



Spatial Models With Inter-Tree Competition From Airborne Laser Scanning Improve Estimates of Genetic Variance

David Pont^{1*}, Heidi S. Dungey², Mari Suontama^{2,3} and Grahame T. Stovold²

¹ Forest Informatics, Scion, Rotorua, New Zealand, ² Forest Genetics, Scion, Rotorua, New Zealand, ³ Tree Breeding, Skogforsk, Umeå, Sweden

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*Correspondence:

David Pont
david.pont@scionresearch.com

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Phenotyping individual trees to quantify interactions among genotype, environment, and management practices is critical to the development of precision forestry and to maximize the opportunity of improved tree breeds. In this study we utilized airborne laser scanning (ALS) data to detect and characterize individual trees in order to generate tree-level phenotypes and tree-to-tree competition metrics. To examine our ability to account for environmental variation and its relative importance on individual-tree traits, we investigated the use of spatial models using ALS-derived competition metrics and conventional autoregressive spatial techniques. Models utilizing competition covariate terms were found to quantify previously unexplained phenotypic variation compared with standard models, substantially reducing residual variance and improving estimates of heritabilities for a set of operationally relevant traits. Models including terms for spatial autocorrelation and competition performed the best and were labelled ACE (autocorrelation-competition-error) models. The best ACE models provided statistically significant reductions in residuals ranging from -65.48% for tree height (H) to -21.03% for wood stiffness (A), and improvements in narrow sense heritabilities from 38.64% for H to 14.01% for A . Individual tree phenotyping using an ACE approach is therefore recommended for analyses of research trials where traits are susceptible to spatial effects.

Keywords: spatial analysis, tree competition, environment, tree phenotyping, airborne laser scanning, heritability, field trial

INTRODUCTION

The development of a precision approach to forestry can improve the efficiency and sustainability of managed forests. The aspiration is to utilize improved tree breeds, planted on the most suitable sites, and managed to optimize production, while minimizing costs and environmental impacts by targeted applications of inputs such as fertilizers (Dungey et al., 2018). A critical requirement for precision forestry is accurate and cost-effective methods to characterize individual trees (Tsafaris et al., 2016; D'odorico et al., 2020). This capability could not only be utilized in trials to support research into improved breeds for tree growth and quality, but also in assessment of trees for inventory of forest stands at different stages of the production cycle. Traditional forest inventory and trial measurement rely on ground-based measurement of traits such as tree diameter, height,

and volume. Such measurements are time consuming and error-prone. Remote sensing offers the potential for high throughput, accurate, and spatially explicit phenotyping, providing an essential foundation for precision management (Fahlgren et al., 2015). At this stage, airborne laser scanning has been most successfully adopted for forest inventory internationally, typically using area-based methods to characterize patches of the order of 0.04 ha in size (White et al., 2013; Maltamo et al., 2014). Alternative methods, identifying and delineating individual trees using ALS, have been developed and evaluated on New Zealand radiata pine stands (Pont, 2016).

Radiata pine (*Pinus radiata* D. Don) is the dominant tree species in the New Zealand forest estate comprising 90% of the planted area (Forest Owners Association, 2019). The New Zealand radiata pine forest estate comprises a monospecific, even aged, intensively managed forest crop. Considerable levels of variation in tree attributes remain, due to genetics, environment, and silviculture (Dungey et al., 2006). Forest tree breeding requires the evaluation of large numbers of trees and sufficient replication due to genetic variability, resulting in trials containing thousands of trees, and occupying several hectares (Dungey et al., 2009).

A standard approach to mitigate the effects of environmental variation in genetics trials is the use of spatial terms in analytical models (Dutkowski et al., 2006). A useful method is the separable first-order autoregressive model (AR1) in two dimensions (Cullis et al., 1998), utilizing inverse distance-weighted correlations across rows and columns in the trial, allowing for differing spatial correlations in the row and column directions. This successfully accounts for various forms of environmental effects in trial analyses (Cullis et al., 2014). Competition is a form of negative autocorrelation, where neighbors of a larger tree are more likely to be smaller, and vice versa (Griffith and Arbia, 2010). Autocorrelative methods such as AR1 models do not distinguish positive and negative autocorrelation and as a result the two effects are confounded (Griffith and Arbia, 2010). In order to accurately account for environmental variation, methods to quantify both positive (site) and negative (competition) autocorrelation are needed (Cappa and Cantet, 2008; Costa et al., 2013; Dong et al., 2020).

Tree traits of primary importance to breeders and forest managers include size, wood quality and disease susceptibility. Height, diameter at breast height (DBH) and total stem volume are widely used fundamental measures of tree size and productivity, able to be estimated from tree-based analyses of ALS (Lindberg et al., 2013; Dalponte et al., 2018). Dothistroma needle blight (*Dothistroma septosporum* (Dorog.) M. Morelet) is a foliar disease causing considerable productivity losses (Watt et al., 2011), and wood stiffness is an wood quality characteristic important for structural uses of timber (Carson et al., 2014). Individual tree crown metrics derived from the ALS were shown to correlate with these aforementioned tree size, disease, and wood quality traits, and to provide accurate estimates of genetic parameters such as heritabilities (Pont, 2016).

Competition metrics express the growth potential of a tree relative to nearby trees, generally considering the size and proximity of those trees (Pretzsch, 2010;

Burkhardt and Tomé, 2012). The inclusion of such competition metrics in analytical models was of interest to partition competition effects from general environmental effects. Spatially registered crown metrics from tree-based analysis of ALS quantifying tree size and locations are suitable for derivation of individual tree competition metrics. In a review of competition metrics for use with individual tree analysis of ALS (Suárez, 2010), distance weighted size ratios were utilized. Such ratios, initially used by Hegyi (1974), were expressed in terms of tree diameters:

$$CI = \sum_{j=1}^n \left(\frac{d_j/d_i}{L_{ij}} \right)$$

where, d_i = DBH of reference tree i , d_j = DBH of competitor tree j , L_{ij} = distance between reference tree i and competitor j .

It is hypothesized that spatial models including autoregressive and competition terms reduce unexplained variation compared to conventional models lacking spatial terms. The ability to more accurately quantify spatial effects reduces model residuals and thereby improves heritability estimates. The study was carried out in a genetics trial, providing the unique opportunity to work within an experimental design of known spacing and documented genetics. Environmental effects due to competition and site related variation were evident in the selected trial, providing the opportunity to examine models accounting for these effects in a controlled setting.

MATERIALS AND METHODS

Genetics Trial Site

The genetics trial BC 35-3 was established in 2007 by the Radiata Pine Breeding Company Ltd., in compartment 76 at Kaingaroa forest (38.53° S, 176.66° E) in the central North Island of New Zealand. The trial was designed to evaluate *Dothistroma* needle blight resistance for families in a breeding program and used an incomplete block design with single tree plots (Dungey et al., 2009). The trial site covered a total area of 2.8 ha and sloped gently (<5 degrees) to the southeast. The trial comprised 75 blocks, with 25 replicates and 3 incomplete blocks per replicate (Figure 1). Each block measured 19.2 × 19.2 m, with tree spacing on a uniform grid of 3.2 × 3.2 m. Blocks were established with 36 trees from different families in a 6 × 6 grid. Six control families were present in every block and the remaining 90 families were assigned across the three incomplete blocks for each replicate, with randomized spatial locations within the blocks and replicates. The surrounding stand was also established with radiata pine in 2007 at a density of 1000 stems ha⁻¹ and thinned to 786 stems ha⁻¹ in 2012.

Initial inspection of the trial data showed evidence of spatial autocorrelation, with reduced height and diameter growth and increased levels of *Dothistroma* infection associated with small gullies within the trial (Figures 2, 3). Favorable conditions for *Dothistroma* are known to occur in gullies, where moist conditions persist, indicating the possibility of reduced tree growth associated with *Dothistroma* infection (Bulman et al., 2004). In addition to observable site effects, the trial had missing

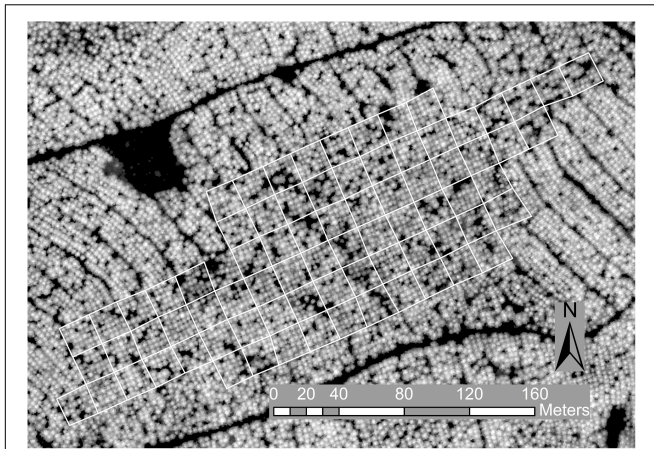


FIGURE 1 | Trial layout with blocks outlined in white on the canopy height model image derived from the ALS data at 0.25 m resolution and used for tree detection.

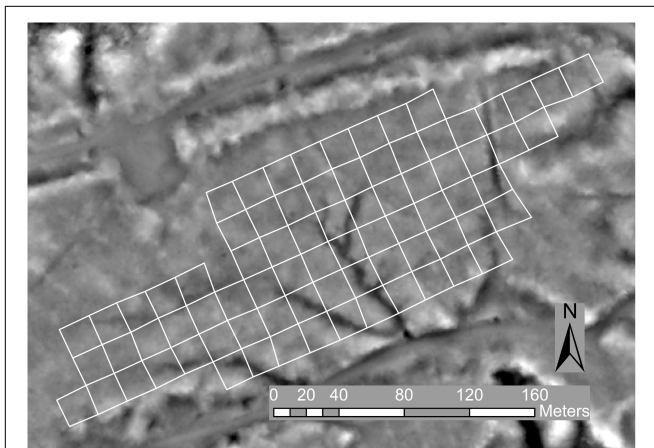


FIGURE 2 | Trial layout with blocks outlined in white on an image of a digital terrain model (derived from the ALS data at 0.8 m resolution) shaded to indicate relative elevation and reveal a number of gullies evident as dark areas.

trees. Missing trees typically occur due to mortality, and in this trial dead, unhealthy, and highly malformed trees were also removed during the 2012 operational thinning of the surrounding stand. The resulting gaps in the trial grid created potential for competition effects (Fins et al., 1992).

Field Measurement of Tree Traits

A ground-based assessment of a number of tree traits was carried out in July 2014 when the trial was aged 7 years, following standard tree breeding measurement methodologies (Jayawickrama, 2001). Measurements of tree diameter at breast height (*DBH*), height (*H*), and outerwood stress wave velocity (*A*), and degree of needle loss caused by *Dothistroma* needle blight (*D*₃₈), were carried out. Tree *DBH* was measured using a fiberglass girth tape with diameter gradations at millimeter intervals (Friedrich Richter Messwerkzeuge GmbH & Co., Speichersdorf, Germany). Tree *H* was measured using a Vertex

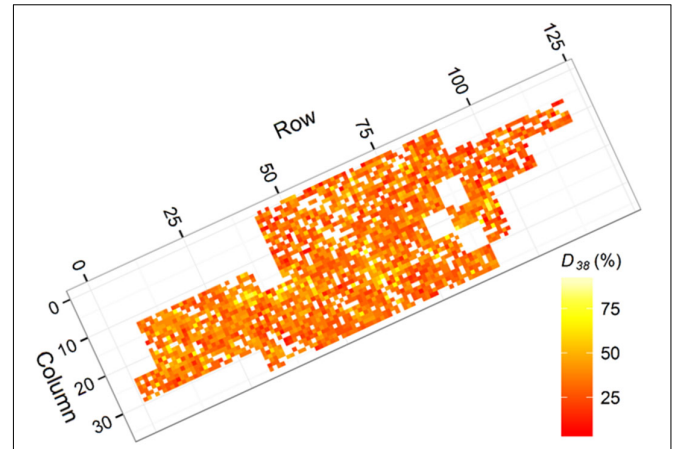


FIGURE 3 | Heatmap presenting ground measured degree of *Dothistroma* infection (*D*₃₈) for each tree (white indicates no data). Areas with elevated infection coincided with the gullies identified within the trial.

IV (Haglof, Sweden). Total stem volume (*V*) was estimated for each tree using the standard volume equation V182 (Goulding, 1995):

$$V = DBH^a \left(\frac{H^2}{H - 1.4} \right)^b e^c$$

where $a = 1.79068$, $b = 1.07473$, $c = -10.03201$, and e is Euler's number.

Outerwood stress wave velocity (*A*) was measured using a HITMAN ST300 (Fibre-gen Ltd., Christchurch, New Zealand) with the probes placed 1 m apart, avoiding knots and defects that could affect readings. The measure *A* is correlated with wood stiffness, an important engineering property for structural uses of timber (Carson et al., 2014). Degree of needle loss (*D*₃₈) was assessed at age 38 months as a percentage of needles infected or lost, estimated visually in 5 percent increments (Van Der Pas et al., 1984). Individual tree *D*₃₈ measurements are presented in **Figure 3** where indication of increased infection in association with gullies crossing the trial (see **Figure 2**) was evident.

Airborne Laser Scanning Data

The discrete return ALS data were acquired in early 2014 using an Optech Pegasus scanner with a pulse rate of 100 kHz, a maximum scan angle of $\pm 12^\circ$, a 25% swath overlap, and a 0.25 m footprint size. The data were georeferenced to the NZGD2000 NZTM coordinate system and all returns were classified as ground and above ground (using Terrascan TerraSolid software). The average point density of the point cloud over the trial area was 17 total returns per m² and 7 last returns per m².

Crown Metrics

A canopy height model (CHM) with 0.25 m resolution was extracted from ALS data collected over the trial and image defects referred to as pits were removed using the standard image processing method *closing* (Ronse and Heijmans, 1991; Andersen et al., 2006). Individual trees were detected and crown boundaries determined on the CHM image using the calibrated

TABLE 1 | Individual tree crown metrics used in candidate competition metrics with most highly correlated tree size trait and Pearson's r .

Abbreviation	Description	Units	Trait r
$CR = \sqrt{\frac{CA_P}{\pi}}$	Crown radius derived from crown area (CA_P).	m	DBH 0.679
CL	Crown length, difference between crown highest point and average height of crown boundary points.	m	H 0.476
GA_P	Two-dimensional ground area of crown growing space from watershed segmentation polygon.	m^2	DBH 0.518
CA_P	Two-dimensional ground area of crown determined from crown boundary polygon.	m^2	V 0.574
A_{CG}	Ratio of crown and growing space areas (CA_P/GA_P).	–	H 0.297
CS_T	Surface area of triangulated crown CHM heights.	m^2	V 0.598
CV_F	The volume between the crown upper surface and the ground (Chen et al., 2007).	m^3	V 0.844
CV_P	The volume between the crown upper surface and the base of the crown.	m^3	DBH 0.541

ITC method (Pont et al., 2015). The method uses watershed segmentation with operator calibration to determine the level of image smoothing and has been shown to provide tree detection accuracy of 95% for New Zealand radiata pine across a range of stand densities and crown sizes. Detected trees were matched to ground trees with an automated least squares approach (Hauglin et al., 2014) and unmatched trees used to identify and manually correct segmentation errors.

Watershed segmentation resulted in growing space polygons, one per detected tree, which completely tiled the image, each including a tree crown and a portion of any adjacent gap between trees. Tree crown boundaries were then delineated within each growing space polygon to exclude any gap area. For tree crowns with no adjacent gaps, growing space and crown polygons were identical. The CHM image gray values within each crown represent heights above ground. Growing space boundaries, crown boundaries, and crown elevation values were used to derive a total of nine crown size metrics (Table 1) correlated with the traits of interest (Pont, 2016). Crown volumes (CV_F and CV_P) quantified three-dimensional crown size, while surface areas from projected polygon outlines (GA_P and CA_P) and from surface areas of three-dimensional crown surfaces (CS_C and CS_T) provided two-dimensional measures of crown sizes. Crown length and radius (CL and CR) provided one-dimensional measures and the ratio of crown and growing space areas (A_{GC}) provided a dimensionless measure of crown size. These crown size metrics were then used in competition metrics described subsequently.

Competition Metrics

Rouvinen and Kuuluvainen (1997) presented a set of competition metrics, CI_{10} , CI_{11} , and CI_{12} , derived from the original by

Hegyi (1974). Those competition metrics were evaluated by Suárez (2010) using ground measured DBH and using DBH estimated from LiDAR CHM crown metrics. Those competition models were generalized in our study to utilize the crown metrics (see Table 1) derived from the ALS CHM as:

$$CIA = \sum_{j=1}^n \left(\frac{c_j/c_i}{L_{ij}} \right)$$

$$CIB = \sum_{j=1}^n \left(\frac{c_j/c_i^2}{L_{ij}} \right)$$

$$CIC = \sum_{j=1}^n \left(\frac{(c_j/c_i)^2}{L_{ij}} \right)$$

where c_i = crown metric for reference tree i , c_j = crown metric for competitor tree j , L_{ij} = distance between reference tree i and competitor j .

Two methods were used for determining the neighboring trees included in the calculation of the competition metrics described above. In the area method (N_A), all trees within a fixed radius were included, an approach used in a number of previous studies (Hegyi, 1974; Pukkala et al., 1994; Rouvinen and Kuuluvainen, 1997; Suárez, 2010). The grid spacing in the trial was used to estimate a radius of 8.273 m to include an average of twenty trees surrounding the central tree. In the boundary method (N_B), only trees sharing a segment boundary (as delineated on the CHM) with the target tree were included (Suárez, 2010). Processing of the CHM included a 50 m buffer around the trial and competition metrics using both neighborhood methods included trees surrounding the trial, a distinction with competition metrics which often only account for trees measured within plots or trials (Dutkowski et al., 2006). The use of 9 crown metrics (Table 1) and 3 model formulations (CIA, CIB, CIC) gave 27 competition metrics. Use of the two neighborhood methods (N_A and N_B) with the 27 metrics gave a total of 54 competition metrics for evaluation.

Spatial Models

The following general individual tree linear mixed model was used as the basis of all spatial models:

$$y = Xb + Zu + e$$

where y is a vector of individual tree observations of a specific trait (H , DBH , V , D_{38} or A), b is a vector of fixed effects, u is a vector of random effects, and e is a vector of random residuals. The terms X and Z correspond to design matrices relating the observations in y to the fixed and random effects in b and u , respectively (Duney et al., 2012).

We fitted a model without spatial terms, as routinely used in estimating variance components and genetic parameters including narrow sense heritabilities, referred to as Base model (B) (Dutkowski et al., 2006). Fixed effects in vector b included the overall mean and a factor with two levels to account for the effects of control versus non-control material. Random terms in vector u included the additive genetic effects of individual

TABLE 2 | Models fitted for each trait to compare improvements from random terms to account for spatial autocorrelation (AR1) and addition of competition covariates derived from analyses of the ALS tree crown metrics.

Model	Abbreviation	Fixed terms	Random terms
Base	B	control	replicate + iblock:rep + pedigree
Base + AR1	BA	control	pedigree + units + AR1
Base + Competition	BC	control	replicate + iblock:rep + pedigree + competition
Base + AR1 + Competition	BAC	control	pedigree + units + AR1 + competition

genotypes for pedigreed material, the effects of replicates and the effects of incomplete blocks within replicates. We also fitted a standard spatial model using an auto-regressive order 1 random term, commonly referred to as AR1xAR1, and abbreviated to AR1 hereafter (Dutkowski et al., 2006). We referred to this standard spatial model as Base plus AR1 (BA). In this model vector e was partitioned into spatially correlated (ζ) and uncorrelated (η) residuals and replicate was removed as a fixed effect. The spatially correlated error ζ , was modeled by using a first-order separable autoregressive process in the row and column directions (Gilmour et al., 1997; Costa et al., 2001; and Dutkowski et al., 2002).

Competition metrics were then introduced as covariates to those models, referred to as Base plus Competition (BC) and Base plus AR1 plus Competition (BAC). Covariate values were standardized by subtracting the mean and dividing by the standard deviation (Butler et al., 2009). Control and the overall mean appeared as the only fixed terms, and the additive genetic effects of individual trees appeared as a random term, in all models. Trees were assigned to grid rows and columns, and missing values added to ensure a complete grid for AR1 models. A nugget effect (referred to as units) was added to models having an AR1 spatial term, as this has been shown to be significant in several studies (Suontama et al., 2015). Incomplete block by replicate was tried as a random term in all models, but it became non-significant when an AR1 spatial term was added, so it was dropped from those models (Dungey et al., 2012). The set of models evaluated are summarized in **Table 2**.

The B and BA models were fitted to each of the 5 traits (H , DBH , V , D_{38} , A), requiring 10 model runs. The BC and BAC models were fitted for the 5 traits by 54 competition metrics, requiring 270 model runs. The total number of model runs being 280.

Model Evaluation

Models can be compared with log-likelihood (LL) ratio tests if they have the same fixed effects, and if one model has a subset of the random effects in the other model (nested models) (Isik et al., 2017). Models with the same fixed effects that are not nested can be compared with information criteria, Akaike's (AIC) or Schwarz's Bayesian Information Criteria (BIC). In our study we evaluated four nested models with the same fixed effects (control only), presented in **Table 2**. We evaluated models under the premise that all models including some spatial component were alternative approaches to accounting for spatial variation compared to the base model. If LL_M and LL_B are the REML

log-likelihoods for a test and base models, respectively, the test statistic (D) is given by:

$$D = 2(LL_M - LL_B)$$

where Akaike Information Criteria (AIC) and Bayesian Information Criteria (BIC) used to rank models (Dutkowski et al., 2006) are derived as follows:

$$AIC = -2LL_{Ri} + 2t_i$$

$$BIC = -2LL_{Ri} + 2t_i \log v$$

where LL is the log-likelihood of the model, t_i is the number of variance parameters in model i , and $v = n - p$ is the residual degrees of freedom.

Narrow sense heritabilities (h^2) were estimated for each model fit, using the additive genetic variance as a ratio of the phenotypic variance, expressed as the sum of the additive and residual variances:

$$h^2 = \frac{Var_A}{Var_A + Var_E}$$

where Var_A is the additive genetic variance and Var_E is the residual variance.

In the case of models with an AR1 term, the residual is represented by the units component (Dutkowski et al., 2002). Models where competition covariates terms were fitted for each trait (BC, and BAC) were ranked by LL and the best model selected. All models tested were ranked by LL (higher being better), and then associated h^2 and residual variance components were examined. Two metrics were derived to express the improvements of spatial models compared to the base model, the change in h^2 , and in residual (ϵ), compared to the standard (base) model, multiplied by 100 to be expressed as percentages:

$$\Delta h^2 = \frac{h_M^2 - h_B^2}{h_B^2}$$

$$\Delta \epsilon = \frac{\epsilon_M - \epsilon_B}{\epsilon_B}$$

where the subscripts M and B represent the spatial and base models, respectively.

RESULTS

Spatial models provided statistically significant improvements in LL over a base model for all traits (H , D , V , D_{38} , and A),

TABLE 3 | ASReml model fit statistics Log-likelihood (LL) and test statistic (D) and results heritability (h^2) with its standard error (SE), by trait and model, ordered by decreasing Log-likelihood (LL) within trait and traits are ordered by decreasing improvement in residual ($\Delta\epsilon\%$) from the best model, improvement in heritability ($\Delta h^2\%$) is also shown.

Trait	Model	LL	D	h^2	SE	$\Delta h^2\%$	$\Delta\epsilon\%$
H	BAC	-1291	<0.001	0.4117	0.0950	38.64	-65.48
	BC	-1381	<0.001	0.3011	0.0679	1.39	-32.90
	BA	-1758	<0.001	0.3425	0.0770	15.34	-24.87
	B	-1800	<0.001	0.2969	0.0660	—	—
DBH	BAC	-8406	<0.001	0.3753	0.0899	33.55	-63.65
	BC	-8440	<0.001	0.2954	0.0657	5.13	-38.90
	BA	-8930	<0.001	0.2950	0.0671	4.99	-8.58
	B	-8948	<0.001	0.2810	0.0636	—	—
V	BAC	5757	<0.001	0.3642	0.0856	22.47	-56.26
	BC	5742	<0.001	0.2980	0.0649	0.21	-31.89
	BA	5347	<0.001	0.3140	0.0678	5.60	-8.87
	B	5334	<0.001	0.2973	0.0640	—	—
D_{38}	BAC	-6024	<0.001	0.4912	0.0931	34.88	-50.31
	BC	-6096	<0.001	0.3546	0.0705	-2.63	-14.43
	BA	-6210	<0.001	0.4926	0.0922	35.28	-40.18
	B	-6276	<0.001	0.3642	0.0713	—	—
A	BAC	1052	<0.001	0.4862	0.1101	14.10	-21.03
	BC	1047	<0.001	0.4221	0.0764	-0.93	-0.30
	BA	1038	0.002	0.4531	0.0819	6.34	-9.63
	B	1033	<0.001	0.4261	0.0772	—	—

the ranking order in **Table 3** was BAC, BC, BA. Spatial BAC models resulted in reductions in residual ranging from -65.48% for H to -21.03% for A , and improvements in h^2 from 38.64% for H to 14.10% for A . Results confirmed prior research that auto-regressive order 1 (AR1) models are able to account for spatial effects from a wide variety of sources (Isik et al., 2017). Results also showed the utilization of a competition covariate in combination with an AR1 term explained additional variation, substantially reducing the residual and improving h^2 for all traits except D_{38} . The tree size traits DBH , H , and V benefited the most from competition covariates, and the greatest improvements in residual and h^2 relative to a BA model were -55% and 29%, respectively from a BAC model for DBH .

The use of competition covariates in spatial models without an AR1 term (BC models) resulted in statistically significant improvements in LL, and reductions in residuals. However, the BC models did not generally result in increased h^2 , the best improvements being 5.13% and -2.63% for D and D_{38} , respectively. The sign and strength of Pearson's correlation coefficients (r) were examined to elucidate the relationships between crown metrics and traits (see **Table 4**).

The crown metric CV_F (see **Table 1**) appeared in the competition metric for the top performing BAC models for all traits except A . Models with competition metrics based on the CV_F crown metric were consistently ranked highest, but only marginally higher than models with the CR and CA_P crown metrics (results not shown). Those three metrics represented crown size in terms of volume, radius, and projected area, respectively. Moderate to strong correlations were observed for

TABLE 4 | Best performing (least Log-Likelihood) crown metrics in BAC models compared to the BA model by trait.

Trait	Model	Crown metric	N/CI	r
H	BAC	CV_F	N_B CIA	-0.5436
	BA			
DBH	BAC	CV_F	N_B CIA	-0.5990
	BA			
V	BAC	CV_F	N_B CIA	-0.5423
	BA			
D_{38}	BAC	CV_F	N_A CIA	0.3971
	BA			
A	BAC	A_{CG}	N_A CIA	0.1328
	BA			

The competition crown metric, neighborhood definition (N) and competition index (CI) used are shown along with Pearson's correlation coefficient (r) for the trait and crown metric.

competition metrics with tree size traits (H , DBH , and V , with r from -0.54 to -0.60) and with disease expression (D_{38} , $r = 0.40$). Results associated higher competition metrics with reduced tree size, and increased disease levels.

Competition metrics based on distance-weighted crown size metrics (CIA , CIB , CIC) were derived using area (N_A) and boundary (N_B) neighborhoods. The CIA formulation, representing a linear distance weighting of crown sizes, appeared in the best BAC models for all traits (**Table 4**) and the boundary neighbourhood definition (N_B) performed best for the tree size traits (H , DBH , and V). The exponentially weighted derivations of competition index (CIB and CIC) were inferior.

DISCUSSION

The Autocorrelation-Competition-Error Approach

Results from our study have confirmed the recognized general utility of AR1 spatial models with a spatially independent units term to take account of spatial environmental variation (Costa et al., 2001; Dutkowski et al., 2006). However, spatial autocorrelation can be positive, representing various site effects such as temperature and aspect, and negative, representing competition effects. Competition effects can result in the mutual masking of these forms of autocorrelation (Griffith and Arbia, 2010). Where negative autocorrelation is left unaccounted for, it can even result in insignificant spatial autocorrelation test statistics. The inclusion of competition effects to reduce residual variation was described in a theoretical approach, focused on competition of genetic origin, and showed failure to account for competition resulted in biased model estimates and increased residual variation (Costa et al., 2013). Our study was a practical demonstration of the presence of both positive (site) and negative (competition) autocorrelation, and the best models combined AR1 and competition terms to explain these respective environmental sources of variation. Models having an explicit competition term and a generic term to account for

positive autocorrelation are referred to as ACE (autocorrelation-competition-error) models. Results confirmed our hypothesis that models including autoregressive and competition terms reduce residuals and improve estimates of heritabilities compared to conventional models without spatial terms.

The success of ACE models was attributed to three key features. Firstly, it was critical to separate negative and positive autocorrelation, representing variation due to competition and other environmental effects, respectively, which were otherwise confounded. Secondly, the inverse-distance weighted competition metrics employed successfully accounted for competition. Thirdly, we observed there are potentially numerous positively auto-correlated environmental effects on tree growth besides competition, which were robustly accounted for by an autoregressive model component. We suggest ACE models as a useful approach to analyses of tree and plant growth due to the ubiquity of both competition and site effects. Thus, we propose that it will be beneficial for modelers to test for, and quantify, those effects with ACE models, when possible, as a useful evolution of the currently recommended practice of applying AR1 models.

The competition and crown metrics utilized were parsimonious, easy to derive, and to interpret, which will aid application of ACE models. The competition metrics were of a widely recognized and applied form, utilizing positions and relative sizes of neighboring trees (Maleki et al., 2015). The crown metrics represented fundamental crown morphological features, and were derived from analysis of the CHM, a model of the upper surface of the canopy derived from the three-dimensional point cloud created by laser scanning (Pont et al., 2013). This is referred to as a raster-based approach, and is contrasted with point- and voxel-based methods which derive numerous measures from the three-dimensional point cloud, a majority of which are statistical measures of point dispersion (Zhen et al., 2016). The latter methods can yield large numbers of metrics, but we note that studies evaluating such metrics have typically found that a more limited set of crown morphological metrics, representing crown features such as diameter, length, area, and volume, were typically among the most useful variables in models estimating tree attributes (Vauhkonen et al., 2016). Raster based metrics derived using the methods described in this study permit the use of widely available point cloud data, either from ALS or photogrammetric methods (Krause et al., 2019), making the methods flexible and amenable to operational uses in forestry. Future research could compare the efficacy of ALS and photogrammetric data sources with ACE models.

Generality of ACE Models

An autoregressive model relates a characteristic of a target tree to the same characteristic of its neighbors, reflecting Tobler's first law of geography (Tobler, 1970). Autoregressive models make no attempt to explain effects or cause, and therein lies their power. We postulate that an AR1 term can effectively account for spatial effects from multiple sources and scales, particularly once a separate term for competition is included. As a hypothetical example of scale independence, consider a group of neighboring trees where height growth is being positively affected by soil fertility at a short scale, and negatively affected by

temperature at a much larger scale. There could also be additional unknown influences on growth, all operating at different scales. An autoregressive model is agnostic to the factors or scales at play and utilizes the integrated result of all such effects on neighboring trees as a robust proxy for the effects on the target tree. The ACE approach could therefore robustly account for environmental variation of unknown sources and scales with an AR1 term, and is also amenable to the addition of terms representing explicit environmental effects as they are elucidated in future research.

Traits Have Distinct Environmental Responses

The ACE approach was shown to be beneficial for a range of traits, but it was also apparent that the relative amounts of variation due to genotype, competition, and site were distinct by trait. Tree *DBH* and *V* apparently had strong overall spatial variation, predominantly due to competition, while *H* also exhibited strong spatial variation due to nearly equal amounts of competition and site effects. The weaker competition effect noted for *Dothistroma* infection agreed with a predominant site effect due to the localized spread of the disease, reliant on a water-borne transmission, and re-infection of trees from fallen needles (Bulman et al., 2013) and the known tendency for the disease to occur in gullies due to increased moisture and reduced air movement (Bulman et al., 2004). The smaller, but evident, competition effect for *D₃₈* could reflect reduced tree growth resulting from the disease, or increased infection of smaller trees.

Applications

There are several important operational applications for tree level phenotyping which could be supported by the ACE modeling approach, ranging from trial, stand, and forest levels, for breeding, research, and management objectives. The use of ALS data provides accurate tree locations and sizes for use in competition metrics. It should be noted the modeling approach is even applicable to conventional ground measurement of trials, where remote sensed crown metrics are not available. In that case competition metrics could be derived from ground measured tree size, or other traits. The use of ACE models including known genetics in analysis of a genetics trial was shown to substantially reduce model residuals and improve heritabilities, potentially improving breeding values, tree selection, and future breeds. The benefits of improved tree breed selection for forest sites are accentuated in the context of climate change (Dungey et al., 2018; D'odorico et al., 2020; De Los Campos et al., 2020). The ACE method is also advocated for use in general research trial analyses to improve accuracy and precision of results by accounting for environmental variation. In this study ACE models were applied to tree size (*H*, *DBH*, *V*), disease expression (*D₃₈*) and wood quality (*A*), representing a set of traits of primary importance to tree breeders and forest managers.

CONCLUSION

Crown metrics utilized in competition metrics substantially reduced residual variation and improved heritabilities for a range of operationally relevant traits. Tree height, *DBH*,

volume, *Dothistroma* infection and stiffness exhibited significant variation attributable to spatial environmental effects. Analyses showed that traits exhibited distinct combinations of genotypic, competition, and site related variation, which needs be considered when modeling. The crown metrics and competition metrics identified in this study were parsimonious, effective, and warrant further investigation.

Analyses of results lead to the proposal of ACE models as a robust and effective approach to account for environmental variation in tree traits. Those models comprise an explicit competition term accounting for negative autocorrelation and a generic spatial term to account for positively autocorrelated site effects. Inclusion of a competition term, which we derived from individual tree crown metrics, was observed to be critical to improving the effectiveness of spatial modeling for environmental effects, avoiding the confounding of negative and positive autocorrelation.

The ACE approach is recommended for wider evaluation in tree and plant growth analyses, particularly for size and disease attributes. The analysis of remotely sensed data using ACE models will be developed and evaluated in future studies to determine utility in improving accuracy of trial analyses, identification of superior trees, tree growth research, and precision forest management.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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AUTHOR CONTRIBUTIONS

DP developed the crown and competition metrics, carried out model fitting, and wrote the core of the manuscript. DP, HD, and MS contributed to development of modeling approach. GS carried out field ground truth data collection. All authors participated in the writing and review of the manuscript, contributed to the article, and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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