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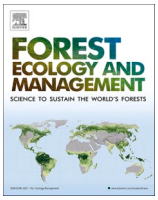

Well-connected trials show low genotype-by-environment interaction in *Pinus radiata*

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ABSTRACT

Selection in the New Zealand radiata pine (*Pinus radiata* D. Don) breeding program relies on wide-scale testing to adequately sample environmental variation. The program uses genomic selection for the early selection of parents for the next breeding cycle, but genomic selection may not perform as expected in the presence of crossover-type genotype-by-environment interaction (GxE) if such environments are poorly represented in the training population. This study uses empirical data to assess the magnitude of GxE to guide the selection and deployment strategy for radiata pine in New Zealand. Data was collected from eight well-connected and replicated cloned full-sib progeny trials across major radiata pine growing regions in New Zealand. We applied a second-order factor analytic model (FA2) with additive and non-additive variance components to characterise GxE. Three model types were used: uncorrected pedigree, marker-corrected pedigree and marker-based relatedness. This study found that the average additive genetic correlations among sites were 0.76 for DBH and 0.94 for DEN when estimated with marker-based relatedness. Models that use marker-based relatedness, without considering non-additive effects, provide a marginally superior fit compared to models that use pedigree or incorporate non-additive effects. Our study suggests that while GxE is present, its magnitude does not warrant regionalising (subdividing) radiata pine breeding zones for the North Island of New Zealand.

1. Introduction

Radiata pine (*Pinus radiata* D. Don) is economically the most important forest plantation species in New Zealand, Chile and Australia, exceeding 1.58 million ha, 1.27 million ha and 0.7 million ha respectively (Ministry for Primary Industries, 2023). Radiata pine breeding in New Zealand began in 1953 through the New Zealand Forest Service (NZFS) using plus-tree material from local landraces, selected primarily for growth and form traits (Shelbourne and Carson, 2019). The New Zealand breeding objective considers four harvest-age traits (Paget, 2022): stem volume, wood density, wood stiffness and branching at rotation age (~28 years). These traits are targeted by five selection criteria: diameter-at-breast height, corewood density, branching score, predicted modulus of elasticity and stem straightness measured at age of 8–10 years after trial establishment. Radiata pine has a narrow native range in five different provenances (locations): Cambria (CA, USA), Guadalupe Island (Mexico), Cedros Island (Mexico), Año Nuevo (CA, USA) and Monterey (CA, USA). Provenance testing involves planting distinct landraces from each provenance across different target environments assess their adaptability, thus informing early selection decisions (White et al., 2007). In the 1950s, approximately 1000 genotypes, identified as plus-trees, were collected from a blend of all five provenances across New Zealand (Shelbourne and Carson, 2019). This avoided the need for provenance selection, given radiata pine's limited natural range.

In New Zealand, radiata pine is grown in a wide variety of environments which are subject to various changes in rainfall, temperature, soil types and silvicultural practices. Over the years, the Radiata Pine Breeding Company (RPBC) has established and measured more than 100 trial sites to evaluate the performance of genotypes across the target population of environments for the prediction of breeding values. The current breeding strategy assumes that genotype-by-environment interaction (GxE) is not a concern in terms of changes in genotype ranking across environments and remains unexplained; however, the

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interaction is managed by wide-scale testing to sample the environmental variation (Paget, 2022).

Regionalised breeding is an alternative to the current breeding strategy. Regionalised breeding involves stratifying a population into multiple sub-populations associated with regions or breeding zones based on high GxE between regions or environmental gradients. Regionalised deployment has been deemed more feasible compared to regionalised breeding because it can use existing regional breeding values to select seed orchard parents for production of control-pollinated seed crop (Johnson and Burdon, 1990) if data is available. In tree breeding, GxE is often deemed significant if genetic correlations between trials planted at different environments are below 0.7, as the reduction in selection intensity would be compensated by better genotype-site matching (Shelbourne, 1972). GxE has been estimated to be high for growth selection criteria (McDonald and Apiolaza, 2009; Shelbourne, 1972; Wu et al., 2008) compared to wood quality selection criteria (Apiolaza, 2012). Despite the presence of significant family x site interactions for growth traits, earlier research found that there would be limited benefit to regionalise the breeding program (Carson, 1991; Johnson and Burdon, 1990). A larger and more recent multi-environment study of 77 undescribed trial sites across south-eastern Australia and New Zealand found high GxE for growth traits (Cullis et al., 2014) which led to the recommendation of regionalised breeding. However, this study had poorly connected trials which could overestimate GxE (Apiolaza, 2012; Li et al., 2018). There has also been no obvious delineation of GxE into specific environmental or geographical zones, so the definition of 'region' in this context has been vague.

Breeding programs rely on the accurate estimates of genetic information for predicting breeding values. The New Zealand radiata pine breeding program has conventionally used pedigree information to estimate breeding values (Henderson, 1975). Pedigree-based additive relationship matrices are prone to mistakes and error rates can often be considerable (Klápště et al., 2022). This can reduce the reliability of GxE estimates (Beaulieu et al., 2022), the accuracy of breeding values (Klápště et al., 2022) and genetic gain (Visscher et al., 2002). Marker-based methods present an alternative to pedigree-based methods and rely on dense Single Nucleotide Polymorphism (SNPs) marker arrays to capture the realised additive genetic relationship between individuals (Meuwissen et al., 2001). Marker-based relationship matrices can also capture historic relatedness that is not recorded in the pedigree (Hayes and Goddard, 2008), capture the Mendelian segregation term (Keller et al., 2011) and with sufficient density improve the reliability of genetic parameter estimates and breeding value accuracy (Beaulieu et al., 2022; Mulder, 2017; Walker et al., 2022). These marker-based relationship matrices are used with phenotypic information in a training population to predict breeding values in the wider breeding population at an early age using genomic information alone, allowing selection at the seedling stage. Understanding GxE is important in this context because the magnitude of GxE will influence the testing strategy. If target environments are not adequately represented in the training population, the presence of GxE suggests that genomic breeding values may be poorly predicted.

The primary focus of this research is to evaluate GxE interaction in the radiata pine breeding program across New Zealand. This study uses a set of eight well-connected and clonally replicated progeny test trials across important radiata pine deployment areas in New Zealand. We compare the use of uncorrected pedigree-based best linear unbiased prediction models (PBLUP) with marker-corrected PBLUP (Klápště et al., 2022) and genomic best linear unbiased prediction (GBLUP) models. The impact of incorporating non-additive genetic variance on GxE is also assessed.

2. Material and methods

2.1. Plant material

Eight clonally replicated full-sib experimental progeny trials were used in the prediction models. Seven sites were in the North Island of New Zealand, and one was in the South Island (Fig. 1) and represented major forestry plantation regions in NZ. There were approximately 15 genotypes (ortets) per full-sib family that were raised to establish hedges for vegetative propagation. Clones were propagated as fascicle cuttings taken from the two- or three-year-old hedge plants and raised as containerised plants (ramets). Overall, there were 1440 genotypes from 49 full-sib families (61 parents) with a single-paired mating design and these genotypes were replicated with 24,546 ramets across and within trial sites (Table 1). Ramets were planted in a 3.1 m x 3.1 m spacing (approximately 1040 stems per hectare). A resolvable incomplete block design (Fisher, 1992) was used in five trials and an 'optimal' design (Butler, 2013) was used in three trials. Incomplete block designs had approximately 15–20 blocks nested within five replicates. Each optimal design trial had 6 ×6 row-column (Prows and Pcols) planting blocks (Psets). There were 6–10 Psets in a trial which were nested in approximately 8–12 larger blocks ('Esets') per trial. Optimal designs were created with the view of using spatially correlated rows (Prow) and columns (Pcol). Prows and Pcols were treated as design features nested within Psets. The mean number of ramets per genotype in each trial site ranged from 2.0 to 4.5. Trials were highly connected with shared parents between trials ranging between 57 and 61 parents, with a total of 61 parents used to form the entire population (Fig. 2). The number of genotypes in common between trial sites ranged between 456 and 1324 genotypes. Some trials had more genotypes and fewer ramets, particularly BC55_2, BC55_3 and BC59_1 which were established one to two years later than the other trials.

This study focused on two key selection criteria for the RPBC's breeding program: 1) diameter-at-breast height (DBH) was measured using diameter tape at a tree height of 1.4 m from the ground, 2) wood density (DEN) was estimated with the maximum moisture content method (Smith, 1954) or the IML-RESI PowerDrill ®.

These selection criteria were chosen to represent traits with low (h^2<0.2) (DBH) (Jayawickrama, 2001) and higher (h^2<0.6) (DEN) (Apiolaza, 2012) narrow-sense heritabilities (h^2). Large phenotypic variances were found in both selection criteria within each trial site (Fig. 3).

Genomic data were generated using two methods on different genotypes 1) using the Axiom NZPRAD02 genotyping array (36,285 SNPs) (Graham et al., 2022) and 2) using a exome-capture genotype-by-sequencing approach where a large number of SNPs were genotyped with a lower quality (Telfer et al., 2019; Telfer et al., 2018). Genomic datasets from the two methods were merged using the PLINK 1.9 software (Chang et al., 2015). SNPs were selected based on the correlation of SNP genotype calls on 295 individuals genotyped on both platforms (>0.90). SNPs with missing data with call rates <95% were also excluded from the analysis. The marker data was further reduced by removing SNPs that had more that 60% of missing data and a minor allele frequency (MAF) of <0.05. Missing data was imputed by the mean genotype method. The remaining marker dataset included 6028 SNPs.

2.2. Statistical analysis

This study used a multivariate model based on pedigree corrected by markers (PBLUP), an uncorrected pedigree (PBLUP-U), and marker-based relationship matrix (GBLUP). Historically, field-recorded pedigrees used by the RPBC are highly likely to have contained errors for various reasons such as misidentified trees, pollen mix up or contamination, recording and handling errors. Therefore, two forms of PBLUP were considered: PBLUP with marker-assisted correction of pedigree errors (denoted as 'PBLUP') and pedigree using parentage as originally

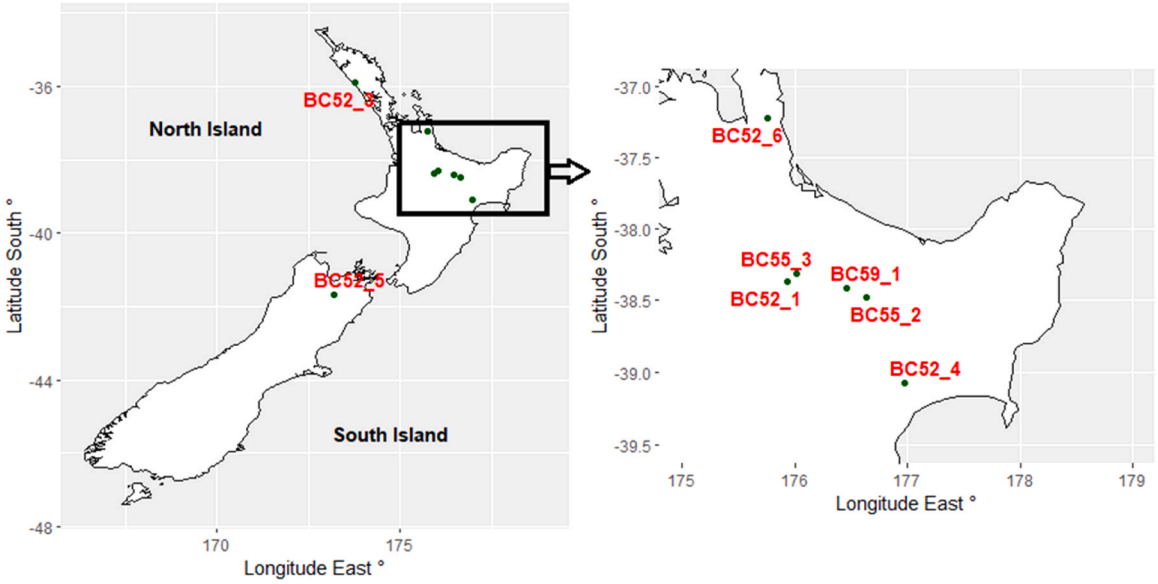

Fig. 1. Geographical location of trials within New Zealand.

Table 1
Summary of trials, locations, designs, and composition.

	BC52_1	BC52_3	BC52_4	BC52_5	BC52_6	BC55_2	BC55_3	BC59_1
Year Planted	2013	2013	2013	2013	2013	2014	2014	2015
Forest	Kinleith	Rotu	Mohaka	Ngaruru	Tairua	Kaingaroa	Kinleith	Kaingaroa
Region	Waikato	Northland	Hawke's Bay	Marlborough	Waikato	Bay of Plenty	Waikato	Bay of Plenty
***Trial Design**	IB	IB	IB	IB	IB	OD	OD	OD
No. Genotypes	635	629	526	634	635	1354	1244	1406
No. Ramets	2130	2804	1751	1705	1567	2538	2610	2884
Ramet/Genotype Ratio	3.36	4.46	3.34	2.72	2.51	2.01	2.22	2.13
Annual Rainfall (mm)[1]	1355	1011	1181	991	1060	729	1063	729
Annual Temperature (°C)[1]	13.4	15.9	13.7	12.9	14.7	13.4	13.3	13.5
NZ Soil Classification[2]	Pumice	Ultic (Clay)	Brown	Brown	Allophanic	Pumice	Pumice	Pumice

*IB – Incomplete block design; OD – Optimal design. [1]Climate data was sourced from NIWA (2023). [2] Soil type data was sourced from Manaaki Whenua - Landcare Research (2023). Ramet/Genotype Ratio is the mean number of ramets per genotype in each trial site.

recorded (denoted as 'PBLUP-U'). Note, PBLUP(U) will be used hereafter to refer to corrected and uncorrected models collectively. See Klápště et al. (2022) for a full description on methodology for the marker-assisted correction of pedigree errors. Approximately 22% of genotypes had discrepancies in parentage when comparing the original pedigree with marker-assisted corrected pedigree. Among these individuals, ~7% of individuals had inconsistencies in the maternal data, ~80% had inconsistencies in the paternal data and ~13% had inconsistencies in both parental data. Breeding values were estimated in a single model, incorporating site and trial design effects using the ASReml-R package Version 4.2 (Butler et al., 2017). To model genotype-by-environment interaction (GxE) different models with varying complexities were tested including unstructured variance, one-factor, and two-factor analytic components (FA1 and FA2). Unstructured variance models failed to converge and were excluded from the analysis. Models were selected based on the Akaike Information Criterion (AIC) (Akaike, 1974) estimated from ASReml-R which was appropriate because all models had equal fixed effects.

2.2.1. Multiple site model

The factor analytic (FA) model was used to estimate genetic correlations and variance components across all trials following Cullis et al. (2014) and Li et al. (2018):

Equation 1

$$y = X\beta + Z_a a + Z_d d + Z_b b + e$$

Where $\boldsymbol{y}$ is a vector for a phenotypic observation for each selection criteria, $\boldsymbol{\beta}$ is a vector of fixed effects containing the overall mean and the mean for each trial site, $\boldsymbol{a}$ is a vector of random additive genetic effects, $\boldsymbol{d}$ is a vector of non-additive genetic effects, $\boldsymbol{b}$ is a vector of experimental design effects and $\boldsymbol{e}$ is a vector of random residual effects. Experimental design effects were fitted as random effects. $\mathbf{X}$, Z_a, Z_d and Z_b are known incidence matrices relating to the observations of effects for $\boldsymbol{\beta}$, $\boldsymbol{a}$, $\boldsymbol{d}$ and $\boldsymbol{b}$ respectively.

2.2.2. Additive genetic effects

In the linear mixed model, the random additive genetic effects ($\boldsymbol{a}$) were calculated as $\text{var}(\boldsymbol{a}) = \mathbf{G}_A = \boldsymbol{\Gamma\Gamma}' + \boldsymbol{\Psi} \otimes \mathbf{A}$ where $\boldsymbol{\Gamma}$ is a t x k (t = number of trials, k = number of factors) matrix of loadings on the covariance scale, $\Psi = \text{diag}[\psi i]$ is a diagonal vector of specific variances, $\otimes$ is the Kronecker product, and $\mathbf{A}$ is the average numerator relationship estimated from a pedigree and calculated in the ASReml-R package (Cullis et al., 2014; Zapata-Valenzuela, 2012). In the context of GBLUP, $\mathbf{A}$ is substituted for additive marker-based relationship matrix ($\mathbf{G}$) which was calculated in the ASRgenomics (Gezan et al., 2022) R package using the VanRaden method (VanRaden, 2008).

As an example, the representation of the matrices for a factor analytic variance-covariance structure with one factor ($k = 1$) is (Zapata--Valenzuela, 2012):

Equation 2

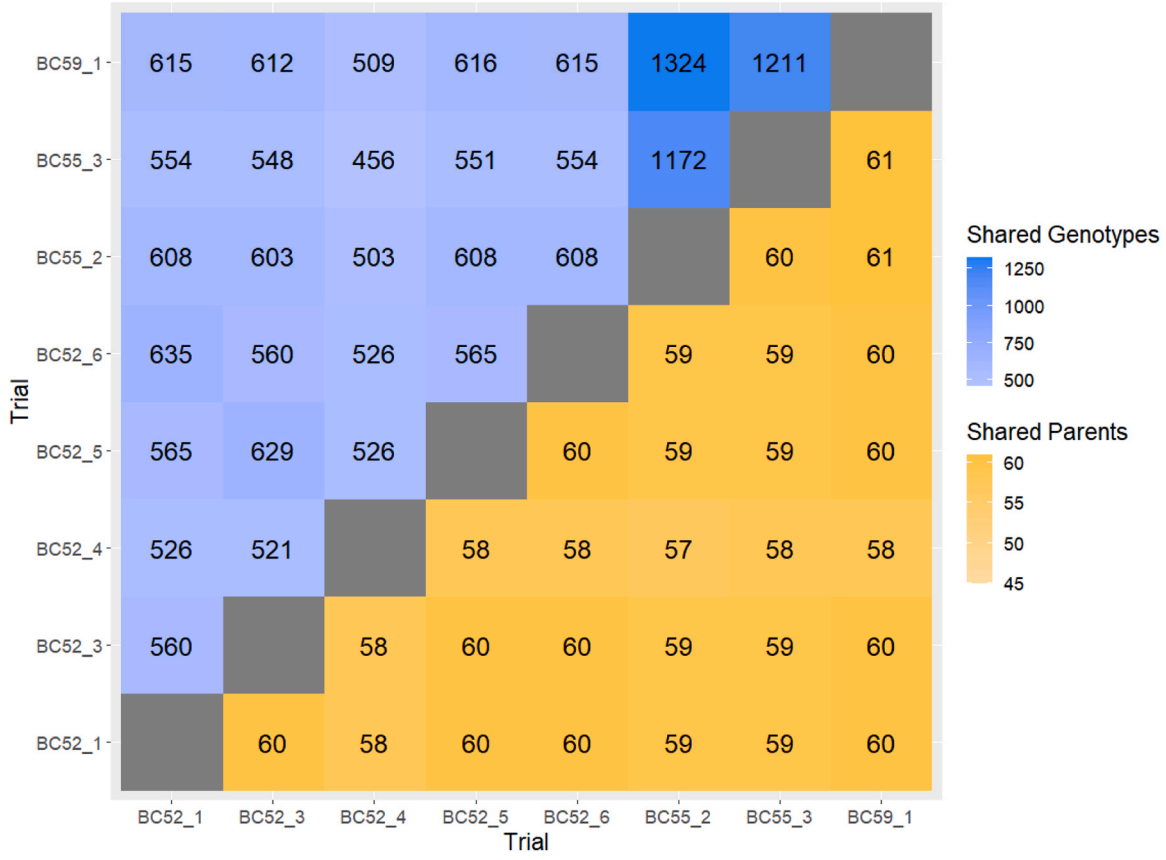

Fig. 2. Summary of concurrence of genotypes and their parents between trial sites.

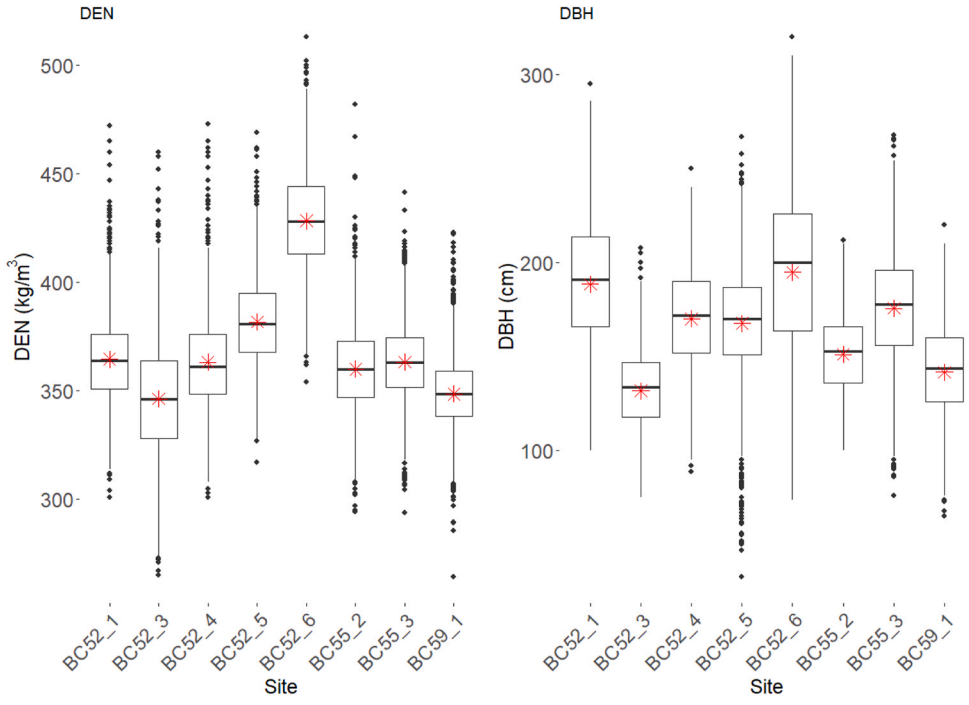

Fig. 3. Distribution of phenotypes for wood density (DEN) and DBH across each trial site. The horizontal box line and red asterisk represent the median and mean, respectively. The boxes represent the interquartile range which contains 50% of the data across each trial site.

$$\mathbf{\Gamma} = \begin{bmatrix} \lambda_1 \\ \lambda_2 \\ \cdot \\ \lambda_8 \end{bmatrix} \mathbf{\Psi} = \begin{bmatrix} \sigma^2_{c1} & 0 & \cdot & 0 \\ 0 & \sigma^2_{c2} & \cdot & 0 \\ 0 & 0 & \cdot & \cdot \\ 0 & 0 & \cdot & \sigma^2_{c8} \end{bmatrix}$$

$$\boldsymbol{G}_A = \begin{bmatrix} \sigma^2_{c1} + \lambda^2_{11} & \lambda_{11}\lambda_{12} & \bullet & \lambda_{11}\lambda_{18} \\ \lambda_{11}\lambda_{12} & \sigma^2_{c2} + \lambda^2_{12} & \bullet & \cdot \\ \bullet & \bullet & \bullet & \bullet \\ \lambda_{11}\lambda_{18} & \cdot & \bullet & \sigma^2_{c8} + \lambda^2_{18} \end{bmatrix} \otimes \mathbf{A}$$

Where λ_i is the loading of factor 1 on a covariance scale for the i^{th} site. $\sigma^2_{c_i}$ is the amount of variance explained by a clone at the i^{th} site loading of factor 1.

2.2.3. Non-additive genetic effects

In all alternative pedigree models, non-additive effects were assumed to be normally distributed with var($\boldsymbol{d}$)~N(0,$\mathbf{G}_{\text{d}} \otimes \boldsymbol{I}$), estimated with a diagonal matrix of the form $\boldsymbol{G}_d = \begin{bmatrix} \sigma^2_{d_1} & \bullet & 0 \\ \bullet & \bullet & \bullet \\ 0 & \bullet & \sigma^2_{d_8} \end{bmatrix}$ where $\sigma^2_{d_i}$ is the non-additive genetic variance for the i^{th} trial and $\boldsymbol{I}$ is the identity matrix. The diagonal structure assumes that each site has a unique non-additive variance and the non-additive effect of the same clone on different sites is independent with no correlation between the non-additive effects between sites. Although the diagonal model is simpler and more strict compared to a model using a compound symmetry structure, it consistently produced lower AIC scores (results not shown) and has been successfully employed in a similar study (Li et al., 2018).

2.2.4. Experimental design and residual effects

Experimental design effects were fitted as random terms in the model. For incomplete block designs replicates and blocks within replicates were included. In 'optimal' design trials, Prows and Pcols were nested within Psets and each Pset was nested within an Eset. Experimental design effects ($\boldsymbol{b}$) were modelled with a multivariate normal distribution of var($\boldsymbol{b}$)~N(0,$\boldsymbol{I}\sigma^2_b$), where σ^2_b is the variance component for each experimental design term. Residual effects ($\boldsymbol{e}$) were modelled with a normal distribution of var($\boldsymbol{e}$)~N(0,$\mathbf{R}\otimes\boldsymbol{I}$) where $\mathbf{R} = \begin{bmatrix} \sigma^2_{e_1} & \bullet & 0 \\ \bullet & \bullet & \bullet \\ 0 & \bullet & \sigma^2_{e_8} \end{bmatrix}$, where $\sigma^2_{e_i}$ is the residual variance for the i^{th} trial.

2.2.5. Additive genetic correlations

Additive genetic correlations were estimated directly from the factor-analytic outputs produced by ASReml-R package which can be expressed as:

Equation 3.

$$r_A = \frac{\sigma_{a_i a_j}}{\sqrt{\sigma^2_{a_i}\sigma^2_{a_j}}}$$

Where $\sigma_{a_i a_j}$is the additive genetic covariance between i^{th} and j^{th} environments, and $\sigma^2_{a_i}$ $\sigma^2_{a_j}$ is the additive genetic variance in the i^{th} and j^{th} environments.

2.2.6. Comparison of models' breeding value predictions

Spearman's rank correlation coefficient was used to analyse rank changes of genotypes' breeding values between GBLUP and PBLUP(U) models. Spearman's rank correlation (Pagano et al., 2022) is suitable for testing the changes in rank for discrete ordinal variables (genotypes) between groups (models), it is less sensitive to outlying data than Pearson's correlation coefficient (Pagano et al., 2022) because it limits outliers to the value of their rank.

2.2.7. Heritability and factor analytic variance percentage

Narrow-sense heritability (h^2_i) for trial site i was calculated as (Li et al., 2018):

Equation 4

$$h^2_i = \frac{\boldsymbol{\sigma}^2_{a_i}}{\boldsymbol{\sigma}^2_{a_i} + \boldsymbol{\sigma}^2_{na_i} + \boldsymbol{\sigma}^2_{b_i} + \boldsymbol{\sigma}^2_{e_i}}$$

Broad-sense heritability (H^2_i) for trial site i was calculated as (Li et al., 2018):

Equation 5

$$H^2_i = \frac{\boldsymbol{\sigma}^2_{a_i} + \boldsymbol{\sigma}^2_{na_i}}{\boldsymbol{\sigma}^2_{a_i} + \boldsymbol{\sigma}^2_{na_i} + \boldsymbol{\sigma}^2_{b_i} + \boldsymbol{\sigma}^2_{e_i}}$$

Where $\boldsymbol{\sigma}^2_{a_i}$ is the diagonal element of $\mathbf{G}_{\text{A}}$ for the i^{th} trial, $\boldsymbol{\sigma}^2_{na_i}$ is the diagonal element of $\mathbf{G}_{\text{d}}$ for the i^{th} trial, $\boldsymbol{\sigma}^2_{b_i}$ is the design effects for the i^{th} trial and $\boldsymbol{\sigma}^2_{e_i}$ includes the diagonal element of $\mathbf{R}$. The means of each of trial was used to calculate heritabilities for multiple environments.

The percentage variance explained by k factors at each site (v_{a_i}) was calculated from equations given by (Smith et al., 2015):

Equation 6

$$v_{a_i} = 100\frac{\sum_{r=1}^{k}\lambda^2_{r_i}}{\sum_{r=1}^{k}\lambda^2_{r_i} + \sigma^2_{c_i}}$$

λ_{ri} is the loading for i^{th} site and r^{th} factor $\sigma^2_{c_i}$ is the amount of variance explained by a clone at the i^{th} site loading of factor 1.

2.2.8. Breeding value accuracy

The accuracy of estimated breeding values was estimated using prediction error variance (PEV) and additive genetic variance by trait obtained from the standard output of the ASReml-R analysis as follows:

Equation 7

$$r = \sqrt{1 - \frac{\text{PEV}}{\boldsymbol{\sigma}^2_a}}$$

3. Results

3.1. Model statistics

Overall, FA2 models provided a better fit for DBH compared with FA1 models based on AIC scores and this was used for the rest of the analysis for both selection criteria (Fig. 4) (see Appendix 1 for a full summary). There was no difference between FA1 and FA2 models for DEN.

Marker-based models (GBLUP) had a better fit compared with marker-corrected (PBLUP) and uncorrected pedigree-based models (PBLUP-U) indicating that they are more likely to accurately capture GxE interaction. As expected, the marker-corrected pedigree improved the model fit over uncorrected pedigree-based models. The difference in AIC between additive-only and additive + non-additive models was marginal and varied between model/selection criteria combinations. In DBH GBLUP, the inclusion of non-additive components slightly improved the model fit, whereas in DEN GBLUP the difference model fit between additive-only and additive + non-additive models was negligible. However, when including the pedigree, additive-only models had a better fit compared to additive + non-additive models for both selection criteria. In this study, the benefit of including non-additive effects in

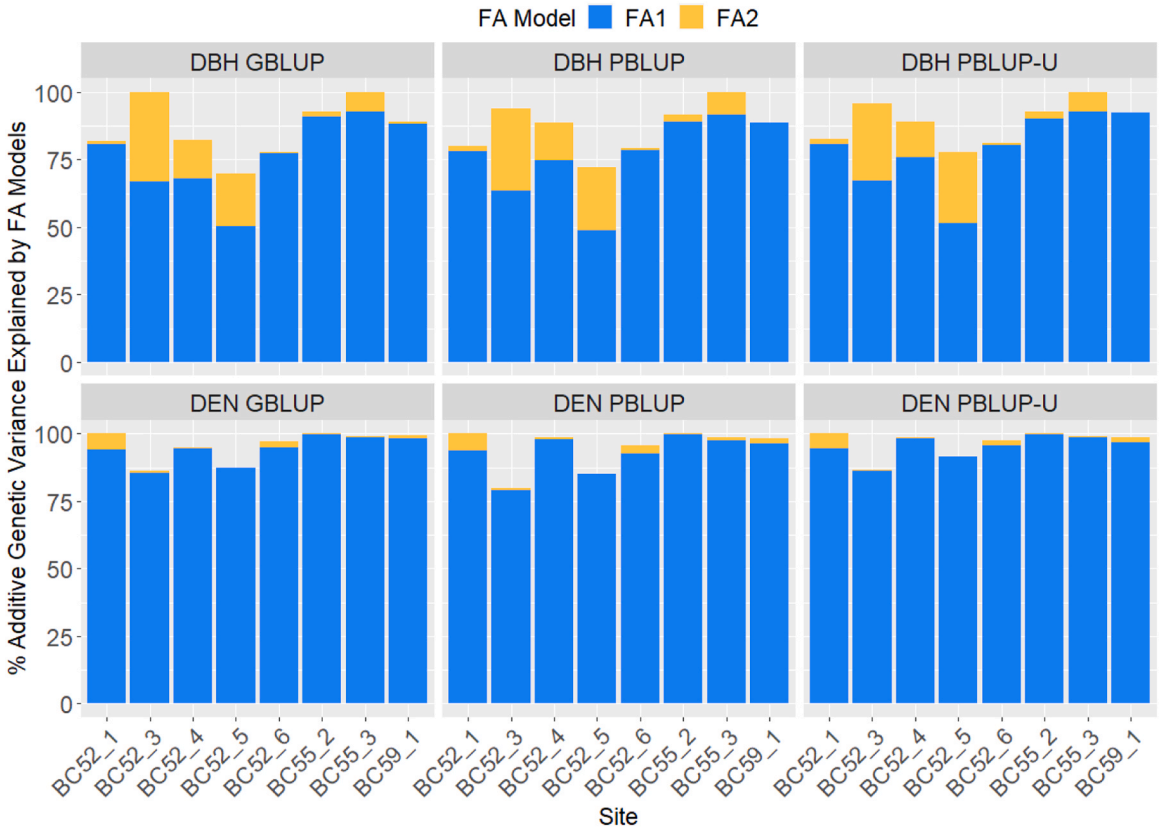

Fig. 4. Percentage of additive variance explained in each site by factor analytic models.

the model did not make a significant difference to improve the characterisation of GxE.

3.2. Variance components and GxE summary

BC52_3 was the only site that had more variance explained by FA2 for DBH in both models compared to DEN (Fig. 4). Increasing the number of k factors from 1 to 2 (FA1 to FA2) did not explain much extra additive genetic variance for DEN (range ~ 0.4–6%) in both marker-based and pedigree-based models. In contrast, increasing the k factors from 1 to 2 explained a greater proportion of additive genetic variance for DBH (range ~ 0.5–30.3%) in both model types. It is evident in trials BC52_3, BC52_4 and BC52_5 (non-pumice soil sites) that the second factor captured an unknown latent variable which explained a significantly greater proportion of additive genetic variance for DBH compared to the other five sites. Increasing the number of k factors also slightly increased the range of additive genetic correlation estimates for DBH (results not shown).

The estimates of additive genetic variance (σ^2_a), narrow-sense heritability (h^2) and broad-sense heritability (H^2), and breeding value accuracy (r) decreased in the following order: uncorrected pedigree-based model, marker-corrected pedigree-based model and marker-based model (Table 2). Breeding value accuracy was lower when using additive + non-additive models compared to additive models. Marker-based models for DBH had a slightly higher range of correlation (r_A) between sites compared to uncorrected pedigree-based models. This was more pronounced when using both additive and non-additive variance components in the model. Estimates of non-additive genetic variance (σ^2_{na}) were higher in DBH compared to DEN, however, in comparison to additive variance (σ^2_a) it was small. Additive-only models had a slightly

Table 2
Summary of variance components for FA2 multi-environment analysis.

Model	[1]SC	h^2 (SE)	H^2 (SE)	σ^2_a	σ^2_{na}	σ^2_e	r_A (A)	r_A (ANA)	r (A)	r (ANA)
GBLUP	**DBH**	0.20 (0.003)	0.22 (0.003)	184.92	17.65	709.24	0.76 (0.56–0.95)	0.74 (0.53–0.94)	0.81	0.77
PBLUP	**DBH**	0.23 (0.003)	0.25 (0.004)	222.16	14.35	709.00	0.76 (0.53–0.95)	0.73 (0.47–0.94)	0.84	0.80
PBLUP-U	**DBH**	0.25 (0.004)	0.27 (0.004)	247.92	16.83	708.62	0.78 (0.55–0.96)	0.75 (0.48–0.95)	0.86	0.83
GBLUP	**DEN**	0.48 (0.005)	0.50 (0.005)	201.45	7.64	212.64	0.94 (0.86–0.99)	0.93 (0.84–0.99)	0.92	0.91
PBLUP	**DEN**	0.50 (0.005)	0.52 (0.005)	221.59	5.25	212.71	0.92 (0.82–0.99)	0.91 (0.81–0.99)	0.92	0.91
PBLUP-U	**DEN**	0.53 (0.005)	0.55 (0.005)	252.32	9.57	212.85	0.95 (0.88–0.99)	0.92 (0.84–0.99)	0.93	0.92

Note: [1]SC = selection criteria, σ^2_a = additive variance, σ^2_{na} = non-additive variance, σ^2_e = residual variance, SE= standard error, r_A = mean additive genetic correlation between sites and r = breeding value accuracy where (A) = additive component only model and (ANA) = additive + non-additive variance component model. Standard errors for heritabilities are given in parentheses.

higher range of genetic correlation between sites compared to models that included non-additive components. Narrow-sense and broad-sense heritability estimates varied considerably from trial to trial (Fig. 5). Marker-based models produced lower narrow-sense and broad-sense estimates of heritability in every trial site for both selection criteria compared to pedigree-based models. A full table of variance components for individual trial sites is provided in Appendix 2.

3.3. Genetic correlations among sites

Shelbourne (1972) proposed a threshold of 0.7 when evaluating whether a genetic correlation is practically significant. When examining the marker-based models only two of the eight trials for DBH fell below the threshold (Fig. 6). With DBH, sites can be split into two groupings those that benefited from the second factor (BC52_3, BC52_4 & BC52_5) and the remainder that did not. The GxE between these two clusters could indicate that the second factor explains an unknown latent environmental variable that is correlated with DBH. The only trial in the South Island of New Zealand (BC52_5, Marlborough Region) had the lowest genetic correlations for both DBH and DEN compared to the 7 other trials that were in the North Island (Fig. 6). There was a pattern of correlation between the sites planted in later years with optimal design layouts (BC55_2, BC55_3 and BC59_1). These sites had the highest additive genetic correlations between each other and were geographically proximate.

Spearman's rank correlation (r_s) was used to test the ranking differences between each model within each selection criteria (Table 3). Both selection criteria had a very high and significant ($p<0.05$) r_s value between all models. DEN had a range of 0.98–1 r_s and DBH had a range of 0.96–0.99 r_s when comparing genomic and pedigree-based models. There were no rank changes between marker-corrected pedigree and uncorrected pedigree models or between additive-only and additive + non-additive models ($r_s \sim 1$). This finding suggests that the same individuals would be selected regardless of whether the pedigree is corrected, or non-additive variance components are included or not.

4. Discussion

4.1. GxE in New Zealand radiata pine

Investigating the extent of GxE interaction for radiata pine in New Zealand is required to guide selection and deployment strategies. The material used in this study was made up of eight cloned full-sib progeny trials across some of the main radiata pine growing regions in New Zealand. Progeny were derived from a diverse genetic base of 61 parents, which is crucial for estimating GxE at the population level. Such well-connected RPBC clonal breeding data have not been available for GxE analysis in New Zealand previously. This study found that additive genetic correlations in marker-based models were moderate to high (mean = 0.76, range = 0.56–0.95) in DBH and high in DEN (mean = 0.94, range = 0.86–0.99).

Genetic correlations between trial sites were higher than most reported in the literature (Carson, 1991; Cullis et al., 2014; Johnson and Burdon, 1990; Li et al., 2018; McDonald and Apiolaza, 2009). Growth traits tend to have a higher GxE compared to wood quality traits (Apiolaza, 2012), however, most studies that report high GxE for growth traits have also had poor connectedness between trials. Simulation studies have found that at least 30% of clones or 50 families (with 10 sibs per family) need to be in common between environments to accurately estimate GxE and lower connectedness leads to lower estimates of genetic correlations and higher standard errors (Li et al., 2018).

Cullis et al. (2014) reported significant GxE with a mean correlation of 0.54 and 25% of correlations being lower than 0.37 in New Zealand and Australia. However, the 77 trials (including some sites in Australia) in the Cullis et al. (2014) study were poorly connected and spanned multiple breeding generations, with the majority of trial pairs having no

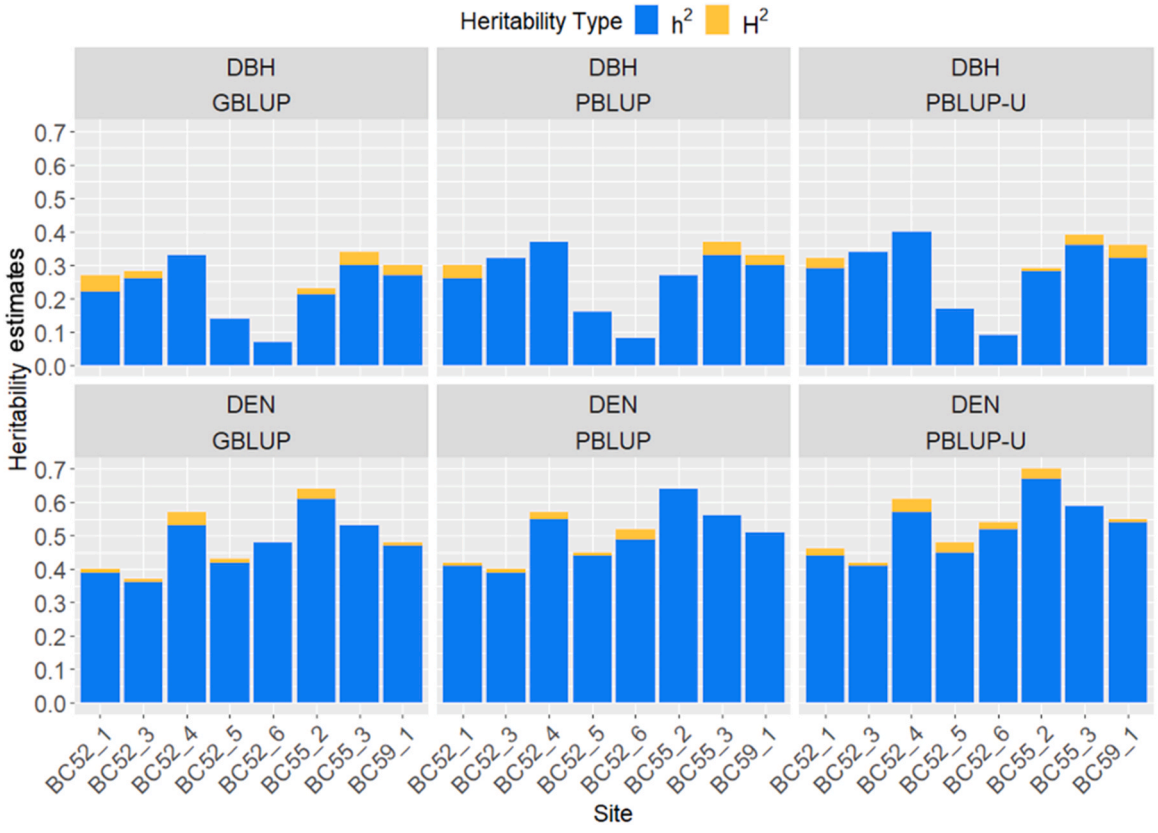

Fig. 5. Summary of heritability estimates across different trial sites.

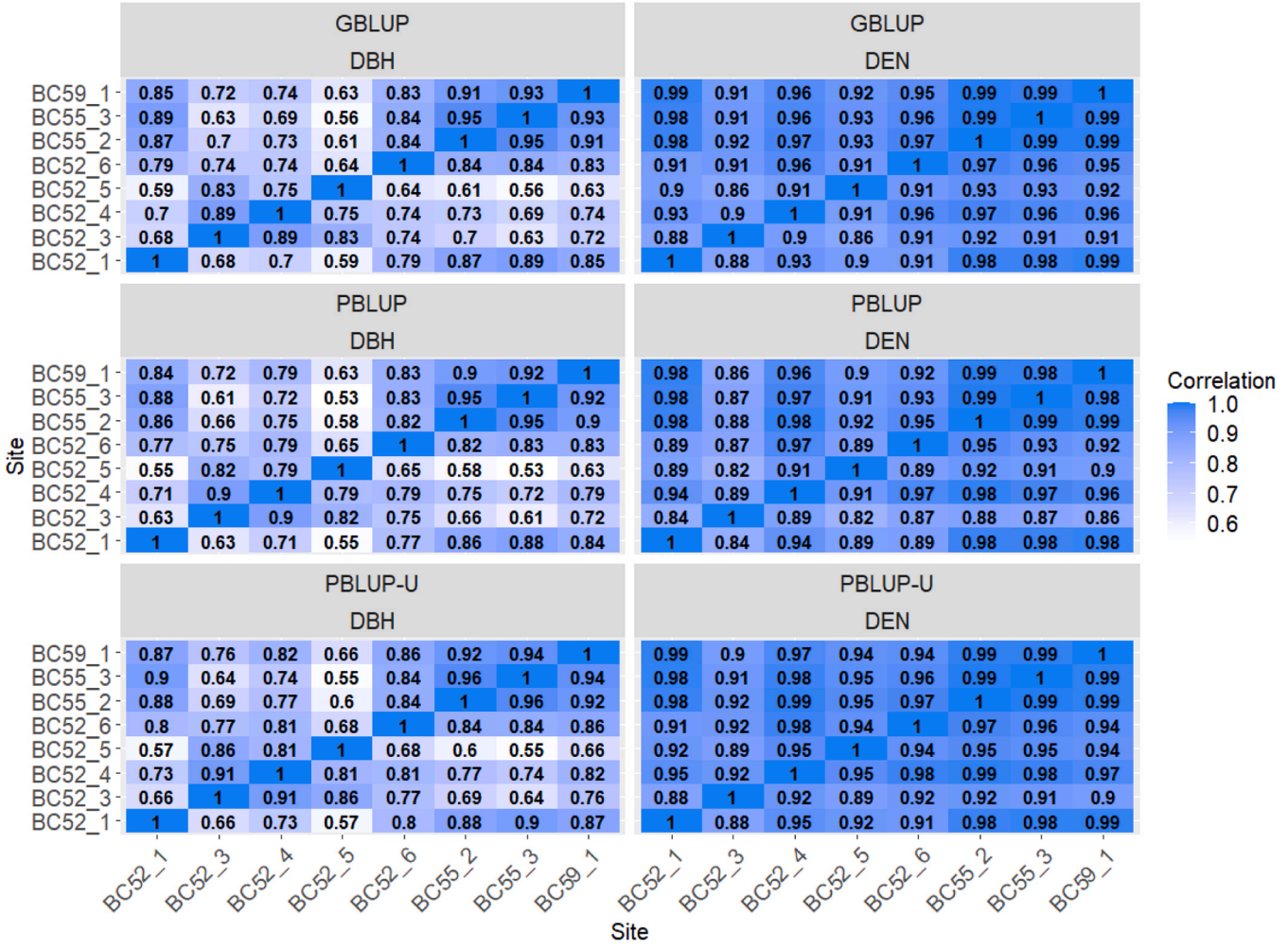

Fig. 6. Additive genetic correlations between sites.

Table 3
Spearman's rank correlations for rankings using different genetic evaluation models.

Model	GBLUP_A	GBLUP_ANA	PBLUP_A	PBLUP_ANA	PBLUP-U_A	PBLUP-U_ANA
GBLUP_A		0.9996	0.9644	0.9642	0.9644	0.9642
GBLUP_ANA	0.9999		0.9669	0.9669	0.9669	0.9669
PBLUP_A	0.9876	0.9876		0.9998	1.0000	0.9998
PBLUP_ANA	0.9876	0.9877	1.0000		0.9998	1.0000
PBLUP-U_A	0.9876	0.9876	1.0000	1.0000		0.9998
PBLUP-U_ANA	0.9876	0.9877	1.0000	1.0000	1.0000	

Note: DBH is represented in the upper diagonal and DEN is represented in the lower diagonal. 'ANA' = additive + non-additive model, 'A' = additive only model

parents in common. Stem volume, which is the breeding objective trait linked to DBH, has been reported to have a genetic correlation range of 0.16–0.96 across four sites in the North Island (Johnson and Burdon, 1990) The largest GxE study for radiata pine in New Zealand across 76 trials found that GxE interaction for DBH was significant, with a genetic correlation range of −0.8–1 with a mean of 0.49 (McDonald & Apiolaza, 2009). When the dataset used by McDonald and Apiolaza (2009) was filtered to a threshold of 50 families in common (17 out of 76 environments), it raised the mean genetic correlation from 0.49 to 0.60, which is closer to estimates in our study. Analysis of three trials in New Zealand with very high connectedness (87% clones in common) had a mean correlation of 0.82 (Baltunis & Brawner, 2010).

4.2. *Regionalising breeding and deployment programs*

Regionalised breeding has been successfully implemented for native loblolly pine (*Pinus taeda*) in the South-Eastern United States (Isik and McKeand, 2019) and native white spruce in Canada (*Picea glauca*) (Cappa et al., 2022; Weng et al., 2019). According to this study, the levels of GxE interactions were not high enough to justify the regionalisation for the North Island deployment area. More trials from the South Island would need to be included to draw conclusions for the entire country. To justify regionalised breeding, there is a requirement for consistent evidence of low correlation between clusters of environmental variables or regions, evidence of improved genetic gain and a greater cost-benefit to the wider industry or breeding program. Detailed economic analysis and genetic gain comparisons were beyond the scope of this study. The Cullis et al. (2014) study, which included trials from

NZ and New South Wales in Australia, showed low correlations between poorly connected trials. Further, there was no obvious clustering of trials based on geography. Studies with high GxE for DBH found that regionalizing the radiata pine breeding program would come at a significant economic cost and would require smaller regional breeding populations with lower selection intensity and less genetic gain compared to a single national program (Carson, 1991). Johnson and Burdon (1990) found evidence of high GxE between clay soils in Northland and pumice soils of the Central North Island but regionalising the breeding program to accommodate this would result in a genetic gain increase from 22% to 24% with a significant economic cost. In Australia, regionalising radiata pine breeding programs between high and genetic gains were almost double in a regionalised program compared to a national program. However, this study did not include an economic analysis (Wu and Matheson, 2005).

Regional breeding values obtained from a nationwide breeding program's multi-environmental data can be used to select seed orchard parents and genotypes for somatic embryogenesis (SE) in regionalised deployment. Regionalised deployment may be more pragmatic than regionalised breeding if control-pollinated seedlots and/or clonal deployment are utilised instead of open-pollinated seedlots (Johnson and Burdon, 1990). This is because control-pollinated seedlots are created by selection of both seed orchard's parents that have high breeding values for a targeted environment (e.g for disease-prone regions). GS-led deployment (with early prediction of unknown phenotypes) has been shown to significantly improve genetic gain in simulation-based studies in seed orchard and clonal deployment pathways (McLean et al., 2023). This information can be used to select parental combinations based on regionalised breeding values in a control-pollinated orchard. Genotypes recovered through SE (Walter et al., 2005) can be tested directly in specific forest estates, which allows for better evaluation of highly-specific local adaptations compared to seed orchard deployment (Carson, 1986). Scaling up the propagation and establishment of locally-tested SE clones can be used to exploit both non-additive genetic and GxE effects, particulary for growth. Genomic selection of somatic embryogenesis clones is often used at the tissue culture phase to decide which genotypes are cryo-banked before further field testing. This takes advantage of high selection intensity and within-family selection from mendelian sampling term estimates. Clonal deployment with GS and no field testing is feasible in theory but has never been implemented because of the financial risk of clonal growth defects such as resin bleeding or internal checking (McLean et al., 2023). However, clonal deployment might be more suitable for regionalised deployment compared to seed orchard options.

4.3. Characterising environmental variables

The use of an extra factor explained a large proportion of extra additive genetic variance for three of the sites. These three sites had a higher correlation amongst each other and were less correlated to those that did not benefit from the second factor. These three sites were quite geographically separated from the remaining sites situated in the North Island and were situated in non-pumice soil regions.

Factor analytic models use unknown latent factors, so genotype-by-environment is observable rather than predictable. Incorporating environmental covariates into the mixed-linear model could make genotype-by-environment predictable (Callister et al., 2024; Tolhurst et al., 2022), which could enhance genetic gain in deployment if environments are matched with genotypes (Dutkowski et al., 2016). It has been established that wood density has a positive relationship with average site temperature e.g. as observed by the latitudinal gradient in NZ, and the inclusion of site temperature increases the fit of a multi-environment model (Apiolaza, 2012). It has also been suggested that total rainfall, minimum and maximum temperatures are the biggest environmental drivers of DBH (Gapare et al., 2015; McDonald and Apiolaza, 2009). Studies in loblolly pine have shown that factor loadings had strong associations with temperature and rainfall that moved across a geographical gradient in the southeastern region of the United States of America (Lauer et al., 2021; Shalizi and Isik, 2019). Currently the RPBC tests material in New South Wales and Tasmania in Australia. Extending this study with a factor analysis to include Australia and more sites across the South Island could determine whether there is a significant interaction between the two countries or between the North and South Island. An extended factor analysis that includes well-connected trials and environmental information such as rainfall, temperature, and soil types across multiple trials may help determine the latent factors that drive GxE and better inform future regional deployment.

4.4. GxE and genomics

When phenotypic information and genomic information is available we found that marker-based models appear to provide a slightly better fit (based on AIC) compared to uncorrected pedigree-based models for this dataset. Unlike marker-based relationship matrices, pedigree-based relationships do not account for the Mendelian sampling term or historical connectedness and this can result in biased estimates of GxE and inflated additive variance estimation (Beaulieu et al., 2022). The inflated additive variance estimation likely overinflated breeding value accuracy and reliability for pedigree-based models in this study. In a small GxE study (two environments) of Norway spruce (*Picea abies*) AIC values were similar in marker-based and pedigree-based models (Chen et al., 2019). However, in a study of white spruce studies using four environments, AIC values indicated that GBLUP models had a better fit compared to pedigree-based models for most selection criteria (Beaulieu et al., 2020; Walker et al., 2022).

It is notable that the comparison between marker- and pedigree-based models in estimating GxE and variance components is dependent on numerous factors including the number of families/progenies, the number of environments, presence of pedigree errors and the reliability/density of SNPs. In this study the presence of errors in the uncorrected pedigree reduced the model fit and overestimated variance components as compared to a corrected-pedigree model. We found that heritability estimates decreased when moving from uncorrected pedigree models to marker-corrected pedigree models, and further decreased when using a marker-based model. This agrees with other radiata pine studies (Li et al., 2019) and meta-analyses of conifers (Beaulieu et al., 2022). Research on the same population used in this study has shown that correcting the pedigree information can increase the accuracy of a pedigree-based relationship matrix (PBLUP) model by 0.07 (Klápště et al., 2022). This improvement in accuracy has been shown to enhance the reliability of using a SNP-corrected pedigree-BLUP model to analyse genotype-by-environment interactions (GxE). Other studies have used single-step BLUP models to combine pedigree and marker information to estimate GxE in lodgepole pine (*Pinus contorta*) and this could also be evaluated in radiata pine (Ukrainetz and Mansfield, 2020). The ability to predict breeding values in an environment where phenotypes are unknown, using genomic and phenotypic information from another environment, is closely correlated with Type-B correlations (Gamal El-Dien et al., 2015), and SNP density is closely linked with predictive ability (Klápště et al., 2022). Therefore, further research could examine the link between SNP density and GxE.

GxE has been characterised in numerous conifer breeding programs. Genomics with or without phenotypes can be used to estimate genetic correlations between environments or to identify SNP effects that change between environments. In radiata pine, SNP associations with selection criteria of interest have been shown to be significant in some environments but not in others (Li et al., 2016). In interior spruce situated in Canada, multi-site models with GxE accounted for produced higher prediction accuracies for growth and wood quality selection criteria compared to a single site model when predicting phenotypes in different sites (Gamal El-Dien et al., 2015). In Norway spruce, genomic-estimated GxE was found to be moderate for growth selection

criteria (r_g = 0.52–0.56) and high for multi-trait growth/wood quality (r_g <0.43) between two different sites in Canada (Lenz et al., 2020).

4.5. GxE and non-additive variance

The benefit of including non-additive genetic variance components was marginal in marker-based models and worsened the fit of pedigree-based models. A higher degree of non-additive genetic variance was identified in low-heritability DBH compared to high-heritability DEN which is consistent with other research (Burdon et al., 1992). However, non-additive genetic variance components only accounted for 8.7% and 3.6% of the total genetic variance for DBH and DEN in marker-based models, respectively. Disentangling epistatic and dominance variance from additive variance accurately usually relies on mating design, well replicated trials with an extensive number of genotypes with the inclusion of genotyped/phenotyped parents. In radiata pine, dominance has been found to be fairly negligible past the age of seven (Dean et al., 2006). Other studies have found that the inclusion of dominance slightly improved the AIC and predictive ability in GxE marker-based models. However, significant dominance effects were predicted in one site whereas the other had limited dominance effects (Chen et al., 2019). In this study, no site demonstrated any significant non-additive genetic effects. However, it must be noted that this study was limited by small family sizes to estimate non-additive effects well.

5. Conclusions

This study used a well-connected, replicated dataset across multiple trial sites to assess the level of GxE to inform radiata pine breeding program and deployment strategies. We found that GxE was low-moderate in DBH and low in DEN when using marker-based models. Poor representation of target environments may result in poor prediction models if GxE is present. While GxE is present, its magnitude does not warrant a regionalised breeding strategy for the North Island deployment area. However, this does not exclude the use of regionalised deployment, which is a more pragmatic approach to manage GxE in NZ radiata pine. Clonal (SE) deployment can more easily exploit GxE than family forestry as it can utilise clonal testing and maximise gain over a local scale. Marker-based models had only a marginally better fit compared to marker-corrected and uncorrected pedigree-based models. The inclusion of non-additive genetic effects had no major impact on the model and did not cause changes in genotype rank. Future research could focus on identifying the underlying environmental variables that drive GxE in radiata pine to improve GS evaluation models and better inform deployment decisions.

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CRediT authorship contribution statement

Jaroslav Klápště: Conceptualization, Formal analysis, Methodology, Project administration, Supervision, Writing – review & editing. **Duncan McLean:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Mark Paget:** Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **Luis A. Apiolaza:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare no conflict of interest.

Data availability

The data that has been used is confidential.

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Ethical approval

Not required.

Appendix

Appendix 1 Summary of Model Fit Statistics with Different Additive Variance-Covariance Structures and Non-Additive Variance Components

Selection Criteria	Model	Additive Model	Non-Additive Component (Y/N)	AIC	Log-likelihood
DBH	GBLUP	FA1	Y	159,254.1	-79,576.03
DBH	GBLUP	FA1	N	159,207.5	-79,545.76
DBH	GBLUP	FA2	Y	159,207.5	-79,545.76
DBH	GBLUP	FA2	N	159,209.0	-79,554.49
DBH	PBLUP	FA1	Y	159,268.3	-79,583.16
DBH	PBLUP	FA1	N	159,270.9	-79,592.44
DBH	PBLUP	FA2	Y	159,231.3	-79,557.63
DBH	PBLUP	FA2	N	159,224.8	-79,562.41
DBH	PBLUP-U	FA1	Y	159,342.0	-79,619.97
DBH	PBLUP-U	FA1	N	159,351.4	-79,632.70
DBH	PBLUP-U	FA2	Y	159,304.7	-79,595.37
DBH	PBLUP-U	FA2	N	159,302.3	-79,602.14
DEN	GBLUP	FA1	Y	115,460.7	-57,679.35
DEN	GBLUP	FA1	N	115,458.6	-57,686.28
DEN	GBLUP	FA2	Y	115,459.0	-57,671.48
DEN	GBLUP	FA2	N	115,458.0	-57,679.01
DEN	PBLUP	FA1	Y	115,494.5	-57,696.24
DEN	PBLUP	FA1	N	115,484.9	-57,699.45
DEN	PBLUP	FA2	Y	115,488.6	-57,686.32
DEN	PBLUP	FA2	N	115,480.9	-57,690.46
DEN	PBLUP-U	FA1	Y	115,621.1	-57,759.55
DEN	PBLUP-U	FA1	N	115,618.9	-57,766.45

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Selection Criteria	Model	Additive Model	Non-Additive Component (Y/N)	AIC	Log-likelihood
DEN	PBLUP-U	FA2	Y	115,617.3	-57,750.65
DEN	PBLUP-U	FA2	N	115,615.2	-57,757.62

Appendix 2 – Summary of Variance Components for Different Models and Selection Criteria for Each Site

Model	SC	Site	h^2	H^2	σ_a^2	σ_{na}^2	σ_e^2
GBLUP	DBH	BC59_1	0.27 (0.006)	0.30 (0.007)	163.08	22.65	424.43
GBLUP	DBH	BC52_1	0.22 (0.009)	0.27 (0.011)	281.13	53.19	931.37
GBLUP	DBH	BC52_3	0.26 (0.008)	0.28 (0.008)	138.62	11.86	384.19
GBLUP	DBH	BC52_4	0.33 (0.008)	0.33 (0.008)	294.57	0.00	593.65
GBLUP	DBH	BC52_5	0.14 (0.009)	0.14 (0.010)	119.69	3.83	757.77
GBLUP	DBH	BC52_6	0.07 (0.003)	0.07 (0.003)	126.45	0.00	1674.66
GBLUP	DBH	BC55_2	0.21 (0.006)	0.23 (0.007)	89.84	12.08	332.47
GBLUP	DBH	BC55_3	0.30 (0.008)	0.34 (0.009)	266.00	37.55	575.38
PBLUP	DBH	BC59_1	0.30 (0.010)	0.33 (0.010)	187.92	25.12	423.80
PBLUP	DBH	BC52_1	0.26 (0.021)	0.30 (0.022)	343.04	44.47	932.62
PBLUP	DBH	BC52_3	0.32 (0.011)	0.32 (0.011)	181.47	0.00	384.30
PBLUP	DBH	BC52_4	0.37 (0.014)	0.37 (0.015)	355.28	0.00	600.47
PBLUP	DBH	BC52_5	0.16 (0.012)	0.16 (0.013)	143.07	3.58	757.61
PBLUP	DBH	BC52_6	0.08 (0.016)	0.08 (0.016)	136.83	3.06	1666.64
PBLUP	DBH	BC55_2	0.27 (0.012)	0.27 (0.012)	119.90	3.69	330.42
PBLUP	DBH	BC55_3	0.33 (0.008)	0.37 (0.008)	309.76	34.88	576.15
PBLUP-U	DBH	BC59_1	0.32 (0.010)	0.36 (0.010)	211.04	30.96	423.60
PBLUP-U	DBH	BC52_1	0.29 (0.021)	0.32 (0.022)	390.77	50.91	933.06
PBLUP-U	DBH	BC52_3	0.34 (0.009)	0.34 (0.009)	203.84	0.00	384.47
PBLUP-U	DBH	BC52_4	0.40 (0.013)	0.40 (0.013)	395.61	0.00	600.39
PBLUP-U	DBH	BC52_5	0.17 (0.013)	0.17 (0.014)	152.42	7.88	757.43
PBLUP-U	DBH	BC52_6	0.09 (0.017)	0.09 (0.018)	157.39	0.59	1663.91
PBLUP-U	DBH	BC55_2	0.28 (0.012)	0.29 (0.012)	126.03	7.83	332.03
PBLUP-U	DBH	BC55_3	0.36 (0.008)	0.39 (0.008)	346.23	36.45	574.08
GBLUP	DEN	BC59_1	0.47 (0.007)	0.48 (0.008)	123.64	4.82	137.02
GBLUP	DEN	BC52_1	0.39 (0.010)	0.40 (0.011)	126.32	6.32	201.55
GBLUP	DEN	BC52_3	0.36 (0.009)	0.37 (0.009)	176.65	8.24	303.46
GBLUP	DEN	BC52_4	0.53 (0.009)	0.57 (0.009)	281.34	21.48	247.86
GBLUP	DEN	BC52_5	0.42 (0.011)	0.43 (0.011)	169.74	4.18	229.15
GBLUP	DEN	BC52_6	0.48 (0.003)	0.48 (0.003)	224.41	2.67	225.99
GBLUP	DEN	BC55_2	0.61 (0.007)	0.64 (0.007)	312.17	13.42	189.66
GBLUP	DEN	BC55_3	0.53 (0.009)	0.53 (0.010)	197.34	0.00	166.44
PBLUP	DEN	BC59_1	0.51 (0.010)	0.51 (0.010)	142.18	1.13	136.27
PBLUP	DEN	BC52_1	0.41 (0.022)	0.42 (0.022)	141.05	4.13	202.50

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Model	SC	Site	h^2	H^2	σ^2_a	σ^2_{na}	σ^2_e
PBLUP	DEN	BC52_3	0.39 (0.012)	0.40 (0.013)	193.91	6.30	303.04
PBLUP	DEN	BC52_4	0.55 (0.013)	0.57 (0.013)	314.29	14.55	248.49
PBLUP	DEN	BC52_5	0.44 (0.012)	0.45 (0.013)	184.96	2.93	229.32
PBLUP	DEN	BC52_6	0.49 (0.015)	0.52 (0.016)	232.00	12.93	226.81
PBLUP	DEN	BC55_2	0.64 (0.011)	0.64 (0.011)	348.93	0.00	189.34
PBLUP	DEN	BC55_3	0.56 (0.008)	0.56 (0.008)	215.41	0.00	165.90
PBLUP-U	DEN	BC59_1	0.54 (0.007)	0.55 (0.008)	163.71	1.01	136.35
PBLUP-U	DEN	BC52_1	0.44 (0.011)	0.46 (0.012)	162.44	4.66	203.06
PBLUP-U	DEN	BC52_3	0.41 (0.009)	0.42 (0.009)	223.93	6.50	303.24
PBLUP-U	DEN	BC52_4	0.57 (0.009)	0.61 (0.009)	351.00	22.66	248.49
PBLUP-U	DEN	BC52_5	0.45 (0.011)	0.48 (0.012)	199.11	12.03	229.24
PBLUP-U	DEN	BC52_6	0.52 (0.003)	0.54 (0.003)	268.86	12.80	227.07
PBLUP-U	DEN	BC55_2	0.67 (0.008)	0.70 (0.008)	403.08	16.91	189.31
PBLUP-U	DEN	BC55_3	0.59 (0.009)	0.59 (0.010)	246.39	0.00	166.06

Note: SC = selection criteria, σ^2_a = additive variance, σ^2_{na} = non-additive variance, σ^2_e = residual variance, r_A (A) = mean additive genetic correlation between sites for model with additive variance components only (range in parentheses), r_A (ANA) = mean additive genetic correlation between sites for model with both additive variance and non-additive components (range in parentheses). Standard errors for heritabilities are given in parentheses.

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