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Identification and joint modeling of competition effects and environmental heterogeneity in three Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) trials

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Abstract (Co)variance matrices for the assumed model, and thus the specification of the dispersion parameters, should take into account both the negative competition and the positive spatial correlations. In this context, we applied several approaches to identify and quantify the genetic and environmental competition effects and/or environmental heterogeneity in three Douglas-fir genetic trials from the British Columbia tree improvement program in total height and diameter at breast height at ages 12 and 35. Then, we applied an individual-tree mixed model to account jointly for competition effects and environmental heterogeneity (competition + spatial mixed model, CSM). We also compared the resulting estimates of all dispersion parameters and breeding values (BVs) with corresponding estimates from three simpler mixed models. Our analysis revealed that strong spatial environmental variation (predominantly at large-scale) covered the effects of competition in the three Douglas-fir progeny trials. While diameter at breast height at age 35 revealed strong competition effects at both genetic and environmental levels, these effects were not as strong for total height. In general, with strong competition genetic effects, the CSM gave a better fit than the simpler models. Ignoring competition effects and environmental heterogeneity resulted in lower additive genetic variances and higher residual variances than those estimated from the CSM. Ignoring competition effects leads to overestimating environmental heterogeneity, while ignoring the environmental heterogeneity leads to underestimating competition effects. Spearman correlations between BVs predicted from the simplest model and total BVs from the CSM were moderate to high. The implications of all these findings for the genetic improvement of coastal Douglas-fir in British Columbia are discussed.

Keywords Total height · Diameter at breast height · Individual-tree mixed model · Indirect genetic effect · Total breeding values

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Introduction

Best linear unbiased prediction (BLUP) of breeding values (BVs) depends largely on how well the correlation structures among the effects in the model are specified. In forest tree breeding, there is often a negative correlation structure caused by competition among trees and a positive correlation structure caused by continuous environmental variation. Competition is defined as the stress suffered by a plant due to the genotypes and the spatial arrangement of neighboring trees (Hinson and Hanson 1962) and is caused by genetic and environmental sources (Magnussen 1989). Concerning the genetic evaluation of trees, competition is an indirect genetic effect (Griffing 1967, 1968a, b). Additionally, as a result of

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variations in soil characteristics and terrain orientation, there are usually two types of spatial environmental variation (or environmental heterogeneity) within forestry field trials: global trend (or large-scale variation) and local trend (or small-scale variation). Specifying both structures (i.e., competition and environmental heterogeneity) within the same model was demonstrated by Costa e Silva and Kerr (2013) and later in Cappa et al. (2015a) using an alternative formulation.

In coastal Douglas-fir, Ye and Jayawickrama (2008) found strong competition in some progeny trials for diameter and volume at ages 15 and 20. Yanchuk (1996) examined the general and specific combining ability of Douglas-fir for total height at ages 7 and 12, as well as volume at age 12. He concluded that competition effects within these field tests may have biased upward the specific combining ability variance for volume by age 12. In contrast, he did not observe this phenomenon in height at the same age. Stoehr et al. (2010) evaluated the effects of spacing and competition in three genetic classes from six low elevation coastal Douglas-fir realized genetic gain trials in British Columbia at ages 3 to 12. They concluded that diameter and volume were fairly sensitive to spacing and competition but height was relatively unaffected. Additionally, strong spatial patterns of variation (mostly small scale) were found in more than 95 % of the 275 first-generation progeny trials in the Pacific Northwest (Ye and Jayawickrama 2008) and in more than 90 % of the 88 trials in British Columbia (Fu et al. 1999).

Spatial analysis has been applied to Douglas-fir genetic trials using different approaches (Thomson and El-Kassaby 1988; Fu et al. 1999; Ye and Jayawickrama 2008). However, despite strong evidence of competition effects for growth traits in Douglas-fir genetic trials (Yanchuk 1996; Ye and Jayawickrama 2008; Stoehr et al. 2010), no empirical studies in this species and only a few in other tree species (Cappa and Cantet 2008; Costa e Silva et al. 2013) attempted to separate genetic and non-genetic competition effects at the individual tree level. Moreover, no studies in Douglas-fir and only a few empirical studies in agronomic crops (Durban et al. 2001; Stringer et al. 2011; Hunt et al. 2013) and in tree species (Magnussen 1994; Resende et al. 2005; Costa e Silva et al. 2013; Cappa et al. 2015a) jointly consider competition (or indirect genetic effect) and spatial variability.

Cappa and Cantet (2007) proposed using tensor products of cubic B-splines based on a mixed model by treating the B-spline functions as random variables (i.e., using a covariance structure for the random knots effects) in a two-dimensional grid. The mixed model with the fit of a two-dimensional surface demonstrated its utility in accommodating complex patterns of environmental heterogeneity (Cappa et al. 2015b). Muir (2005) derived the mixed model equations with competition effects to analyze data from test trials of forest trees, but he did not consider varying the number of competing neighbors in a trial. Cappa and Cantet (2008) also presented a mixed

linear model that included direct and competition additive genetic effects, as well as environmental competition effects, where the competition effects of neighbors are expressed in the phenotype of a focal tree by means of the "intensity of competition" (IC). The ICs allow standardizing of the variance of the effects of competition within the phenotypic variance, so that the model can account for unequal number of neighbors because of either mortality or border locations. Costa e Silva and Kerr (2013) extended the calculation of ICs to account for unequal inter-row and inter-column distances. Cappa et al. (2015a) presented an extension of the individual-tree mixed model with additive direct genetic effects, and genetic and environmental competition effects. (Cappa and Cantet 2008) by incorporating a two-dimensional smoothing surface (Cappa and Cantet 2007) that accounts for environmental heterogeneity.

As part of the coastal Douglas-fir tree improvement program, a large number of full-sib progeny trials were established across the southern coast of British Columbia, Canada, in eight series from 1976 to 1986. Because of the large number of genetic entries, the recognized environmental heterogeneity (Fu et al. 1999), and the evidence of genetic competition (Yanchuk 1996) in these trials, the data provide us with a good opportunity to identify and jointly model the effects of competition and spatial heterogeneity. The main objectives of the present study are (1) to identify and quantify the effects of competition at genetic and environmental levels and environmental heterogeneity using different diagnostic tools; (2) to apply the individual-tree mixed model proposed by Cappa et al. (2015a) for estimating genetic parameters with joint consideration of genetic and environmental competition effects and environmental heterogeneity; (3) to compare the resulting estimates of all dispersion parameters and predicted BVs for the joint model with those from three simpler individual-tree mixed models, namely standard (no competition and spatial continuous effects), competition (Cappa and Cantet 2008), and spatial (Cappa and Cantet 2007); and (4) to determine the impact of simultaneously adjusting for competition genetic effects and environmental heterogeneity on selection of individuals (forward selections) in the Douglas-fir tree breeding program.

Material and methods

Genetic material, trial description, and quantitative traits

The data used in this study are from the British Columbia coastal Douglas-fir tree improvement program. They include eight test series with various numbers of six-parent disconnected half diallels. A detailed description of the genetic materials can be found in Yanchuk (1996). Each of the 8 series was established on 11 different sites (i.e., in total 88 test sites) from 1976 to 1986. They are distributed along the southern

Pacific coast of British Columbia and on Vancouver Island (Fu et al. 1999). A randomized complete block design with four replicates of four-tree row plots per full-sib family was employed at each site with an initial spacing of 3.0 × 3.0 m. The current study uses data from the three progeny test sites of series 3, which demonstrated the highest heritabilities. These trials are established at Adams River near Campbell River (50° 24′ 42″ north, 126° 09′ 37″ west), Fleet River (48° 39′ 25″ north, 128° 05′ 05″ west), and Lost Creek (Chilliwack) (49° 22′ 15″ north, 122° 14′ 07″ west). Using the Biogeoclimatic Ecosystem Classification (BEC) system (Pojar et al. 1987), the sites were identified, respectively, as montane very wet site, submontane moist maritime site, and submaritime very wet site. At the three sites, total height (TH) in centimeter using a laser hypsometer and diameter at breast height (DBH) in millimeter were measured at ages 12 and 35. All three sites were thinned at age 15 from four-tree to three-tree plots by removing the shortest tree, a standard practice across all test series. Table 1 provides some general information about the three trials.

Identification and quantification of competition and environmental heterogeneity effects

A central first step in the joint analysis of competition and spatial variability is a pre-analysis to determine the significance of both effects within each site. In this study, we employed several diagnostic tools to identify and quantify the competition effects (at genetic and environmental levels) and environmental heterogeneity. First, we fitted an individual-tree mixed model with fixed effects of genetic group and block, random effects of plot, breeding value, and full-sib family (see standard model [1] below), and residual covariance structure following a first-order autoregressive process for rows and columns (AR(1) × AR(1); autoregressive model) using the ASReml program (Gilmour et al. 2006). The sign and magnitude of the autocorrelation parameters for row and column can reveal the presence of competition effects at residual level and/or environmental heterogeneity. Dutkowski et al. (2002) stated that environmental heterogeneity emerges at autocorrelation coefficients greater than 0.3 and become more definite at 0.6. Resende et al. (2005) indicated that high (>0.3) positive autocorrelation coefficient estimates reveal that environmental heterogeneity is predominant over competition, and negative (<−0.3) autocorrelation coefficient estimates indicate competition effects at the residual level probably together with environmental heterogeneity. Therefore, autocorrelation coefficients larger than 0.3 and smaller than −0.3 were used to identify dominant environmental heterogeneity and competition effects at residual level, respectively. Additionally, we used a graphical diagnostic tool, the two-dimensional sample variograms from the autoregressive model at each combination of trait-age within each site, as

Table 1 Location, site characteristics, design information, means, and standard deviations for the diameter at breast height (DBH) and total height (TH) measured at ages 12 and 35 across the three coastal Douglas-fir progeny trials

Site	Montane very wet		Submontane moist maritime		Submaritime very wet	
Latitud (north)	50° 24′ 42″		48° 39′ 25″		49° 22′ 15″	
Longitude (west)	126° 09′ 37″		128° 05′ 05″		122° 14′ 07″	
Altitude (m)	576		561		424	
AMP	2363		3397		2421	
AMT	7.6		8.3		7.3	
MTCM (°C)/MTWM (°C)	0.7/15		2.1/16.2		−0.1/15.6	
Age	12	35	12	35	12	35
No. of trees with records	2367	2093	2592	2263	2462	2058
No. of parents	78		78		78	
No. of families	165		165		165	
Experiment design	RCB		RCB		RCB	
No. of replicates	4		4		4	
No. of diallels	10		10		10	
No. of row	49		53		90	
No. of column	99		65		55	
Spacing (m)	3 × 3		3 × 3		3 × 3	
Mean DBH (SD) (mm)	88.6 (21.9)	**312.1 (63.6)**	92.3 (19.6)	270.8 (51.9)	**104.0 (30.5)**	264.8 (67.0)
Mean TH (SD) (cm)	624.2 (113.5)	2332.2 (248.0)	705.1 (119.7)	**2533.9 (258.7)**	726.7 (161.4)	2405.4 (353.5)

The highest growth across sites at ages 12 and 35 are highlighted in bold

AMP annual mean precipitation, *AMT* annual mean temperature, *MTCM* minimum mean temperature of the coldest month (usually January), *MTWM* maximum mean temperature of the warmest month (usually August). The highest growth across sites at ages 12 and 35 of age are highlighted in bold

suggested by Gilmour et al. (1997). On the other hand, strong spatial patterns expressed in global trends (i.e., high and positive autocorrelation coefficients) may reduce the evidence of spatial patterns in small scale (i.e., local trends) and/or competition effects (e.g., Kempton 1982; Brownie and Gumpertz 1997; Durban et al. 2001). Although simultaneous autoregressive models (like the equal-roots third-order autoregressive model-EAR(3)-) could be used to identify simultaneously spatial trend and competition at the residual level, we fitted the autoregressive model for the de-trended data, i.e., by subtracting the fitted spatially dependent residuals from the original phenotypic data (Ye and Jayawickrama 2008). Second, for each trait-age combination at each site, we calculated the Pearson correlation coefficients between the residuals of the focal trees after fitting the standard model (see Eq. [1]) and the phenotypic means of the focal tree's neighbors under various configurations: (1) the m (maximum 8) first-order neighbor trees (i.e., adjacent to one another in the diagonal and in the same planting row or column), (2) the m (maximum 2) row-neighbor trees, (3) the m (maximum 2) column-neighbor trees, and (4) the m (maximum 4) diagonal-neighbor trees. Statistically, significant positive (or negative) correlations between two adjoining trees provide evidence of environmental heterogeneity (or competition). Then, we plotted these residuals versus the phenotypic means as suggested by Durban et al. (2001). To account for the distance and the number of competitive individuals either row-column wise or diagonally, the average of the phenotypic means of the row-, column-, and diagonal-neighbor trees were multiplied by the ICs (Cappa and Cantet 2008) as a weight before calculating the Pearson correlation coefficients. The growth traits studied (i.e., DBH and TH) are more sensitive to recent competition than at early ages (Gould et al. 2011), i.e., the sum of growth over the entire life of the study. Therefore, we calculated the difference between ages 12 and 35 for DBH (DBH growth) and TH (TH growth). Finally, we examined the direct and competition additive correlation (Cappa and Cantet 2008) to study the competition effects at genetic level from the competition model (see competition mixed model [2]). A high and negative correlation between both types of genetic effects (higher than −0.3) suggests strong genetic competition (e.g., Muir 2005).

Statistical models of analysis

Each trait-age combination within each Douglas-fir trial was analyzed using the following individual-tree mixed models.

1. Standard mixed model (TM):

$$y = X\beta + Z_l l + Z_a a + Z_f f + e \qquad (1)$$

where the vector y contains the phenotype of individual i ($i = 1, \ldots, n$; n is the total number of trees with recorded data); the vector β includes the fixed effects of blocks and genetic groups to account for the means of the different diallels; l is the vector of random plot effects; a is the vector of random additive genetic effects (i.e., breeding values) distributed as $N\sim(0, A\,\sigma^2_a)$, where A is the expected relationship matrix from the pedigree information and σ^2_a is the additive genetic variance; f is the vector of random full-sib genetic effects (corresponding to specific combining ability, SCA) distributed as $N(0, I\,\sigma^2_f)$, where I is the identity matrix and σ^2_f is the family variance; and e is the vector of random error; X, Z_l, Z_a, and Z_f are incidence matrices relating the observations (y) to the model effects β, l, a, and f, respectively. The vector e is distributed as $e\sim N(0, I\,\sigma^2_e)$ where σ^2_e is the residual variance.

2. Competition mixed model (CM):

$$y = X\beta + Z_l l + Z_d a_d + Z_c a_c + Z_p p_c + Z_f f + e \qquad (2)$$

where the effects β, l, f, and e and matrices X, Z^l, and Z^f were specified as described above. We follow closely Cappa and Cantet (2008) to describe the CM. In Eq. [2], a^d and a^c are the vectors of direct and competition random additive genetics effects (i.e., breeding values), respectively, and Z^d and Z^c are the corresponding incidence matrices relating the observations in y to the direct and competition breeding values. Every row (i) of Z^d has all elements equal to zero except for a 1 in the corresponding column. Similarly, each row i of matrix Z^c has all elements equal to zero except in the positions corresponding to the m^i neighbors of the tree i, with values f^{ij}, $j = 1, \ldots, m^i$. These positive coefficients can be interpreted as the intensity of competition (IC) that each neighbor exerts over the phenotype of the ith tree (see further details in Cappa and Cantet 2008). The covariance matrix of a^d is $A\sigma^2_{Ad}$ where σ^2_{Ad} is the variance of the direct additive genetic effects. Also, $a^c\sim N(0, A\sigma^2_{Ac})$, where σ^2_{Ac} is the variance of the competition breeding values, and $\text{cov}(a^d, a^c) = A\,\sigma_{AdAc}$, where σ_{AdAc} is the covariance between direct and competition breeding values. Every row of the incidence matrix Z^p has elements equal to zero except for a 1 in the column belonging to a^{pj} of the nearest j neighbor competitor tree. The vector p^c includes the environmental competition effects (or permanent environmental competition effects; Cappa and Cantet 2008; Cappa et al. 2015a) distributed as $p^c\sim N(0, I\,\sigma^2_p)$, where σ^2_p is the variance of environmental competition effects.

3. Spatial mixed model (SM):

$$y = X\beta + Bb + Z_a a + Z_f f + e \qquad (3)$$

where the effects β (including only genetic group effects), a, f, and e and matrices X, Z_a, and Z_f were specified as described above. We follow closely Cappa and Cantet (2007) to describe SM. In Eq. [3], the term Bb is the matrix expression approximating the two-dimensional surface with a tensor product of B-spline bases (Eilers and Marx 2003). The vector b is assumed to be normally distributed with mean zero and covariance matrix $U\sigma_b^2$. The scalar σ_b^2 is the variance of the B-spline coefficients for rows and columns, and the U matrix is the covariance structure in two dimensions for the B-splines coefficients. A tridiagonal U matrix, originally proposed by Green and Silverman (1994, p. 13) and then used by Durban et al. (2001) to fit a fertility trend, was used in this study. Three SM with different numbers of knots for rows and columns, 10×10, 20×20, and 30×30, were fitted for each trait-age combination within each trial. The model including 20×20 or 30×30 knots had the better fits (based on the smallest deviance information criterion, see below), i.e., captured most of the spatial variability and was used for further comparison. For this SM, we dropped the fixed block and random plot effects (i.e., the design effects) as they became non-significant.

4. Competition + spatial mixed model (CSM):

$$y = X\beta + Bb + Z_d a_d + Z_c a_c + Z_p a_p + Z_f f + e \qquad (4)$$

All vectors of fixed and random effects and matrices of Eq. [4] were specified above. We followed closely Cappa et al. (2015a) to describe the CSM. For this CSM, we also dropped the design effects as they were non-significant.

Bayesian inference and models comparison

The Bayesian approach via Gibbs sampling was used to estimate the parameters in the four individual-tree models studied following closely Cappa and Cantet (2007, 2008) and Cappa et al. (2015a). Conjugate prior densities were chosen for all parameters. To reflect a prior state of uncertainty for the fixed effects while keeping the posterior distribution proper, we selected $\beta \sim N\,(0, K)$ with K, a diagonal matrix with large elements ($k_{ii} > 10^8$). For the prior distributions of σ_a^2, σ_b^2, σ_p^2, σ_f^2, and σ_e^2, we used a scaled inverted chi-square with hypervariances δ_a^2, δ_b^2, δ_p^2, δ_f^2, and δ_e^2 and degrees of freedom υ_a, υ_b, υ_p, υ_f, and υ_e, respectively. The additive (co)variance matrix of breeding values (G_0) follows a priori an inverted Wishart (IW) distribution with prior covariance matrix G_0^* and degree of belief υ_g. Therefore, the joint and conditional posterior densities are Gaussian for β, a, b, a_d, a_c, a_f, and p_c; scaled chi-square for σ_a^2, σ_b^2, σ_p^2, σ_f^2, and σ_e^2; and scaled inverted Wishart distribution for G_0.

A single Gibbs chain of 210,000 (SM with 30 knots for row and column and CSM) and 1,010,000 (SM with less than 20 knots, TM, and CM) samples was drawn, and the first 10,000 iterates were discarded as *burn-in*. Thus, 200,000 and 1,000,000 additional samples were used for computing the summary from the marginal posterior distribution. Marginal posterior densities for all parameters were estimated by the Gaussian kernel method (Silverman 1986, chap. 2). Convergence was monitored by plotting the iterations against the mean of the draws up to each iteration (running mean plots) and using the Z criterion of Geweke (1992) for each parameter. Mean, mode, median, standard deviation, and 95 % high posterior density interval (95 % HPD) were then calculated with "*Bayesian Output Analysis*" (BOA version 1.0.1; Smith 2003) for all parameters from the individual marginal posteriors, under the free software R (http://www.r-project.org/).

The deviance information criterion (DIC; Spiegelhalter et al. 2002) was computed to compare the fit of each model. The DIC criterion is defined as

$$DIC = \bar{D}(\theta_M) \; + \; p_D$$

where $\bar{D}(\theta_M)$ is the posterior mean of the deviance and p_D is the "effective number of parameters." Hence, the DIC combines a measure of model fit ($\bar{D}(\theta_M)$), with a measure of model complexity (p_D). A smaller DIC value indicates a better fit and lower degree of model complexity. The total genetic contribution to the genetic mean value of a population or total tree breeding value (TBV_i) from the CSM model [4] was calculated following Costa e Silva and Kerr (2013); Eq. 14), i.e., $TBV_i = a_{di} + \left(n_R f_{ijR} + n_C f_{ijC} + n_D f_{ijD} \right) a_{ci}$, where $\left(n_R f_{ijR} + n_C f_{ijC} + n_D f_{ijD} \right)$ is the sum of the products of the means across all focal individuals in each Douglas-fir trial; n_R, n_C, n_D is the average number of their neighbors; and f_{ijR}, f_{ijC}, f_{ijD} is the average intensity of competition in the row, column, and diagonal directions, respectively. The values of the expression $\left(n_R f_{ijR} + n_C f_{ijC} + n_D f_{ijD} \right)$ for the three Douglas-fir trials at age 35 were 1.31, 1.85, and 1.37 for the montane very wet, submontane moist maritime, and submaritime very wet progeny trials, respectively. Additionally, to study the impact of simultaneously adjusting for competition genetic effects and environmental heterogeneity on selection decisions, Spearman rank correlations were calculated between the predicted tree BVs from the TM and the TBVs from the CSM for DBH at age 35. The proportions of common individuals (offspring) in the top 10 % (209, 226, and 206 trees for the montane very wet, submontane moist maritime, and submaritime very wet sites, respectively) from the TM and CSM models were also compared.

FORTRAN computer programs (available upon request) were employed to carry out the Bayesian inference, solve the mixed models equations, and obtain corresponding accuracies of all model analyses.

Results and discussion

Survival and growth

Overall mean survival across the three sites was 94 % at age 12 and slightly lower at age 35 (81 %) (Table 1). The submontane moist maritime site demonstrated the highest survival rates at both assessment ages. Trees at the submaritime very wet site had the best growth at age 12 but lagged behind those at the montane very wet site at age 35.

Identification of competition and environmental heterogeneity

Strong environmental heterogeneity (autocorrelation coefficient >0.8) was detected in 22 of the 24 cases studied (Table 2). The sample variograms for residuals after fitting an AR(1) × AR(1) model show that the spatial pattern of the variation was usually a global trend (e.g., Supplementary Fig. S1a). There were no negative autocorrelation coefficients for any trait at ages 12 and 35 for the three sites (Table 2). In general, there was an increase in autocorrelation coefficients in both row and column directions from ages 12 to 35, which probably mirrors the cumulative effect of growth on good sites (Magnussen 1990). However, for DBH at the submontane moist maritime site, the column autocorrelation coefficients decreased substantially from ages 12 to 35 (from 0.89 to 0.27), which may have resulted from stronger negative correlations indicating competition due to faster diameter growth at this site (Table 1). Strong global trends may mask patterns of small-scale (i.e., local trends) environmental variation and

competition effects (e.g., Kempton 1982; Brownie and Gumpertz 1997; Durban et al. 2001). After these predominant global trends were removed from the original data, i.e., using the de-trended data, most of the autocorrelation coefficients among neighboring units became negative in both directions (Table 2). Moreover, strong competition effects in row and column directions were shown in DBH at age 35 at all three sites (negative autocorrelation coefficients from −0.08 to −0.38), suggesting that competition is dominant over the environmental heterogeneity at small scale. The trait TH at age 35 at the submontane moist maritime site also showed strong competition effects in row (autocorrelation coefficients −0.54) and column (autocorrelation coefficients −0.81) directions when the de-trended data were used. An example of sample variogram showing a competitive effect at residual level is given in Supplementary Fig. S1b. This is consistent with the results reported by Ye and Jayawickrama (2008) that strong aboveground competition starts from ages 10~15 in most Douglas-fir progeny trials in the Pacific Northwest. Ye and Jayawickrama (2008) also reported negative autocorrelation coefficients for diameter and volume at age 15 or 20 when studying the efficiency of the AR(1) × AR(1) model of 275 Douglas-fir progeny trials in the US Pacific Northwest.

Pearson correlation coefficients among the residual of the ith focal tree after fitting the standard model and the phenotypic mean of m (maximum 8) first-order neighbor trees were also calculated (Table 3; Supplementary Fig. S2). Estimated negative correlations confirm the tendency revealed by the autocorrelation coefficients that competition is present for DBH at age 35 in the three Douglas-fir trials. The mean correlation coefficients are ranging from −0.19 to −0.36 (Supplementary Fig. S2). In general, Pearson correlation between the residual of the ith focal tree and the phenotypic mean of m (maximum 4) diagonal-neighbor trees was weaker than that between the ith focal tree and the mean of m (maximum 2) row- and column-neighbor trees for all the trait-age combination, which reflect that competition can vary as a function of the distance between

Table 2 Autocorrelation coefficients for row (ρ_{row}) and column (ρ_{col}) for diameter at breast height (DBH) and total height (TH) at ages 12 and 35 for the original phenotype and the de-trended data (subscript dt) from the autoregressive model (see text) using the ASReml program (Gilmour et al. 2006)

Trait	Age	Site Montane very wet		Submontane moist maritime		Submaritime very wet	
		ρ_{row}	ρ_{col}	ρ_{row}	ρ_{col}	ρ_{row}	ρ_{col}
DBH	12	0.76	0.95	0.86	0.89	0.90	0.91
DBH$_{\text{dt}}$	12	−0.01	−0.04	−0.09	−0.05	−0.05	−0.10
DBH	35	0.95	0.98	0.98	0.27	0.90	0.89
DBH$_{\text{dt}}$	35	−0.38	−0.33	−0.27	−0.24	−0.08	−0.14
TH	12	0.86	0.96	0.86	0.90	0.87	0.89
TH$_{\text{dt}}$	12	−0.02	0.00	−0.08	−0.03	−0.06	−0.08
TH	35	0.96	0.97	0.96	0.99	1.00	1.00
TH$_{\text{dt}}$	35	−0.05	0.01	−0.04	−0.07	−0.54	−0.81

Table 3 Pearson correlation coefficients between the residual or phenotype of the ith focal tree and the phenotypic mean of m (maximum 8) first-order neighbors trees (r_{rp} or r_{pp}), average of row and column residual autocorrelation coefficients for the original phenotypic data (ρ), de-trended data (ρ_{dt}) from the autoregressive model (see text) using the ASReml program (Gilmour et al. 2006), correlation between direct and competition additive genetic effects from the competition model (r_{AdAc}), and intensity of competition for diameter at breast height (DBH) and total height (TH) at ages 12 and 35

Site	Trait	Age (year)	r_{rp}	r_{pp}[a]	ρ	ρ_{dt}	r_{AdAc}	Competition[b]
Montane very wet	DBH	12	−0.03	0.01 ns	0.86	−0.03	0.16	+ +
Submontane moist maritime	DBH	12	0.06	0.22**	0.88	−0.07	0.06	+
Submaritime very wet	DBH	12	0.08	0.16**	0.91	−0.08	0.14	+
Montane very wet	DBH	35	−0.36	−0.39**	0.97	−0.36	−0.32	+ + + + +
Submontane moist maritime	DBH	35	−0.29	−0.29**	0.63	−0.26	−0.47	+ + + +
Submaritime very wet	DBH	35	−0.19	−0.21**	0.90	−0.11	−0.72	+ + +
Montane very wet	TH	12	0.05	0.10**	0.91	−0.01	0.32	+
Submontane moist maritime	TH	12	0.09	0.23**	0.88	−0.06	0.34	Nil
Submaritime very wet	TH	12	0.12	0.24**	0.88	−0.07	0.35	Nil
Montane very wet	TH	35	−0.03	0.04 ns	0.97	−0.02	0.28	+ +
Submontane moist maritime	TH	35	−0.08	−0.06**	0.98	−0.06	−0.07	+ +
Submaritime very wet	TH	35	0.01	0.06**	1.00	−0.68	0.09	+

ns not statistically significant ($p > 0.05$)

[a] The p values showing difference from zero:

[b] Conclusion based mainly on the information from r_{rp} and r_{pp}

*Statistically significant, $0.01 < p < 0.05$; **statistically highly significant, $p < 0.01$

the focal tree and its neighbors (Supplementary Fig. S2). In addition, the mean Pearson correlations for 35-year-old DBH at the montane very wet site were stronger than those at the other two sites (Table 3; Supplementary Fig. S2), likely due to the faster diameter growth (Table 1).

Similar results (i.e., high $R^2 = 0.96$ across the combination trait-age and the three trials) were obtained when the Pearson correlation coefficients were calculated between the phenotype values (instead of the residual values) of the focal tree and the phenotypic means of the m (maximum 8) neighbor trees (Table 3; Supplementary Fig. S3). When DBH and TH growth (i.e., the difference in these traits between ages 12 and 35) were used as response variables following Gould et al. (2011), Pearson correlation coefficients were stronger and more negative (results not shown), suggesting that competition became stronger as trees got older (or larger).

At early ages, trees may compete for water and nutrients, but after canopy closure they compete mainly for light (Brotherstone et al. 2011). In our work, first-order neighbor trees were used in both CM and CSM models; thus, the implicit assumption is that light is a more important factor than water and nutrients (Magnussen 1989). This assumption can be regarded as reasonable since, as mentioned above, crown closure for Douglas-fir usually starts after age 10 in the Pacific Northwest (Ye and Jayawickrama 2008). However, in single-tree plots or small row plot designs (like the four-tree row plot used in this study), the sharing of these resources can never be equal because the interacting plants are genetically different (Stringer et al. 2011). Positive correlation between adjoining trees suggests that they are less competitive but more cooperative in responding to their shared environment, while negative correlation indicates that they compete with each other as one tree's gain is the other tree's loss. These two types of trees are classified as two categories of ideotypes, i.e., crop ideotype and competition ideotype, respectively (White et al. 2007).

In general, differences in the autocorrelation coefficients (Table 2) and Pearson correlation coefficients between the residual of the ith focal tree and the phenotypic mean of m first-order neighboring trees (Supplementary Fig. S2) in the direction of the rows and columns were small. However, and in particular to the DBH trait at age 35, these differences follow the same trend of lower values for rows than for columns, except for DBH at the submontane moist maritime site age 35 where much smaller autocorrelations were estimated for rows (0.98) than those for columns (0.27). Thus, the observed trend of stronger negative autocorrelation coefficients and residual Pearson correlation coefficients between rows than between columns, suggests that inter-family competition (i.e., competition between trees from different families) was often stronger than intra-family competition (i.e., competition between adjoining trees from the same family). However, research in Douglas-fir and other forest tree species showed considerable disagreement on whether genetic relatedness between adjoining trees increase (Sakai et al. 1968; Gould et al. 2011) or decrease (von Euler et al. 1992; Boyden et al. 2008; St. Clair and Adams 1991) the intensity of competition.

When competition is present, it may exist at both residual and genetic levels (e.g., Stringer et al. 2011; Brotherstone et al. 2011; Costa e Silva et al. 2013). At age 12, correlations between direct and competitive additive genetic effects from competition model were all positive, whereas at age 35, they were negative and strong (especially for DBH). Negative correlation between additive direct and competition genetic effects indicates competition for a limited resource at genetic level, where an individual with a positive heritable effect on its own growth has, on average, a negative heritable effect on the growth of its neighbors (Costa e Silva et al. 2013). Our work is one of the first empirical studies applying a competition genetic model to forest genetic trials. Therefore, making comparisons with other forest studies is limited. However, for DBH, the estimated correlations in the present study were somewhat lower than those reported by Cappa and Cantet (2008) for *Pinus taeda* (−0.79) at age 13 and tree spacing of 3.5 m × 3.5 m and by Costa e Silva et al. (2013) for *Eucalyptus globulus* (−0.92, average across 2 and 4 years and planting spacing of 5.0 m × 2.125 m).

The genetic basis for response to competition depends on the trait measured (expression) (von Euler et al. 1992). As we observed, DBH was more sensitive to competition than TH at both non-genetic (i.e., residual) and genetic level in the three Douglas-fir trials. These results confirm findings from previous studies in Douglas-fir (Ye and Jayawickrama 2008; Stoehr et al. 2010) and other forest tree species (Sakai et al. 1968; Magnussen 1989; Hannrup et al. 1998; Dutkowski et al. 2006). Concerning forest genetic evaluation, Gould et al. (2011) suggested that selection based on TH rather than DBH may help produce families that have consistent performance across different competitive environments.

It has been reported that competition effects become consistently stronger as the trees become older (e.g., Kusnandar 2001; Stoehr et al. 2010; Costa e Silva et al. 2013). In our study, we observed a general increase in the competition effect from age 12 to 35 for de-trended phenotypic values in DBH and TH at the three sites (Tables 2 and 3; Supplementary Fig. S2), suggesting an increase in interaction among individuals over time; thus, trees that are truly superior will exert their superiority over others due to an inherent higher growth rate and/or a stronger competitive advantage (Stoehr et al. 2010). For example, the average autocorrelation coefficients across row and column for the de-trended DBH data became more negative at all sites (Table 3). The presence of weak (at age 12) and strong (at age 35) tree-to-tree competition for DBH is also shown in the Supplementary Fig. S4 for the three trials.

Model comparison

When strong competition was dominant over the environmental heterogeneity (i.e., for DBH at age 35), CSM showed better fit (i.e., smaller DIC) than simpler models with no competition and spatial continuous effects or either of these effects alone (i.e., TM, CM, and SM; Table 4). The only exception is for DBH at age 35 at the submontane moist maritime site where CM was the model with the best fit (Table 4). Generally speaking, CSM is the model of choice when both competition effects and environmental heterogeneity are expected to be strong. Similar results have been reported in crop species (Stringer et al. 2011; Hunt et al. 2013) and forest tree species (Resende et al. 2005 and Costa e Silva et al. 2013) when competition and environmental spatial effects are present regardless of whether the spatial trend predominated over competition or vice versa.

However, when competition effects were weak (e.g., for all traits at age 12 and TH at age 35; Table 3), the fits of the models were inconsistent across traits and ages. For TH at age 35, TM was the best at the montane very wet and submontane moist maritime sites. At age 12, TM was the best for DBH at the montane very wet site and TH at the submontane moist maritime site, while CM was the best for DBH at the submaritime very wet site. The causes of these results are not clear, but they suggest that the first important step in analyzing joint competition and environmental heterogeneity effects is to identify the significance of these effects. Through simulation, Costa e Silva and Kerr (2013) compared a base model (not fitting competition at either the residual and genetic levels), a spatial autoregressive model for the residual, a genetic competition model, and a competition spatial model using likelihood ratio tests. They concluded that the ability to detect the correct model depends on the r_{AdAc}, the magnitude of the σ^2_{Ac}, and genetic relatedness levels within a neighborhood for a given level of survival. This ability

Table 4 Deviance information criterion (DIC) calculates for each combination trait-age and all models fitted

Site	Model	Trait-age			
		DBH		TH	
		12	35	12	35
Montane very wet	TM	**10,250**	11,253	**13,494**	**13,268**
	CM	10,307	11,267	13,789	13,505
	SM	10,387	11,029	13,696	13,349
	CSM	10,349	**10,722**	13,611	13,377
Submontane moist maritime	TM	9281	11,449	12,614	**14,293**
	CM	9210	**11,325**	12,425	14,366
	SM	9207	11,558	12,506	14,391
	CSM	**9054**	11,347	**12,259**	14,346
Submaritime very wet	TM	11,499	11,259	15,236	13,911
	CM	**11,366**	11,263	15,179	14,275
	SM	11,531	11,063	14,864	13,801
	CSM	11,404	**10,922**	**14,800**	**13,695**

Smallest DICs (i.e., better fits) are highlighted in bold. See text for traits' and models' abbreviations

appeared to diminish when the r_{AdAc} became less negative, the σ^2_{Ac} decreased for a given magnitude of r_{AdAc}, and the level of relatedness decreased for a given magnitude of the r_{AdAc} and σ^2_{Ac}. Additionally, a decrease in the survival rate (from 100 to 80 %) seemed to reduce the ability to detect the most appropriate model for a given genetic relatedness. In our study, low negative (−0.07) and low to moderate positive (from 0.06 to 0.35) r_{AdAc} values (i.e., weak recognizable competition effect at genetic level) were observed for all traits at age 12 and TH at age 35 (Table 3). The additive genetic relatedness is also relatively high (i.e., control pollination mating with four tree row plots). These results may have limited the ability to identify the best model for jointly modeling the competition and environmental heterogeneity effects for those traits. Moreover, Cappa et al. (2015a), also in a simulation study, concluded that the worst performance of the CSM was under a scenario with weak competition effects. However, strong and negative values of the r_{AdAc} for DBH at age 35 (Table 3) assure that CSM is the most appropriate model for this trait.

The appropriate choice of model is likely influenced by how well the competition and environmental effects can be separated analytically (Durban et al. 2001). In the cases presented here for DBH at age 35, the better fit by the CSM is aided by the fact that both processes are strong and were detected operating at different spatial scales, i.e., the competition effects at small scale and the environmental heterogeneity at large scale.

Based on the identification and quantification of competition and environmental heterogeneity (summarized in Table 3) and the DIC values (Table 4), we retained only DBH at age 35 to conduct all the analyses in relation to the study of the impact of simultaneously adjusting for competition genetic effects and environmental heterogeneity on the variance components and selection decisions.

Impact of simultaneously adjusting for competition and environmental heterogeneity effects on variance components

Posterior means and standard deviations for σ^2_{Ad}, σ^2_{Ac}, r_{AdAc}, σ^2_p, σ^2_f, σ^2_{plot}, σ^2_b, and σ^2_e are shown in Table 5 and Supplementary Fig. S5. TM yielded smaller posterior σ^2_{Ad} estimates than those estimated from CSM for DBH (from

Table 5 Posterior means (standard deviation) for the additive variance for direct effects (σ^2_{Ad}), additive variance for competition breeding values (σ^2_{Ac}), correlation between direct and competitive additive effects (r_{AdAc}), variance of environmental competition effects (σ^2_p), family variance (σ^2_f), plot variance (σ^2_{plot}), variance of the knot effects (σ^2_b), and error variance (σ^2_e) for diameter at breast height (DBH) at age 35

Trial		TM	CM	SM	CSM
Montane very wet	σ^2_{Ad}	371.77 (109.77)	259.30 (70.54)	429.50 (128.06)	752.42 (186.80)
	σ^2_{Ac}	–	491.91 (117.64)	–	1073.65 (167.36)
	r_{AdAc}	–	−0.32 (0.18)	–	−0.66 (0.09)
	σ^2_p	–	166.22 (49.24)	–	177.32 (57.53)
	σ^2_f	129.49 (44.66)	108.66 (36.84)	121.04 (40.21)	110.48 (35.15)
	σ^2_{plot}	362.58 (77.90)	45.64 (17.88)		–
	σ^2_b	–	–	2453.28 (520.44)	144.07 (90.83)
	σ^2_e	3124.30 (140.01)	3461.78 (348.47)	3012.29 (130.15)	2154.82 (155.43)
Submontane moist maritime	σ^2_{Ad}	373.12 (85.10)	387.67 (83.39)	462.05 (108.61)	622.46 (138.91)
	σ^2_{Ac}	–	181.22 (50.51)	–	276.54 (80.40)
	r_{AdAc}	–	−0.47 (0.13)	–	−0.59 (0.11)
	σ^2_p	–	141.90 (38.59)	–	168.55 (48.13)
	σ^2_f	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	σ^2_{plot}	196.56 (44.41)	152.37 (37.95)	–	–
	σ^2_b	–	–	360.21 (234.85)	134.15 (73.58)
	σ^2_e	2123.33 (101.99)	1989.30 (124.43)	2150.31 (100.51)	1733.67 (123.91)
Submaritime very wet	σ^2_{Ad}	419.67 (125.18)	417.69 (124.58)	460.40 (141.10)	828.61 (256.62)
	σ^2_{Ac}	–	60.37 (23.84)	–	117.32 (50.93)
	r_{AdAc}	–	−0.72 (0.12)	–	−0.84 (0.08)
	σ^2_p	–	252.26 (72.43)	–	310.19 (89.46)
	σ^2_f	133.83 (44.05)	128.61 (43.18)	141.47 (45.75)	125.93 (40.68)
	σ^2_{plot}	139.49 (48.92)	41.43 (18.39)	–	–
	σ^2_b	–	–	217.83 (180.17)	148.42 (98.44)
	σ^2_e	3842.32 (153.17)	4024.22 (312.77)	3849.12 (154.89)	3258.84 (214.00)

See text for models' abbreviations

40.1 to 50.6 %, across trials), while σ^2_e estimates were higher than those estimated from CSM for DBH (from 17.9 to 45.0 %, across trials). This observation is due to competition effects and environmental heterogeneity not entirely accounted for by TM. In a simulation study where the competition was dominant over environmental trend (i.e., $r_{AdAc} = -0.9$), and with level of relatedness (full-sib mating design and multi-tree row plots, i.e., medium relatedness level) and survival similar to those of this work, Costa e Silva and Kerr (2013) showed higher direct additive variance estimates (approximately 55 %) and lower error variance estimates (approximately 48 %) when a base model was fitted (see Fig. 3 in Costa e Silva and Kerr 2013). When studying diameter in a 19-year-old Sitka spruce clonal trial in Scotland, Brotherstone et al. (2011) also reported a 19.9 % increase in σ^2_{Ad} and a 10.5 % reduction in σ^2_e after adjusting a simple competition model proposed by Bijma (2007) jointly with an AR(1) × AR(1) covariance structure for the residual. There was evidence of a global trend in the latter model, but this effect was not formally accounted for. Moreover, the posterior means of σ^2_{Ad} from CSM were higher and σ^2_e smaller than those estimated from SM for DBH (Table 5; Supplementary Fig. S5). Therefore, these empirical results show that by not fitting competition effects (i.e., TM or SM), a consistent decrease resulted in the estimated posterior mean of σ^2_{Ad} and an increase in the estimated posterior mean of σ^2_e (Table 5; Supplementary Fig. S5). Given the strong genetic competition effects for this trait (especially when r_{AdAc} was stronger than −0.72), these patterns of variation in both variance components estimated (i.e., σ^2_{Ad} and σ^2_e) can be explained by the negative sign and the absolute value of σ_{AdAc} relative to the small value of σ^2_c, which gives more weight to the second than the third term in the expression of the genetic covariance between two records (see Eq. [26] in Cappa and Cantet 2008, p. 52). Then, these sources of (co)variation (i.e., σ_{AdAc} and σ^2_c) not accounted for the model (i.e., TM or SM) are absorbed into the error term and result in an increment of σ^2_e. This phenomenon is particularly large in multi-tree plot field designs (Cappa and Cantet 2008; Costa e Silva and Kerr 2013). A similar phenomenon has been observed by Cappa and Cantet (2008) in loblolly pine trial data when comparing models with and without fitting competition genetic affects, by Costa e Silva and Kerr (2013) when comparing the base model with the model that fits both competition and spatial effects using an AR(1) × AR(1) residual structure, and by Cappa et al. (2015a) using the same empirical dataset as Cappa and Cantet (2008) when comparing TM with CM and CSM models.

Estimates of σ^2_b from SM were grossly overestimated compared with those estimated from CSM (Table 5; Supplementary Fig. S5), suggesting that ignoring the genetic and environmental competition effects leads to overestimating environmental heterogeneity. Cappa et al. (2015a) showed the same results using an empirical dataset of loblolly pine, i.e., the SM yielded estimates of σ^2_b that were higher than those of

CSM. A similar trend due to ignoring competition effects has been observed by Costa e Silva and Kerr (2013), where the variance for the correlated residual effects increased by approximately 65 % (see Fig. 4 in Costa e Silva and Kerr 2013).

The CM yielded posterior σ^2_{Ad}, σ^2_{Ac}, and σ^2_p estimates smaller than those estimated from CSM for DBH (from 37.7 to 65.5 %, from 34.5 to 54.2 %, and from 6.3 to 18.7 % for σ^2_{Ad}, σ^2_{Ac}, and σ^2_p, respectively). Moreover, the estimated posterior means r_{AdAc} from the CM indicated weaker negative correlations than those estimated from the CSM (Table 5; Supplementary Fig. S5). These differences from the CM and CSM tended to be larger when the estimated correlation (r_{AdAc}) from the CM was weaker. For example, for DBH at the trial montane very wet, the estimated r_{AdAc} was −0.32 and −0.66 (i.e., 53.3 %) for the CM and CSM model, respectively. On the contrary, for the same trait at the submaritime very wet site, those values were −0.72 and −0.84 (i.e., 14.3 %) for the CM and CSM, respectively. Therefore, ignoring the environmental heterogeneity leads to underestimating genetic and environmental competition effects. These underestimates were greatest for the strongest competition effects (last column Table 3). Our results are similar to those reported by Durban et al. (2001), where ignoring the fertility trends resulted in underestimates of competition effects, and similar to the simulation results of Costa e Silva and Kerr (2013) (see Figs. 5 and 6 in Costa e Silva and Kerr 2013).

Impact of simultaneously adjusting for competition and environmental heterogeneity effects on selection

Competition and environmental heterogeneity may affect the effectiveness and efficiency of genetic selection. Therefore, from a tree breeder's point of view, a relevant question is whether or not the predicted tree BVs from TM and the predicted TBVs from CSM lead to a different ranking. In our study, Spearman rank correlation between these predicted BVs was positive and from moderate to high for DBH at all sites (from 0.58 to 0.95). Lower correlations values are directly associated with highest σ^2_{Ac} and highest ratio $\sigma^2_{Ac}/\sigma^2_{Ad}$, suggesting that strong contribution of the competition genetic effects on TBVs leads to a change in the ranking. In fact, as we expected, Spearman rank correlations between BVs estimated from the TM and direct BVs from the CSM were higher than those between the TM and the TBVs from the CSM. These correlations varied from 0.81 to 0.94 for DBH across the studied trials (results not shown). Additionally, the Spearman rank correlation between BVs from the TM and the SM were always very high (from 0.97 to 0.99, results not shown), indicating that similar selection will result from both models. Assuming 100 % survival and using simulated data with similar relatedness and additive covariance matrix of breeding values (r_{AdAc} from −0.3 to −0.9 and ratio $\sigma^2_{Ac}/\sigma^2_{Ad}$ = 10 and 50 %), Costa e Silva and Kerr (2013) found similar

Spearman correlations between predicted BVs from the base model and TBVs from a model including both competition and spatial effects (see Tables 3 and 4 in Costa e Silva and Kerr 2013). Although our empirical study showed moderate to high correlations between predicted tree BVs from the TM and the TBVs from the CSM, the absolute values changed. Given the high and negative competition BVs, the TBVs (the total genetic contributions to their population) of the selected individuals were overestimated for the simplest model (i.e., TM). When the differences between the predicted tree BVs from the TM and the TBVs from the CSM were calculated for DBH at age 35, their distribution were very skewed, with many small and large positive values (results not shown). These results confirm the inefficiency of simpler models currently used in forest tree-breeding programs when there is genetic competition and environmental heterogeneity within forest genetic trials, and highlight that the CSM provide a more realistic prediction of future performance, as concluded by Brotherstone et al. (2011). Moreover, the ranking among the top 10 % individuals from TM and CSM showed differences. The proportion of common individuals within the top 10 % of the selected trees between the BVs of TM and TBVs from CSM varied from 45.9 to 88.9 % for DBH at age 35. These differences demonstrate that simpler models may have a substantial direct impact on selection decisions and genetic progress.

Implications for the coastal Douglas-fir British Columbia tree improvement program and conclusions

In British Columbia, stand volume predictions for growth projections and allowable cut determinations are based on site index, which is determined by heights of dominant trees. Therefore, we made early selections based on height and incorporated the estimated (or predicted) height gains to project stand volume at rotation (Xie and Yanchuk 2003). Since TH is not strongly affected by competition, the effects of competition on stand volume projection are minimized by early selection and by selection for height. Indirect evidence for this also comes from our realized gain trials where estimated gains at age 12 are in line with the observed gains based on progeny testing (Stoehr et al. 2010).

A summary of the findings and implications to be drawn from the current study is as follows:

1. It has been shown that both competition and environmental heterogeneity effects are present in the same forest genetic Douglas-fir progeny trials.
2. Strong spatial patterns of variation (predominantly large-scale spatial variation) generate positive correlations that hide the competition effects in the three Douglas-fir progeny trials.
3. While DBH at age 35 revealed strong competition effects at both genetic and environmental levels, these effects were weak for TH.
4. In general, with strong competition genetic effects, the CSM gave a better fit (lower DIC value) than the simpler models (i.e., TM, CM, and SM). Thus, we recommend using CSM in the estimation of dispersion parameters and prediction of BVs in forest trees.
5. Ignoring the genetic and environmental competition effects leads to overestimating environmental heterogeneity, i.e., the SM yielded higher random knots variance estimates than those of the CSM.
6. Ignoring the environmental heterogeneity leads to underestimating genetic and environmental competition effects, i.e., the CM yielded smaller direct and competition additive correlation (from 6.3 to 53.3 %) and environmental competition variance estimates (from 6.3 to 29.4 %) than the CSM.
7. Spearman correlations for DBH between BVs estimated from the TM and TBVs from the CSM were moderate to high (from 0.58 to 0.95).

Finally, this empirical example confirms the results obtained in the study of Cappa et al. (2015a) using simulated and real data from a loblolly pine progeny trial, and shows the importance of accounting simultaneously for competition and spatial effects to understand the dynamics of both phenomena and their effects on the estimation of genetic parameters and predicted BVs in single forest genetic trials.

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