = (\Lambda_a \Lambda_a^T + \Psi_a)$. The FA model can be fit with different levels of k .

Cullis et al. (2014) provides guidance on determining the appropriate value of k using estimates of the proportion of genetic variance captured by the model, and the distribution of genetic variance for trials that was explained by the model. The variance explained by each individual trial for k multiplicative terms in Equation 6 was calculated as:

$$[8] \quad v_{a_j} = 100 \sum_{r=1}^k \lambda_{a_{rj}}^2 / \left(\sum_{r=1}^k \lambda_{a_{rj}}^2 + \Psi_j \right)$$

The overall genetic variation explained by the FA model can be calculated as $\bar{v}_a = 100 \text{tr}(\Lambda_a \Lambda_a^T) / \text{tr}(G_a)$.

For computational simplicity in fitting FA models, the upper triangle of the Λ_a matrix is set to zero which has no biological significance or interpretation (Cullis et al. 2010). It is more meaningful to transform the factor loadings and factor scores to the principle component representation known as rotated factor loadings and rotated factor scores. The rotated loadings and scores are orthogonal. The first factor accounts for the majority of the variation, the second accounts for the next highest and is orthogonal to the first. The REML estimates of the loadings from ASReml can be rotated as $\Lambda_a^* = \Lambda_a V_a$, and factor scores can be rotated as $f_{ap}^* = (V_a^T \otimes I_{m_p}) f_{ap}$ where, V_a is the singular value decomposition of Λ_a (Cullis et al. 2010).

Assigning sites to breeding groups

Groups of sites with low GxE for growth traits (high Type B genetic correlations; see Burdon 1977) will have a set of genotypes that perform similarly across all sites in the group, and a subset of genotypes that consistently perform best. In British Columbia, climate variation accounts for the majority of variation in populations across the range of tree species, and can be used to explain patterns of local adaptation (Rehfeldt et al. 1999; Wang et al. 2006; Rehfeldt and Jaquish 2010; Wang et al. 2010). Next, we attempted to use the G_a matrix for the best FA model to identify groups of sites (called breeding groups) such that mean Type B genetic correlations within groups are high and between groups are low. We then used climate models to explain where the breeding population for each breeding group should be deployed given historical and expected future climates.

Equation 8 was used to calculate the percent of site additive genetic variation explained by the best FA model. All sites that were described poorly by the model (<50% of the additive genetic variation explained by the model) were removed from the next stage of the analysis. Hierarchical cluster analysis using the *hclust* procedure in R and the ward.D2 method was used to cluster sites based on the G_a matrix, using $s = 2$ to 12 number of clusters (breeding groups) and the mean Type B genetic correlation

between groups was calculated for each level of s . The criteria for determining the optimum number of breeding groups (s) was i) a within-group mean Type B genetic correlation >0.7 , and ii) the point at which the benefit of adding an additional group diminishes as indicated by a decrease in slope of the plot of mean within-group genetic correlations.

Using climate models to describe breeding groups

Next, we attempt to describe breeding groups using climate models in order to better understand the potential size and distribution of the breeding zone associated with each group and the potential impact of climate change. For this we used the following approach: i) use multiple regression models to predict factor loading values based on climate variables, ii) train a regression tree model to predict the most appropriate breeding group based on a particular combination of site factor loadings, iii) apply the multiple regression models from (i) to a provincial grid dataset of climate variables to predict factor loadings across the landscape, and vi) use the predicted factor loadings in (iii) as an input for the regression tree model in (ii) to predict breeding group across the landscape.

Multiple regression with the following linear model was used to model rotated factor loadings:

$$[9] \quad y_k = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3$$

where, y is the rotated factor loading of order k , β_0 is the intercept, β_1 , β_2 and β_3 are coefficients, and x_1 , x_2 and x_3 are climate variables. A set of weakly-correlated annual and seasonal climate variables from ClimateBC (version 5.31) was created by applying hierarchical cluster analysis to the correlation matrix for climate variables across sites and choosing one variable from each of 9 clusters for annual variables and 16 clusters for seasonal variables. The nine more weakly correlated annual climate variables were used to model the first two factor loadings, while seasonal variables were better at explaining the third factor loading. All three-variable models were attempted using the *leaps* package in R and the best model was selected based on the highest R^2 . For regression tree analysis the random forest package in R

was used to create a model to predict genetic groups (dependent classification variable) based on the rotated factor loadings (independent predictor variables) with the model set to classification mode with 10,000 trees. The multiple regression models for the three rotated factor loadings were applied to a 1.6 km gridded point dataset with geographic (latitude, longitude and elevation) and climate normals from 1961 to 1990 (ClimateBC version 5.31) to predict factor loading values across the province which were subsequently used as input for the random forest regression tree model to assign each point to a breeding group.

In order to determine the rate of misclassification associated with the multiple regression-regression tree (MRRT) approach, we used the MRRT models to predict a breeding group for each test site in the MET dataset based on its rotated factor loadings. The predicted groups from the MRRT models were compared to the actual groups assigned based on cluster analysis of the G_a matrix. This validation approach provides an estimate of overall error and indicates which groups are most vulnerable to misclassification.

The effect of climate change on breeding zones was determined by applying the multiple regression and random forest models (MRRT) to an ensemble of 15 general circulation models from ClimateBC (version 5.31) for 2055 based on the Representative Concentration Pathway (RCP) 8.5 scenario which assumes high greenhouse gas emissions and is the most pessimistic scenario employed by the Intergovernmental Panel on Climate Change (IPCC 2014).

Results

Single-site analysis

The average individual tree heritability for height growth based on single-site analyses for OP and CP sites was 0.31 and 0.11, respectively. The distribution of heritability estimates for OP sites was wider and shifted to the right compared to CP sites (Figure 2).

Factor analytic

The FA3 model explained over 80% of the overall additive genetic variation and 82% of sites were well modelled (over 50% of the additive variance could be explained; Figure 3). Furthermore, the matrix of Type B genetic correlations (G_a) for the FA3 model was well-structured with several easily identifiable groups of sites that had high genetic correlations (Figure 4). The G_a matrix for lower order models did not adequately explain the additive (co)variance in the data, and higher order models (FA4) were overly complex. Therefore, the FA3 model was chosen for further consideration in the development of breeding groups and zones. The mean standard error of all Type B genetic correlations was 0.10 and ranged from 0.014 to 0.26. The Type B genetic correlations between pairs of sites that shared more common base parents (higher connectivity) had lower standard errors indicating a link between connectivity and the precision of estimates ($r = -0.34$ between the number of common parents and standard error of the genetic correlation between sites). However, there was no significant relationship between the magnitude of the genetic correlations and connectivity ($r = 0.13$). The mean genetic correlation among OP sites was 0.66 (range from 0.28 to 0.99), among CP sites was 0.49 (range from 0.006 to 0.86) and between CP and OP sites was 0.44 (range from -0.27 to 0.79). The mean standard error of the genetic correlation estimates among OP sites was 0.08 (range from 0.01 to 0.23), among CP sites was 0.10 (range from 0.04 to 0.21) and between OP and CP sites was 0.12 (0.05 to 0.26).

Using hierarchical cluster analysis (Figure 5A) with different numbers of clusters ($s=2$ to 12), all s values >2 had mean within group Type B genetic correlations of greater than 0.7. Furthermore, the benefit of adding an additional group to the cluster analysis was assessed as the change in average within-group

genetic correlation. The change in mean genetic correlation began to decline from $s = 4$ to 5, and although still positive indicated a decreasing benefit of adding additional groups (Figure 5B). The goal was to find the smallest number of groups that describe the structure of the G_a matrix rather than maximizing the average within-group genetic correlation. Therefore, the cluster result with $s=4$ was selected for determining breeding groups. The number of sites within each breeding group ranged from four to eight (Table 2).

Climate modelling and misclassification rate

The relationship between factor loadings and climate variables indicate that GxE is driven by temperature and humidity late in the growing season (data not shown). The best three-variable regression models for the MRRT analysis had R^2 values that ranged from 0.34 to 0.71 (Table 3). The first factor loading (λ_1) was explained by a combination of annual temperature and precipitation, while the second loading (λ_2) was explained best by a combination of variables related to the frost-free period and precipitation as snow. The third loading (λ_3) was explained by summer and autumn temperatures, along with autumn moisture deficit. The out of bag error rate for the random forest regression tree component of the MRRT analysis was 8.7%, with two sites misclassified. One site from group 1 was misclassified as group 2, and one site from group 4 was misclassified as group 1.

The expected misclassification rate of the MRRT analysis was 39% which indicates the percent of sites that were misclassified using the MRRT analysis compared to the actual breeding group from the cluster analysis of the G_a matrix. Group 4 was particularly vulnerable with three of the four sites (75%) misclassified as group 3. Sites in group 1 were misclassified into groups 2 and 3 (29% misclassification rate), sites in group 2 misclassified as group 3 (25% misclassification rate) and sites in group 3 were misclassified into groups 2 and 4 (38% misclassification rate). All of the misclassifications are "moderate" in nature (*i.e.*, none are group 1 to group 4 or group 2 to group 4 errors).

Breeding zones and climate change

Sites within groups are classified into similar ecosystem units (based on the biogeoclimatic ecosystem classification system for British Columbia, which is also known as BEC), and share similar climate and elevation profiles (Table 2). Sites in group 1 have a wide geographic range with high-elevation sites in the south and low-elevation sites further north (Figure 6A). The sites in group 1 also have slightly higher mean annual temperature (MAT) and mean annual precipitation (MAP), representing regions of the province that are relatively warm and wet. Group 2 has only four sites with three in the south and one in the north (Figure 6B). These sites are, on average, the warmest and driest. Sites in group 3 represent regions that are cold and dry (Figure 6C), while sites from group 4 represent regions that are cold and wet (Figure 6D).

The average Type B genetic correlation of sites within breeding groups was 0.76 and ranged from 0.67 to 0.83 (Table 4). The average correlation of sites between groups was 0.46 and ranged from 0.20 to 0.72. The highest between-group correlation was observed for groups 2 and 3 (0.72), while the lowest was between groups 2 and 4 (0.20).

The largest projected breeding zone based on climate normals (1961 to 1990) was for breeding group 4 with an estimated area of 51.5 M ha, while the smallest zones were for groups 1 and 2 at 15.8 M ha and 9.0 M ha, respectively (Table 5). The breeding zones have similar climate profiles to the sites that they represent. Based on current and future projections in climate change, it is expected that the area for group 1 and 2 zones will change by 129% and 276%, respectively (Table 5). The zones for groups 3 and 4 will contract significantly, and all four zones will expand north and move to higher elevations (Figure 7).

Discussion

General data analysis

401 The elegant approach for analysing large MET forestry datasets proposed by Cullis et al. (2014) is ideal
402 for modelling patterns of GxE interactions across the deployment area of a species. The combination of
403 the ARA model and factor analytic (FA) allow for the analysis of large and complex MET datasets that are
404 common to tree breeding programs. Without this technique, MET datasets would be partitioned into
405 smaller subsets for analysis and Type B genetic correlations estimated for all pairs of sites separately
406 (Baltunis et al. 2010; Apiolaza 2012; Raymond 2011), which results in greater bias in the estimates. The
407 sensitivity of this approach to variation in the number of common parents and additive genetic variation
408 between sites remains unclear. For this example, the first split in the dendrogram for the cluster analysis
409 based on the G_a matrix separated OP and CP sites. It is unclear whether this accurately reflects patterns
410 of GxE, or differences in connectivity and additive genetic variation. During the course of this analysis,
411 several modelling approaches were used to investigate these issues including an analysis using data for
412 all tested families (Appendix 1) rather than just elite families, doing separate MET analyses for OP and
413 CP testing cycles, including genetic groups as fixed effects for OP sites and fitting testing cycle as a fixed
414 effect in the model. When testing cycles were analyzed separately, the patterns in the G_a matrix reflect a
415 north-south split. However, due to the nature of the testing scheme, it is impossible to separate the
416 confounding effects of test environment and number of common families since tests in similar
417 environments (north versus south) shared more families than tests from different environments. All
418 other approaches resulted in similar patterns in the G_a matrix with OP and CP sites being clustered more
419 often than would be expected. The approach and model used and reported here was the most
420 appropriate given the proposed questions regarding the nature of GxE for an advanced generation
421 breeding program. Upon closer examination of the cluster groups it is apparent that sites within groups
422 were from similar ecosystems and shared similar climate profiles (Table 2). Sites within groups had
423 higher mean genetic correlations and lower Euclidean distance estimates (estimated based on eight
424 annual climate variables) than between groups (Table 4), and patterns of mean Euclidean distance and

genetic correlations were similar. Furthermore, second-cycle testing (CP tests) targeted different environments from first-cycle tests due to predictions about future harvesting and reforestation programs and access to available testing sites. For example, first-cycle OP tests for southern breeding populations were generally located lower in the valley on homogenous sites, while second-cycle CP tests were established at higher-elevations which reflect more northern environments and these types of patterns are reflected in the groupings from the MET analysis. Given that sites within groups share similar ecosystem and climate profiles, and knowing that OP and CP testing were conducted over very different environments, we believe that the MET analysis is robust and patterns in the G_a matrix truly reflect patterns of GxE across the breeding program for lodgepole pine.

The goodness-of-fit criteria for determining FA model fit provided a trade-off between selecting overly simple or complex models. Higher order models capture more of the additive genetic variation overall and at the individual site level, but we found that the patterns of Type B genetic correlations were difficult to interpret. The FA1 and FA2 models did a poor job of modelling GxE in certain segments of the dataset. The FA3 model, which met the criteria outlined by Cullis et al. (2014), had a correlation structure with strong patterns and easily identifiable groups (Figure 4) while capturing an adequate proportion of the additive variation in the data (Figure 3). Smith et al. (2015) report that other model-selection approaches such as residual maximum likelihood ratio tests (REMLRT) and Akaike and Bayesian (AIC and BIC) information criteria can also be used, but result in the selection of models that are overly complicated or simple. Moreover, comparing FA(k) models with the unstructured model is a superior approach but not practical because fitting an unstructured model for large MET datasets is difficult.

The FA model produces a set of factor loadings and factor scores that when combined can be used to determine the breeding value for each tree, at each site (Smith et al. 2001; Cullis et al. 2014). The number of factor loadings and factor scores is determined by the order of the model. Each site has a

unique set of factor loadings that, in some way, reflect the conditions that influence the performance of individual genotypes. It is likely that a combination of environmental conditions underlie the factor loadings for each site, such as soil conditions, presence of pests and pathogens, and climatic variables. For gymnosperms in temperate environments, climate is a significant force of natural selection and local adaptation (Rehfeldt 1988; Rehfeldt et al. 2006; Wang et al. 2006), and consequently it is expected to show a strong relationship with factor loadings. These relationships can help understand the drivers of GxE in forest tree breeding populations and across the deployment area for a breeding program. Other biotic and abiotic factors can be included to help identify the contributing factors of GxE, if such information exists.

It is important to make a connection between test sites and the deployment area in order to optimize the use of genetic resources. In this example, the connection between test sites and deployment area is made through climate modelling which is ideal for assessing the potential impacts of climate change. Rapid climate change will affect the performance of genotypes through time resulting in climate change induced GxE. It is not only important to consider the past performance of a genotype in a particular environment based on test data, but also the potential performance should they be subject to elevated rates of change in climatic variables. As such, deployment areas should be adjusted in order to match groups of genotypes with expected future environments, while at the same time carefully considering the vulnerability of young seedlings to the current conditions. This type of modelling can help prioritize investment for different breeding populations and delineate appropriate deployment zones. Other studies have proposed systems for seed transfer and assisted migration based on common garden experiments of natural populations (Wang et al. 2006; Wang et al. 2010), however, the use of large MET analyses is more appropriate for the deployment of material from advanced generation breeding programs since it is based on actual field performance of the breeding population.

471 Implications for the lodgepole pine breeding program

472 There are strong differences in the magnitude of heritability estimates for height growth between CP
473 and OP sites (Figure 2) which are likely due to inflated additive variance estimates for test populations
474 with half-sib families collected from wild stands. Xie et al. (2007) suggest that the coefficient of
475 relatedness among trees within half-sib families from natural stands is higher than expected due to
476 breeding among close relatives within a local geographic area. In order to account for this, they adjust
477 the coefficient of relatedness ($\frac{1}{8}$ versus the conventional $\frac{1}{4}$) when determining heritability and include
478 provenance as a fixed effect in the mixed linear model. Other contributing factors to inflated heritability
479 estimates were higher levels of genetic variation, more efficient experimental design, or a combination
480 of these factors in some testing series. We attempted to control inflated heritability estimates in the OP
481 tests by grouping families based on their geographic location and elevation, and including a fixed effect
482 for provenance in the mixed linear model. This helped reduce the magnitude of estimates for OP sites
483 which were still high (mean of 0.31 and maximum of 0.67). Including a realized relationship matrix based
484 on molecular markers with more accurate estimates of relatedness between sibs will help improve
485 estimates of additive variance. The magnitude of heritability estimates in subsequent cycles of testing
486 with control-pollinated material are considerably lower, since the coefficient of relatedness among sibs
487 (full and half-sibs) is more closely approximated by the estimated values resulting in a more accurate
488 estimate of additive variance. Accurate estimates of additive variation are important for breeding value
489 estimation that in turn are used for predicting the genetic value of genotypes. Inflated additive variation
490 results in inflated breeding values and expected gains which are unreasonable and misleading.

491 The goal of this project was to accurately characterize patterns of GxE interactions across the
492 deployment area for the entire lodgepole pine breeding program in British Columbia, Canada. The first
493 generation of progeny testing included base parents with a wide range of genetic quality and only the

top parents were selected for the deployment and advanced-generation breeding populations. In order to understand the effect of GxE on the advanced generation breeding program, all families of base parents that were not used as parents for second-generation breeding and testing were removed from the OP datasets. Results then reflect the performance of the closed, elite breeding and deployment populations that will be the basis of all future testing and operational use. Adding families from non-elite base parents may provide more precise estimates of GxE that reflect patterns only found in natural populations.

It became apparent that performance of genotypes across the deployment area for lodgepole pine in British Columbia is strongly influenced by the length of the growing season and specifically temperatures and precipitation in fall (September to November; Table 3). This suggests that adaptation for fall cold hardiness is still prevalent in the breeding population, and limits the use of certain high-performing genotypes from southern sources that are adapted to environments with longer growing seasons and low risk of late-season frost damage further north or in colder climates. Growth rates and breeding values for elite southern material are often very high when grown on northern sites with shorter growing seasons and higher risk of late-season frost, but often have lower survival rates than locally-adapted material (Ukrainetz, personal observation). Based on our findings, it is apparent that late season frost and the length of the growing season are the most important factors to consider for the deployment of elite material and advancement of breeding populations of lodgepole pine, which is consistent with the influence of climate on genetic variation of natural populations and results from analysis of the entire test population (Appendix 1). Rehfeldt (1988) found that frost-free period was a significant factor in determining population differentiation along environmental gradients, and population variation of lodgepole pine is often well correlated with temperature (Rehfeldt et al. 1999; Wang et al. 2006; O'Neill et al. 2008; Wang et al. 2010).

517 The misclassification rate of the random forest model based on the factor loadings from the MET
518 analysis was very low (8.7%), but much higher when the model was applied to predicted factor loadings
519 from the MRRT analysis (25-75%). Sites that were misclassified were often placed into groups that were
520 similar in terms of climate variation. For example, group 4 which is made of sites that better reflect
521 northern environments with shorter growing seasons was quite vulnerable to misclassification. There
522 were only four sites in this group, and 75% were misclassified into group 3 which is the most similar in
523 terms of climate variation. When modelling breeding groups across the province we expect a certain
524 amount of error associated with the regression models and the random forest model. The significance of
525 the error is based on the patterns of misclassification. Misclassification into groups that are more similar
526 climatically with similar patterns of Type B genetic correlations is less of a concern than misclassification
527 into groups with disparate environments. Breeders know that genetic variation and climate are clinal,
528 and some level of misclassification at the zone boundaries is acceptable. Our model validation shows
529 that most misclassification occurs between groups with similar climate and patterns of Type B genetic
530 correlations. The most vulnerable group was group 4 with only four sites. Sites within group 4 reflect
531 northern and high-elevation environments, although the within group climate profile was weak
532 suggesting that this group is not well-defined (Figure 6D).

533 Provincial models based on climate normals (1961 to 1990) for the four breeding groups suggest that
534 the breeding population for group 4 (Figure 6D) was historically very important followed by groups 3
535 and 1 (Table 5 and Figure 6). Group 4 represents the cold and wet locations in BC, and the random forest
536 regression tree model likely groups all environments beyond the bounds of the data into this group
537 making it appear more important but likely requires refinement. Climate change is apparent and more
538 importantly is expected to be rapid, resulting in some climate change-induced GxE interaction over time.
539 The models using climate change data show that the southern breeding groups (groups 1 and 2) will
540 expand significantly and become more important in the future. For example, in the near future, the area

appropriate for selections from groups 3 and 4 will shrink considerably. This suggests that more investment should be made for the breeding populations derived from groups 1 and 2 (Figure 7A and B). The assisted gene flow of southern breeding populations to northern or colder environments will need to balance the short-term risk of cold damage to seedlings with the long-term benefits of improved growth and adaptation captured by accounting for past and future climate change (Ukrainetz et al. 2011).

The results from this exercise have provided insight into how to restructure the breeding and deployment program for lodgepole pine in British Columbia. Forward and backward selections should be made based on performance on sites within breeding groups. These selections should be further tested at locations within new breeding zones to confirm performance. Using this analysis we can make predictions about growth performance of families within and between breeding groups, but not survival. In British Columbia, wide transfers of seed from southern sources to northern locations or from low to high elevation is considered risky due to increased susceptibility of frost damage. Some breeding groups have very wide geographic distributions that may be considered risky. The MET analysis predicts that selections on southern sites will perform well in northern locations based on growth performance but does not consider tree health, form or survival. The growth and health of a tree at a particular location results from the impact of multiple insults accumulated from biotic and abiotic factors and the interaction of the genetic component of a tree with these factors results in patterns of GxE across the landscape. It is important to test selections across the range of environments within each breeding group prior to deployment. These results also show that selections on sites in warmer, more southern environments will be more important in the future given the projections in climate change models. Moreover, projected breeding zones using climate change predictions (Figure 7) can be used to implement assisted migration in the deployment populations and adjust the testing program. It also shows that more resources should be directed to test material selected on southern sites for future

deployment over a wider geographic area. All annual and seasonal climate variables were included in our modelling approach, including mean climate variables and extremes, but mean climate variables were selected because they explained a higher proportion of the variation in the data. However, it is extreme climate events, and the frequency of these events, that can have important impacts on trees across the landscape and the results presented here should be interpreted with caution when developing new deployment scenarios.

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668 **Tables:**

669 Table 1: Summary of lodgepole pine progeny test sites.

Site	Year	Gen	Zone	Series	Trees	Families	Females	Males	Blocks	T/F/S	T/F/B	HT
DARD	1984*	OP	TO	3	13,339	410	410		8	32	4	326.0
MISS	1984*	OP	TO	3	14,632	449	449		8	32	4	339.8
PENA	1984*	OP	TO	3	14,679	452	452		8	32	4	231.5
ANZU	1985*	OP	BV	2	9451	297	297		8	32	4	259.2
CHOW	1985*	OP	BV	2	9515	300	300		8	32	4	366.0
GRAM	1985*	OP	BV	2	8649	296	296		8	28	4	326.9
BOWR	1985*	OP	PG	2	9769	307	307		8	32	4	370.5
INDI	1985*	OP	PG	2	9395	301	301		8	32	4	452.7
MOFF	1985*	OP	PG	2	9586	302	302		8	32	4	309.9
CRIP	1987	OP	CP	2	8715	274	274		8	32	4	389.0
TACH	1987	OP	CP	2	8488	269	269		8	32	4	312.2
WICP	1987	OP	CP	2	8928	280	280		8	32	4	407.1
BISO	1987*	OP	NE	2	8061	290	290		7	28	4	415.6
EAST	1987*	OP	NE	2	8153	275	275		8	32	4	412.5
HARI	1987*	OP	NE	2	8881	286	286		8	32	4	400.9
BLAC	1988	OP	FI	2	6655	228	228		8	32	4	306.9
TUTU	1988	OP	FI	2	7998	265	265		8	32	4	310.6
WIFI	1988	OP	FI	2	8704	273	273		8	32	4	325.9
REDP	1990	OP	DP	1	1148	36	36		8	32	4	129.8 †
WIDP	1990	OP	DP	1	1149	37	37		8	32	4	121.7 †
REOP	1990	OP	OP	1	1152	36	36		8	32	4	109.5 †
WIOP	1990	OP	OP	1	1152	37	37		8	32	4	121.2 †
COTT	2000	OP	EK	1	892	25	25	3	8	32	4	374.3
PERR	2000	OP	EK	1	860	25	25	3	8	32	4	553.3
POMM	2000	OP	EK	1	877	26	26	3	8	32	4	374.4
HELA	2000	OP	NST	1	3663	116	116	4	8	32	4	316.1
HELC	2000	OP	NST	1	3701	116	116	4	8	32	4	334.7
ABBO	2002	CP	PG	1	6133	137	61	53	9	45	5	487.2
CHIE	2002	CP	PG	1	5590	125	57	51	9	45	5	275.5
WIPG	2002	CP	PG	1	5934	133	59	52	9	45	5	324.4
GRIZ	2004	CP	BV	1	8400	179	72	52	10	50	5	316.5
LORN	2004	CP	BV	1	8675	181	73	52	10	50	5	102.3 †
PINK	2004	CP	BV	1	6225	164	69	49	8	40	5	346.5
BONN	2005	CP	NE	1	5700	118	52	49	10	50	5	327.2
HAWK	2005	CP	NE	1	6215	127	53	50	10	50	5	319.4
INON	2005	CP	NE	1	5990	124	53	50	10	50	5	361.2
FLYF	2005	CP	TO	1	5885	122	43	44	9	50	5	410.8

REDC	2005	CP	TO	1	5710	121	42	43	10	50	5	241.6
THRE	2005	CP	TO	1	5475	119	42	43	10	50	5	214.6
CURV	2006	CP	CP	1	6508	143	66	50	10	50	5	532.9 ‡
MUGA	2006	CP	CP	1	5745	131	62	49	10	50	5	409.6 ‡
REED	2006	CP	CP	1	6200	140	65	49	10	50	5	405.0 ‡

Site = test site code; Year = year of planting (* = planted in multiple years); Gen = generation of testing (OP = open pollinated; CP = control pollinated); Zone = breeding zone; Series = number of planting series; Trees = number of trees planted; Families = number of families included on the site (half-sib families for OP sites, and full-sib families for CP sites); Females = number of trees for seed collections; Males = number of pollen donors; Blocks = number of blocks within planting series; T/F/S = median number of trees per family per site; T/F/B = median number of trees per family per block; HT = average height at 10 years from planting (†5 years; ‡ 11 years).

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Table 2: Assigned breeding group for each site based on hierarchical cluster analysis of the G_a matrix from the MET analysis along with site geographic, ecological and climate data.

Site	Group	Elevation	BEC	MAT	MAP
ABBO	1	960	ICHwk2	3.8	649
FLYF	1	1400	MSdm1	3.1	778
GRIZ	1	915	SBSmc2	2.0	571
HARI	1	1330	ICHmk1	3.5	761
HAWK	1	1535	ICHdm	2.9	914
INON	1	1450	ESSFwc1	3.1	927
PINK	1	1000	SBSmc2	1.7	594
BISO	2	1165	ICHmk1	3.7	770
CHOW	2	840	SBSdw3	2.4	536
EAST	2	1200	ICHmw3	3.7	594
MISS	2	1365	ICHmk1	3.1	726
BOWR	3	985	SBSwk1	3.1	808
CRIP	3	865	SBSdw3	1.3	679
DARD	3	1275	MSxk2	2.9	478
GRAM	3	975	ICHmc1	1.6	747
INDI	3	880	SBSvk	3.2	889
PENA	3	1295	IDFdk1	3.1	559
TACH	3	840	SBSdw3	1.8	605
TUTU	3	715	SBSmk2	1.9	692
CHIE	4	725	SBSmk1	3.1	733
CURV	4	810	SBSwk2	1.1	587
REED	4	1067	SBSmk1	0.5	1011
WILL	4	760	SBSwk1	3.2	852

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BEC = biogeoclimatic ecosystem classification; MAT = mean annual temperature; MAP = mean annual precipitation.

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684 Table 3: The coefficients for multiple regression models between factor loadings and climate normals.

Factor Loading	Model Results	Variable	Coefficient	t-value	p-value
λ_1		Intercept	43.10	0.061	0.55
		MCMT	-14.27	-3.25	0.0043
		TD	-10.52	-2.30	0.033
		MAP	0.051	-2.08	0.052
R^2	0.46				
F-statistic	5.46				
p-value	0.007				
λ_2		Intercept	-750.87	-4.54	<0.001
		FFP	2.63	5.59	<0.001
		bFFP	3.27	4.20	<0.001
		PAS	-0.08	-3.75	0.001
R^2	0.71				
F-statistic	16.08				
p-value	<0.001				
λ_3		Intercept	-107.97	-2.25	0.037
		Tave_sm	6.71	2.01	0.059
		Tmin_at	-9.61	-2.23	0.038
		CMD_at	0.68	2.33	0.031
R^2	0.34				
F-statistic	3.24				
p-value	0.045				

685 MCMT = mean coldest month temperature; TD = temperature differential; MAP = mean annual precipitation; FFP =
 686 frost-free period; bFFP = beginning of the frost-free period; PAS = precipitation as snow; Tave_sm = average
 687 summer temperature; Tmin_at = minimum autumn temperature; CMD_at = Hargreaves climate moisture deficit in
 688 autumn.

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690 Table 4: The number of test sites associated with each group (N) with the number of OP and CP sites
691 (within brackets). The upper diagonal shows the within-site mean genetic correlation and above the
692 diagonal the mean between-group genetic correlations with the range of genetic correlations within
693 brackets. The lower diagonal is the mean Euclidean distance (based on eight annual climate variables)
694 within-groups and below the diagonal are the mean Euclidean distances between groups.

Group	N (OP, CP)	1	2	3	4
1	7 (1, 6)	0.67 (0.45-0.86) 2.9	0.60 (0.36-0.92)	0.49 (0.05-0.73)	0.26 (-0.28-0.71)
2	4 (4, 0)	3.2	0.83 (0.72-0.91) 2.3	0.72 (0.53-0.90)	0.20 (-0.11-0.38)
3	8 (8, 0)	3.5	3.4	0.80 (0.65-0.99) 2.9	0.50 (0.22-0.72)
4	4 (1*, 3)	4.4	4.5	4.3	0.73 (0.66-0.82) 3.8

695 *WILL is a mix of OP and CP trials located at the same farm field site.

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699 Table 5: The total area for each breeding group based on climate normals from 1961 to 1990, and an
700 ensemble of climate change scenarios projected to 2055 along with the percent change in area
701 predicted under climate change.

Breeding group	Area 1961-1990 (M ha)	Area 2055 (M ha)	% change
1	15.8	36.2	129
2	9.0	33.8	276
3	17.5	5.1	-71
4	51.5	18.7	-63

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Figures:

Figure 1: The number of common base parents shared between test sites for all progeny test sites in the lodgepole pine breeding program in British Columbia, Canada.

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710 Figure 2: The smoothed distribution (kernel density estimate) of heritability estimates based on single-
711 site analyses of all lodgepole pine progeny test sites.

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Figure 3: Frequency distribution of site additive genetic variance explained by a factor analytic model of order k.

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719 Figure 4: A heatmap showing patterns of genetic correlations based on the G_a matrix for the FA3 model.

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Figure 5: Dendrogram for the cluster analysis of the G_a matrix for the FA3 model with cluster groups indicated by the grey boxes and corresponding group number (A), and mean within-group genetic correlation for each level of s (number of clusters) based on hierarchical cluster analysis (B).

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729 Figure 6: The projected distribution of breeding zones based on climate normals (1961 – 1990). The
 730 coloured circles indicate the location of progeny test sites for each breeding group (A = breeding group
 731 1; B = breeding group 2; C = breeding group 3; D = breeding group 4).

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735 Figure 7: The predicted distribution of breeding zones based on an ensemble of climate change
736 scenarios projected to 2055. The coloured circles indicate the location of progeny test sites for each
737 breeding group (A = breeding group 1; B = breeding group 2; C = breeding group 3; D = breeding group
738 4).

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Appendix 1: Results for the multi-environment trial analysis using full information.

Background

The article outlines a method to model patterns of GxE for an advanced generation breeding program which removes parents that were not used in advanced generation breeding, and their associated progeny, from the MET dataset. The resulting model better reflects the elite breeding population that will be employed for seed deployment and future breeding. However, the MET dataset can include parents and progeny from all tested families to improve the precision of Type B genetic correlations and a model that reflects the broader testing population for the breeding program.

Appendix 1 provides the results of an analysis using parents and progeny from all tested families in the MET dataset. The procedures outlined in the main article are used with slight modifications to the MET dataset as outlined below.

Multi-environment trial dataset

The MET dataset considered for this analysis had 1,359 base parents tested on 28 sites with an average of 237 parents per site which ranged from 84 to 561. The average number of common parents between sites (connectedness) was 55, which ranged from 2 to 439.

Factor analytic model results

The FA2 and FA3 models explained over 80% of the additive genetic variation in the model (83% and 87%, respectively). Both models explained individual-site additive variance well (Figure A1). This was evaluated as the number of sites for which >50% of the additive genetic variation was captured (82% of sites for the FA2 model and 96% for the FA3 model). After examination of the Type B genetic correlation (G_a) matrix for each model, the FA3 model was selected for further analysis (Figure A2).

Figure A1: Frequency distribution of site additive genetic variance explained by a factor analytic model of order k .

Figure A2: A heatmap showing patterns of genetic correlations based on the G_a matrix for the FA3 model.

The mean standard error of all Type B genetic correlations was 0.07 and ranged from 0.006 to 0.19. The mean standard error of the genetic correlation estimates among OP sites was 0.05 (range from 0.006 to 0.11), among CP sites was 0.09 (range from 0.04 to 0.19) and between OP and CP sites was 0.08 (0.02 to 0.16).

Figure A3: Dendrogram for the cluster analysis of the G_a matrix for the FA3 model with cluster groups indicated by the grey boxes and corresponding group number (A), and mean within-group genetic correlation for each level of s (number of clusters) based on hierarchical cluster analysis (B).

Cluster analysis

Using hierarchical cluster analysis with s number of clusters from 2 to 12, all solutions with $s > 2$ had mean within-group Type B genetic correlations > 0.7 and the benefit of adding an additional group to the cluster analysis plateaued at $s = 4$ (Figure A3). The number of sites within each breeding group ranged from 5 to 8 (Table A1 and A2). The mean within-group genetic correlation for the four-cluster model was 0.76 and ranged from 0.57 to 0.87 (Table A2). The mean between-group correlation was 0.56 and ranged from 0.36 to 0.72.

Climate modelling

The best three-variable regression models for the multiple regression, regression tree (MRRT) analysis had R^2 values that ranged from 0.45 to 0.75 (Table A3). The first and second factor loadings (λ_1 and λ_2) were explained best by similar annual climate variables while the third factor loading (λ_3) was best modelled using seasonal variables for autumn moisture deficit, precipitation in summer and degree days greater than 0 in autumn. The out of bag error rate for the random forest regression tree component of the MRRT analysis was 22.2% with six sites out of 27 misclassified.

Table A1: The assigned breeding group for each site based on hierarchical cluster analysis of the Ga matrix from the FA3 model using a MET dataset with all tested parents and progeny.

Site	Group	Elevation	BEC	MAT	MAP
ABBO	1	960	ICHwk2	3.8	649
ANZU	1	1116	SBSmc2	1.7	607
FLYF	1	1400	MSdm1	3.1	778
GRIZ	1	915	SBSmc2	2.0	571
INON	1	1450	ESSFwc1	3.1	927
MOFF	1	1075	SBPSmk	3.2	626
MUGA	1	690	SBSmk2	2.0	704
PINK	1	1000	SBSmc2	1.7	594
BISO	2	1165	ICHmk1	3.7	770
DARD	2	1275	MSxk2	2.9	478
EAST	2	1200	ICHmw3	3.7	594
HARI	2	1330	ICHmk1	3.5	761
MISS	2	1365	ICHmk1	3.1	726
PENA	2	1295	IDFdk1	3.1	559
BOWR	3	985	SBSwk1	3.1	808
CHOW	3	840	SBSdw3	2.4	536
CRIP	3	865	SBSdw3	1.3	679
GRAM	3	975	ICHmc1	1.6	747
HAWK	3	1535	ICHdm	2.9	914
INDI	3	880	SBSvk	3.2	889
TACH	3	840	SBSdw3	1.8	605
TUTU	3	715	SBSmk2	1.9	692
BLAC	4	735	SBSmk2	1.5	625
CHIE	4	725	SBSmk1	3.1	733
CURV	4	810	SBSwk2	1.1	587
REED	4	1067	SBSmk1	0.5	1011
WILL	4	760	SBSwk1	3.2	852

BEC = biogeoclimatic ecosystem classification; MAT = mean annual temperature; MAP = mean annual precipitation.

Table A2: The number of test sites associated with each group (N) with the number of OP and CP sites (within brackets). The upper diagonal shows the within-site mean genetic correlation and above the diagonal the mean between-group genetic correlations with the range of genetic correlations within brackets. The lower diagonal is the mean Euclidean distance (based on eight annual climate variables) within-groups and below the diagonal are the mean Euclidean distances between groups.

Group	N (OP, CP)	1	2	3	4
1	8(2,6)	0.57 (0.41-0.77) 2.9	0.52 (0.29-0.83)	0.60 (0.09-0.74)	0.49 (0.22-0.80)
2	6(6,0)		0.87 (0.72-0.95) 2.6	0.72 (0.51-0.93)	0.36 (0-0.57)
3	8(7,1)			0.83 (0.74-0.90) 2.9	0.70 (0.37-0.91)
4	5(2*,4)				0.82 (0.73-0.93) 3.9
		4.3	4.9	3.9	

The expected misclassification rate of the MRRT analysis was 44% which indicates the percent of sites that were misclassified using the MRRT analysis compared to the actual breeding groups from the cluster analysis of the G_a matrix. Most misclassified sites were between groups 3 and 4 or groups 1 and 3. Groups 1, 3 and 4 represent cooler climates and misclassification between these groups is less risky than misclassification of group 2.

Table A3: The coefficients for multiple regression models between factor loadings and climate normals.

Factor Loading	Model Results	Variable	Coefficient	t-value	p-value
λ_1		Intercept	91.79	1.41	0.17
		MCMT	-12.61	-3.04	0.006
		TD	-8.95	-2.17	0.041
		AHM	-2.12	-2.28	0.033
R^2	0.48				
F-statistic	6.97				
p-value	0.002				
λ_2		Intercept	21.92	0.65	0.52
		MCMT	10.47	4.64	<0.001
		TD	4.44	1.97	0.061
		MAP	-0.046	-3.55	0.002
R^2	0.75				
F-statistic	22.71				
p-value	<0.001				
λ_3		Intercept	-78.33	-3.30	0.003
		CMD_at	1.60	4.01	<0.001
		PPT_sm	0.17	2.17	0.041
		DDGT0_at	0.26	3.45	0.002
R^2	0.45				
F-statistic	6.22				
p-value	0.003				

MCMT = mean coldest month temperature; TD = temperature differential; AHM = annual heat:moisture index; MAP = mean annual precipitation; CMD_at = Hargreaves climate moisture deficit in autumn; PPT_sm = summer precipitation; DDGT0_at = degree days greater than 0 in the autumn.

The sites within each breeding group are classified into similar ecosystem units based on the biogeoclimatic ecosystem classification system for British Columbia and share similar climate envelope profiles (Table A1). Sites in group 1 have a wide geographic distribution and represent sites at high elevation in southern regions and low elevation in northern regions (Figure A4A). Group 2 sites represent southern, low-elevation environments (Figure A4B), group 3 represents mid-elevation regions in the south and drier environments in the north (Figure A4C), and group 4 represents high-elevation southern regions and far northern environments (Figure A4D). For all sites, climate change is expected to drive the climate envelope for each group further north and up in elevation (Figure A5). Based on this model, breeding group 2 (Figure A5B) will be most widely adapted under future conditions (Table A4). Group 4 will have the largest reduction in area. Groups 1 and 3 remain relatively stable with small shifts over time.

Table A4: The total area for each breeding group based on climate normals from 1961 to 1990, and an ensemble of climate change scenarios projected to 2055 along with the percent change in area predicted under climate change.

Breeding group	Area 1961-1990 (M ha)	Area 2055 (M ha)	% change
1	7.1	6.1	-13.6
2	14.0	55.4	297.1
3	10.9	12.3	13.3
4	62.0	20.0	-67.7

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Figure A4: The projected distribution of breeding zones based on climate normals (1961 – 1990). The coloured circles indicate the location of progeny test sites for each breeding group (A = breeding group 1; B = breeding group 2; C = breeding group 3; D = breeding group 4).

Figure A5: The predicted distribution of breeding zones based on an ensemble of climate change scenarios projected to 2055. The coloured circles indicate the location of progeny test sites for each breeding group (A = breeding group 1; B = breeding group 2; C = breeding group 3; D = breeding group 4).