Phenotypic assessment and quantitative genetic analysis of two Douglas-fir progeny tests

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EXECUTIVE SUMMARY

Two Douglas-fir progeny trials planted in Kaingaroa and Gowan Hill in 1996 were assessed in 2007 and re-assessed in February 2017. These two progeny trials are also training populations in a genomic selection project for Douglas-fir. A portion of the selections made after the 2007 assessment at Gowan Hill were no longer acceptable in terms of tree form, especially for stem straightness. Therefore an additional re-assessment was proposed to update knowledge of the quality of trees at these sites.

Information on the heritability for DBH and stem straightness at both sites indicated that good genetic gains will be achieved for these traits. Selection for improved needle retention would be possible by indirect selection using DBH because of a high genetic correlation between these two traits. Generally, genetic correlations between DBH and tree form indicated that selecting for tree growth does not result in improved tree form. Considerable differences among the performance of provenances were observed for all traits at both sites. Oregon and Washington provenances showed superior quality for an overall breeding goal compared with Californian provenances. Genotype by environment interaction was noticeable for DBH and stem straightness.

Application of genomic selection is expected to increase accuracy of selections from this population, which were highest at 0.65 for stem straightness at Gowan Hill using pedigree-based methods. Genetic correlations between traits at age 11 years and again at age 21 years indicated that age11 year data are adequate for selecting the next generation of trees. Only a limited amount of additional information for genetic evaluation was obtained at age 21 years. However, this study, produced a considerable amount of new information for planning a Douglas-fir breeding strategy regarding early selection (age 11 years), genetic associations of selection criteria and provenance performances that can be utilised in future work.

INTRODUCTION

The Douglas-fir breeding programme in New Zealand is in its second generation. Four breeding targets were agreed upon at the Specialty Wood Products (SWP) breeding workshop held in June 2016 at Christchurch. These targets were: growth, form, stiffness, and needle retention, (i.e. resistance to Swiss Needle Cast (SNC)). Estimated heritabilities for these four traits are generally moderate, so there is good potential for genetic improvement (Dungey et al., 2012).

Two Douglas-fir progeny trials were planted in Kaingaroa (Central North Island) and Gowan Hill (Southland) in 1996. They were assessed in 2007 and were re-assessed in February 2017. These two progeny trials also form part of the training populations in a genomic selection project for Douglas-fir. These re-assessments were conducted to provide updated phenotypic data for the genomic selection training populations and also to undertake re-selections at Gowan Hill. These re-assessments and the re-selection focused on the breeding targets of growth and form. Stiffness was not re-assessed because data collected from previous assessments made on 12-year-old trees at Kaingaroa and on 11-year-old trees at Gowan Hill were still considered valid.

A third site in this series was planted in Golden Downs in 1996 (and selected at age 11 years). This site was inspected in May 2017 to see if any further assessments/selection were required. The results of this inspection are reported separately (Stovold, 2017). It was concluded that no further assessments/selections were needed at this site but a follow-up on progeny testing of the parents was recommended.

The genetic data collected during the re-assessment were analysed to obtain estimates of breeding values and genetic parameters as well as predicting genotype by environment interactions. These data was also used to estimate age-age genetic correlations.

The aim of this report is to: (1) estimate heritability and genetic correlations between traits within each site; (2) estimate genetic correlations between the sites to determine any indication of a genotype by environment interaction; and (3) investigate how differences between the latitudes of origin of the tree material at the two sites may affect growth and form. This work will produce estimates of BLUP breeding values that can be used to create the next generation of Douglas-fir.

METHODS

The material used to plant the Kaingaroa and Gowan Hill trials in 1996 was collected from populations in three States (California, Oregon and Washington State) along the western coast of the USA that ranged in latitude from 36° to 48° N (Dungey et al., 2012). Tree diameter at breast height (DBH) was measured at ages 11 (DBH11) and 21 years (DBH21). Trees were also assessed for straightness (STR) and malformation (MAL) at the same ages. Straightness was scored on a scale of 1 to 9 (Carson, 1986). Malformation data were subsequently transformed to binary values where the ninth degree was assigned a value of 1 and all other data were assigned a value of 0. Acoustic velocity (VEL) was measured at age 11 years only, and branching (BR), acceptability (AC) and needle retention (NR) (measured only at Kaingaroa) at age 21 years only. Acoustic velocity was an indirect measure of wood stiffness.

Variance components and heritabilities of these traits were estimated using a mixed linear model implemented in ASReml-R statistical package (Butler, et al., 2009) as follows:

$$y = X\beta + Zp + Zg + Zr + Zr(s) + e$$

where y is vector of measurements, β is vector of fixed effects such as intercept, p is vector of random provenance effects following var(p)~N(0,$I\sigma_p^2$), where I is identity matrix and σ_p^2 is provenance variance, g is vector of random tree nested within provenance effect following var(g)~N(0,$A\sigma_g^2$), where A is average numerator relationship matrix (Wright, 1922) and σ_g^2 is additive genetic variance, r is vector of random replication effects following var(r)~N(0,$I\sigma_r^2$), where σ_r^2 is replication variance, the r(s) is vector of random set effects nested within replication effects following var($r(s)$)~N(0,$I\sigma_{r(s)}^2$), where $\sigma_{r(s)}^2$ is set nested within replication variance, e is vector of random residuals following var(e)~N(0,$I\sigma_e^2$), where σ_e^2 is residual variance, X and Z are incidence matrices assigning effects from fixed and random vectors to measurements in vector y.

Genetic correlations between traits within site and between traits across sites were estimated using bivariate mixed linear model implemented in ASReml-R statistical package (Butler, et al., 2009) as follows:

$$Y = X\beta + Zp + Zg + Zr + Zr(s) + e$$

Where Y is matrix of measurements, p is random vector of provenance effects following *var(p)~N(0, G1)*, where G1 is provenance variance-covariance structure following $G1 = \begin{bmatrix} \sigma_{p_1}^2 & \sigma_{p_1 p_2} \\ \sigma_{p_2 p_1} & \sigma_{p_2}^2 \end{bmatrix} \otimes I$, where $\sigma_{p_1}^2$ and $\sigma_{p_2}^2$ are provenance variances for 1st and 2nd trait, $\sigma_{p_1 p_2}$ and $\sigma_{p_2 p_1}$ are provenance covariances between 1st and 2nd trait, $\otimes$ is Kronecker product, g is random vector of tree nested within provenance effects following *var(g)~N(0, G2)*, where G2 is tree nested within provenance variance-covariance structure following $G2 = \begin{bmatrix} \sigma_{g_1}^2 & \sigma_{g_1 g_2} \\ \sigma_{g_2 g_1} & \sigma_{g_2}^2 \end{bmatrix} \otimes A$, where $\sigma_{g_1}^2$ and $\sigma_{g_2}^2$ are tree nested within provenance variances for 1st and 2nd trait, $\sigma_{p_1 p_2}$ and $\sigma_{p_2 p_1}$ are tree nested within provenance covariances between 1st and 2nd trait, r is random vector of replication effects following *var(r)~N(0, G3)*, where G3 is replication variance-covariance structure following $G3 = \begin{bmatrix} \sigma_{r_1}^2 & 0 \\ 0 & \sigma_{r_2}^2 \end{bmatrix} \otimes I$, where $\sigma_{r_1}^2$ and $\sigma_{r_2}^2$ are replication variances for 1st and 2nd trait, $r(s)$ is random vector of set nested within replication effects following *var(r(s))~N(0, G4)*, where G4 is set nested within replication variance-covariance structure following $G4 = \begin{bmatrix} \sigma_{r(s)_1}^2 & 0 \\ 0 & \sigma_{r(s)_2}^2 \end{bmatrix} \otimes I$, where $\sigma_{r(s)_1}^2$ and $\sigma_{r(s)_2}^2$ are set nested within replication variances for 1st and 2nd trait, e is random vector of residual effects following *var(e)~N(0, R)*, where R is residual variance-covariance structure following $R =$

$$\begin{bmatrix} \sigma_{e_1}^2 & \sigma_{e_1 e_2} \\ \sigma_{e_2 e_1} & \sigma_{e_2}^2 \end{bmatrix} \otimes I,$$ where $\sigma_{e_1}^2$ and $\sigma_{e_2}^2$ are residual variances for 1st and 2nd trait, $\sigma_{e_1 e_2}$ and $\sigma_{e_2 e_1}$ are residual covariances between 1st and 2nd trait. The narrow sense heritabilities for traits following normal distribution were estimated as follows:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

The narrow sense heritability for binary traits was estimated as follows:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \phi \dfrac{\pi^2}{3}}$$

Where ϕ is over/under dispersion coefficient and π is 3.14159. The genetic correlations were estimated in terms of Pearson's product moment as follows:

$$r_g = \frac{\sigma_{g_1 g_2}}{\sqrt{\sigma_{g_1}^2 \sigma_{g_2}^2}}.$$

Breeding value accuracy was estimated as follows:

$$r = \sqrt{1 - \frac{PEV}{(1 + F_i)\sigma_g^2}}$$

where PEV is prediction error variance (Mrode, 2014) and F_i is inbreeding coefficient of the ith individual.

RESULTS

The minimum, maximum and mean values for each of the traits assessed are shown in Table 1. Mean tree diameter was smaller at Kaingaroa than at Gowan Hill at age 11 years and this difference was still apparent at age 21 years.

Table 1. Minimum, maximum and mean values for the non-binary assessment traits measured at Gowan Hill and Kaingaroa at age 11 and/or age 21.

Site	Trait		Mean	Min	Max
Gowan Hill	**DBH11**	[mm]	169.46	11	271
	STR11	[1-9 scale]	5.38	1	9
	VEL11	[m/s]	2.01	1.465	2.552
	DBH21	[mm]	303.62	150	800
	STR21	[1-9 scale]	4.52	1	9
	BR21	[1-9 scale]	3.54	1	9
Kaingaroa	**DBH11**	[mm]	144.85	30	290
	STR11	[1-9 scale]	6.38	1	9
	VEL11	[m/s]	3.81	2.331	4.902
	DBH21	[mm]	269.32	133	530
	STR21	[1-9 scale]	6.57	1	9
	BR21	[1-9 scale]	3.14	1	10
	NR21	[0-6 scale]	2.99	0	6

The genetic component of each trait was divided into a provenance and a tree-within-provenance part. Both parts were statistically significant for most traits. However, the provenance part was relevant only for DBH where provenance-level heritability ranged from 0.116 to 0.136 at Gowan Hill and from 0.121 to 0.202 at Kaingaroa. All other traits had a very small heritability at the provenance level, ranging from 0 for VEL at Kaingaroa to 0.061 for AC at Gowan Hill. The heritability for the tree-within-provenance component was generally higher compared with the provenance level counterpart, ranging from 0.05 for MAL11 to 0.459 for STR21 at Gowan Hill and from 0.014 for MAL11 to 0.765 for VEL11 at Kaingaroa. The accuracy of estimated breeding values was low to moderate, ranging from 0.115 for VEL11 to 0.649 for STR21 at Gowan Hill and from 0.168 for MAL11 to 0.557 for DBH at Kaingaroa (Tables 2 and 3). Accuracy of breeding values reflected the magnitude of heritabilities for the various traits, with the exception of acoustic wave velocity at age 11 years, which had a large standard error.

Table 2. Variance components, heritability at provenance and individual tree level, their standard errors in brackets, breeding values accuracy and model fit in terms of log likelihood for traits measured at the Gowan Hill and Kaingaroa sites

Gowan Hill	DBH11	STR11	MAL11	VEL11	DBH21	STR21	BR21	MAL21	AC21
Provenance	139.5 (45.21)	0.138 (0.054)	0.080 (0.034)	0.001 (0.001)	411.8 (138.5)	0.119 (0.057)	0.044 (0.020)	0.148 (0.058)	0.161 (0.067)
Prov(Tree)	212.2 (34.38)	0.878 (0.132)	0.183 (0.066)	0.009 (0.004)	834.9 (133.3)	1.771 (0.228)	0.342 (0.076)	0.394 (0.090)	0.445 (0.103)
Rep	45.30 (13.58)	0.404 (0.114)	3.184 (0.923)	0.002 (0.001)	88.28 (28.11)	0.182 (0.055)	0.093 (0.031)	0.069 (0.028)	0.093 (0.036)
Rep(Set)	14.93 (4.765)	0.090 (0.021)	0.135 (0.035)	0.003 (0.001)	15.27 (13.69)	0.071 (0.021)	0.062 (0.017)	0.000 (na)	0.027 (0.032)
Residual	670.6 (31.03)	2.078 (0.115)	1.000 (na)	0.015 (0.004)	2301 (118.3)	1.966 (0.185)	2.408 (0.081)	1.000 (na)	1.000 (na)
h^2 prov	0.136 (0.038)	0.044 (0.017)	0.022 (0.009)	0.048 (0.035)	0.116 (0.035)	0.031 (0.014)	0.015 (0.007)	0.049 (0.019)	0.061 (0.023)
h^2 gen	0.208 (0.034)	0.284 (0.041)	0.050 (0.017)	0.350 (0.162)	0.235 (0.038)	0.459 (0.054)	0.122 (0.027)	0.122 (0.025)	0.151 (0.030)
BV accuracy	0.522	0.557	0.257	0.115	0.532	0.649	0.416	0.312	0.307
logL	-23927.15	-6237.59	-8168.27	748.32	-26480.76	-6679.79	-5957.34	-8121.54	-8449.89
Kaingaroa	**DBH11**	**STR11**	**MAL11**	**VEL11**	**DBH21**	**STR21**	**BR21**	**MAL21**	**AC21**
Provenance	304.9 (90.09)	0.038 (0.017)	0.069 (0.029)	0.000 (0.000)	474.3 (156.2)	0.037 (0.024)	0.047 (0.025)	0.075 (0.035)	0.078 (0.037)
Prov(Tree)	404.7 (61.36)	0.421 (0.081)	0.061 (0.058)	0.089 (0.024)	1027 (202.9)	0.695 (0.152)	0.320 (0.106)	0.128 (0.082)	0.158 (0.083)
Rep	45.62 (14.46)	0.035 (0.015)	0.047 (0.021)	0.000 (0.000)	77.40 (29.52)	0.024 (0.017)	0.296 (0.091)	0.056 (0.025)	0.084 (0.035)
Rep(Set)	18.68 (6.686)	0.063 (0.016)	0.052 (0.023)	0.005 (0.005)	30.50 (25.36)	0.081 (0.028)	0.177 (0.036)	0.000 (na)	0.055 (0.034)
Residual	800.9 (52.16)	1.877 (0.078)	1.000 (na)	0.027 (0.020)	2432 (181.0)	2.220 (0.141)	2.299 (0.110)	1.000 (na)	1.000 (na)
h^2 prov	0.202 (0.048)	0.016 (0.007)	0.016 (0.007)	0.000 (0.000)	0.121 (0.035)	0.012 (0.008)	0.018 (0.009)	0.018 (0.008)	0.019 (0.009)
h^2 gen	0.268 (0.042)	0.180 (0.034)	0.014 (0.014)	0.765 (0.179)	0.261 (0.051)	0.236 (0.050)	0.120 (0.039)	0.030 (0.019)	0.037 (0.019)
BV accuracy	0.557	0.468	0.168	0.147	0.443	0.422	0.329	0.184	0.202
logL	-22414.93	-5122.34	-6831	322.296	-15541.09	-3538.765	-3440.263	-4153.145	-4127.256

Table 3. Variance components, heritability at provenance and individual tree level, their standard errors in brackets, breeding value accuracy and model fit in terms of log likelihood for traits measured at the Kaingaroa site

Kaingaroa	NR21
Provenance	0.027(0.010)
Prov(Tree)	0.075 (0.019)
Rep	0.007 (0.004)
Rep(Set)	0.027 (0.006)
Residual	0.319 (0.019)
h² prov	0.064 (0.022)
h² gen	0.178 (0.045)
BV accuracy	0.374
logL	-198.93

Needle retention was assessed at the Kaingaroa site only. The results showed a heritability of 0.17, which indicates possible improvements could be made by breeding when needle retention is used as a selection criterion. However, there were highly positive genetic correlations between this trait and DBH at age 11 years at the provenance level, and with DBH at age 21 years at the tree level. These genetic correlations indicate that indirect selection using DBH as a criterion would also result in improved needle retention and better resistance to Swiss Needle Cast. Needle retention was also highly positively correlated with branching at age 21 years at the provenance level and acceptability at both ages and both levels.

The traits of DBH, MAL and STR were measured at 11 years and again at 21 years so it was possible to estimate age x age correlations for these traits. The age x age correlations were high at the provenance level, ranging from 0.977 for STR to 0.984 for DBH at Gowan Hill and from 0.984 for DBH to 0.999 for STR at Kaingaroa. Slightly lower correlations were found at the tree-within-provenance level ranging from 0.866 for DBH to 0.933 for STR at Gowan Hill and from 0.888 for STR to 0.964 for DBH at Kaingaroa.

Pairwise trait correlations within each age were also estimated for each site (Tables 4a, 4b, 4c). The results at age 11 years show a negative relationship between DBH and most other measured traits at both sites and at both levels. The only exception was a slightly positive, but non-significant, relationship with VEL at Kaingaroa. STR showed strong positive correlation with MAL at the provenance level at both sites and at the tree-within-provenance level at Kaingaroa. However, there was only a moderate, and non-significant, tree-within-provenance correlation between STR and MAL at Gowan Hill. Correlations between STR and VEL or MAL and VEL at both levels and both sites were not significant.

The results at age 21 years show that DBH was negatively correlated with BR at both levels and sites. There was no correlation between DBH and STR at the tree-within-provenance level at Gowan Hill, but otherwise DBH was negatively correlated with STR. The correlation between DBH and AC was positive at Kaingaroa while slightly negative at Gowan Hill at both levels but these correlations are not statistically significant. On the other hand, AC was highly correlated with both STR and BR at Gowan Hill but only moderately so at Kaingaroa. The form traits (BR, STR and MAL) showed very strong pair-wise correlations to each other at both levels at Gowan Hill while only moderate correlations at Kaingaroa. However, STR and MAL showed strong correlations at both sites and only BR was moderately related to those traits at Kaingaroa (Table 3 and 4). We are speculating that the stronger correlation between quality of branching (BR) and stem form (STR or MAL) at Gowan Hill is probably due to presence of snow where unfavourable type of branching keep heavy snow coverage at tree crowns and put pressure on stem straightness. These strong relationship (showed in terms of genetic correlations) resulted in more weights putted on stem form in in Gowan Hill while on productivity in Kaingaroa when acceptance (AC) was scored which is reflected in pattern observed in genetic correlations. This speculation will be further discussed with the forest owner.

The genetic correlations between sites (Table 5), define the level of GxE interaction. There was an increase in GxE for production traits with increasing age where the genetic correlation for DBH at age of 11 years was 0.61 at provenance and 0.68 at tree-within-provenance and decreased to 0.59 at provenance and 0.43 at tree-within-provenance level at age of 21 years. On the other hand, the genetic correlation between sites for STR increased from 0.38 at age of 11 years to 0.93 at age of 21 years at provenance level, and from 0.83 at age 11 years to 0.97 at age of 21 years at the tree-within-provenance level. The BR21 and VEL11 traits had genetic correlations between sites of around 0.7 (Table 5).

Table 4a. Genetic correlation between traits (their standard errors in parentheses) measured at the Gowan Hill site, estimated at provenance level (above diagonal) and tree-within-provenance level (below diagonal).

gen\prov	DBH11	STR11	MAL11	VEL11	DBH21	STR21	BR21	MAL21	AC21
DBH11	1	-0.774 (0.118)	-0.188 (0.279)	-0.852 (0.151)	0.984 (0.010)	-0.719 (0.156)	-0.714 (0.160)	-0.617 (0.181)	-0.037 (0.299)
STR11	-0.384 (0.099)	1	0.700 (0.202)	0.243 (0.397)	-0.641 (0.168)	0.977 (0.032)	0.694 (0.174)	0.843 (0.110)	0.688 (0.184)
MAL11	-0.070 (0.145)	0.231 (0.134)	1	-0.189 (0.445)	-0.113 0.0286)	0.902 (0.150)	0.848 (0.167)	NA	NA
VEL11	-0.188 (0.281)	-0.272 (0.288)	0.046 (0.337)	1	-0.713 (0.230)	0.252 (0.425)	0.164 (0.408)	0.376 (0.376)	0.007 (0.437)
DBH21	0.866 (0.034)	0.017 (0.109)	0.186 (0.141)	-0.153 (0.282)	1	-0.549 (0.217)	-0.646 (0.183)	0.276 (0.262)	-0.14 (na)
STR21	-0.366 (0.092)	0.933 (0.030)	0.382 (0.120)	-0.198 (0.254)	0.032 (0.101)	1	0.759 (0.172)	0.978 (0.068)	0.616 (0.289)
BR21	-0.438 (0.124)	0.508 (0.113)	-0.015 (0.169)	0.021 (0.302)	-0.396 (0.126)	0.500 (0.100)	1	0.765 (0.157)	0.638 (0.229)
MAL21	-0.367 (0.116)	0.623 (0.092)	NA	0.017 (0.291)	-0.44 (0.883)	0.748 (0.071)	0.735 (0.074)	1	NA
AC21	-0.231 (0.123)	0.857 (0.068)	NA	-0.107 (0.296)	-0.14 (na)	0.973 (0.017)	0.748 (0.069)	NA	1

Table 4b. Genetic correlation between needle retention and other traits (their standard errors in parentheses) measured at the Kaingaroa site, estimated at provenance level and tree-within-provenance level.

| gen\prov	DBH11	STR11	MAL11	VEL11	DBH21	STR21	BR21	MAL21	AC21
DBH11	1	0.337 (0.260)	-0.039 (0.250)	-0.999 (na)	0.985 (0.008)	-0.181 (0.313)	-0.152 (0.284)	-0.535 (0.222)	0.849 (0.114)
STR11	-0.089 (0.121)	1	0.624 (0.260)	0.999 (na)	0.236 (0.278)	0.999 (na)	0.336 (0.326)	0.544 (0.296)	0.839 (0.192)
MAL11	-0.110 (0.119)	0.922 (0.048)	1	0.999 (na)	-0.08 (0.264)	0.877 (0.182)	0.481 (0.285)	NA	NA
VEL11	0.113 (0.209)	-0.259 (0.258)	0.255 (0.223)	1	-0.999 (na)	0.999 (na)	0.999 (na)	0.999 (na)	0.999 (na)
DBH21	0.964 (0.014)	-0.129 (0.137)	-0.055 (0.143)	0.002 (0.213)	1	-0.235 (0.323)	-0.374 (0.274)	-0.657 (0.232)	0.607 (0.266)
STR21	-0.236 (0.129)	0.888 (0.065)	0.854 (0.163)	-0.171 (0.244)	-0.143 (0.146)	1	0.536 (0.341)	0.907 (0.271)	-0.135 (0.340)
BR21	-0.362 (0.158)	-0.060 (0.182)	0.367 (0.212)	0.147 (0.275)	-0.345 (0.178)	-0.162 (0.193)	1	0.651 (0.276)	0.213 (0.375)
MAL21	-0.222 (0.114)	0.786 (0.078)	NA	0.247 (0.183)	0.267 (0.105)	0.828 (0.053)	0.471 (0.156)	1	NA
AC21	0.795 (0.050)	0.859 (0.053)	NA	0.210 (0.154)	0.849 (0.041)	0.999 (na)	0.525 (0.107)	NA	1

Table 4c. Genetic correlation between traits (their standard errors in parentheses) measured at Kaingaroa site, estimated at provenance level (above diagonal) and tree-within-provenance level (below diagonal)

| NRA21	DBH11	STR11	VEL11	DBH21	STR21	BR21	MAL21	AC21
Prov	0.622 (0.146)	0.408 (0.262)	0.999 (na)	0.197 (0.250)	0.321 (0.325)	0.711 (0.217)	0.203 (0.305)	0.678 (0.193)
Gen	0.392 (0.126)	0.332 (0.151)	0.03 (0.236)	0.778 (0.048)	0.506 (0.150)	0.080 (0.203)	0.126 (0.234)	0.697 (0.156)

Table 5. Genetic correlations between sites (their standard errors in parentheses)

Trait	Prov	Prov(Gen)
DBH11	0.610 (0.148)	0.681 (0.082)
STR11	0.379 (0.261)	0.827 (0.085)
MAL11	NA	NA
VEL11	0.999 (na)	0.672 (0.324)
DBH21	0.588 (0.167)	0.429 (0.118)
STR21	0.933 (0.130)	0.970 (0.078)
BR21	0.696 (0.251)	0.678 (0.179)
MAL21	NA	NA
AC21	NA	NA

The effect of provenance latitude on DBH, STR or MAL at both ages is shown for each site in Figure 1. In general, the highest DBH was found in trees from provenances between 38° and 42° N at Kaingaroa in both ages. At Gowan Hill, the southern-most provenance performed the worst and there was also a continuous decrease in productivity with increasing latitude. However, the provenances with the greatest increase in DBH often had the poorest form (both STR and MAL). This pattern was present at both sites and was more obvious in 21-year-old trees (Figure 1). There was no provenance effect for VEL11, Table 1. Similarly, provenances from latitudes around 38° to 40° N had the poorest BR and AC, and improved with increased latitude at both sites. The pattern was more obvious at Kaingaroa than at Gowan Hill (Figure 2). Needle retention at Kaingaroa was best for provenances at 42° N and above (Figure 2). Provenances below 42° N showed the poorest needle retention.
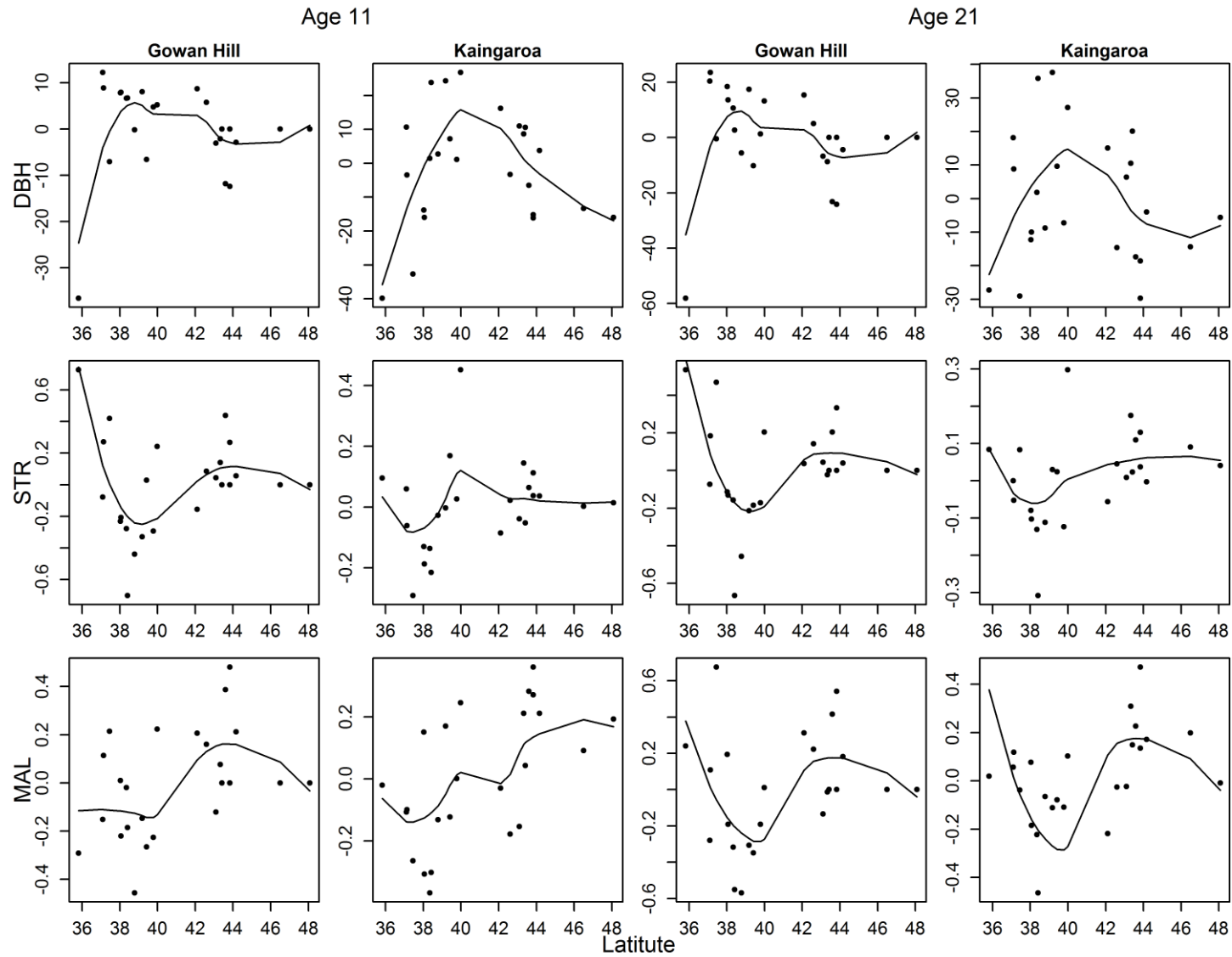
Figure 1. Provenance effects along the latitude of origin for DBH, STR and MAL at Gowan Hill and Kaingaroa at ages 11 and 21 years.
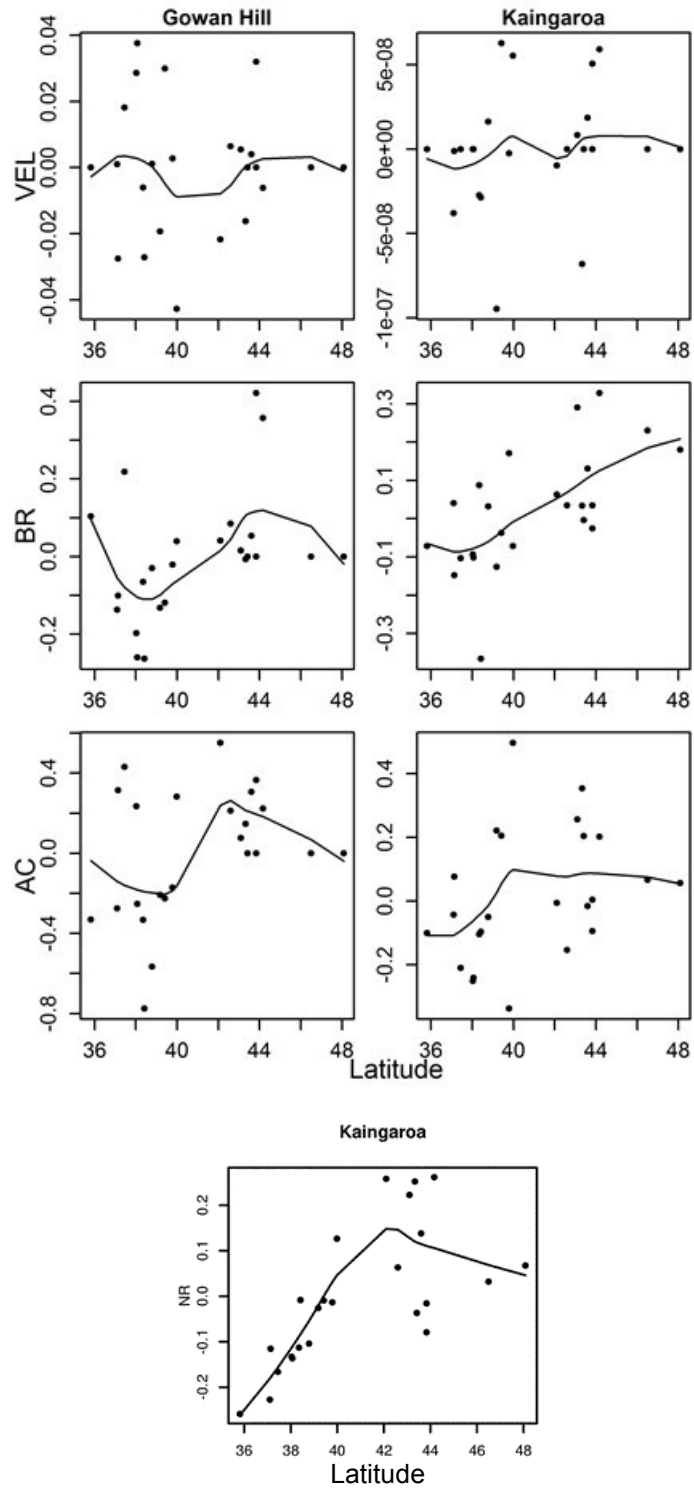
Figure 2. Provenance effects along the latitude of origin for VEL, BR and AC at Gowan Hill and Kaingaroa at age of 21 years and for NR at Kaingaroa at age 21 years.

DISCUSSION

Swiss Needle Cast (SNC) is more prevalent at warmer sites such as Kaingaroa in the North Island compared with cool sites like Gowan Hill in the South Island. Infection by SNC may have resulted in the smaller diameter growth at Kaingaroa. However, the faster growth at Gowan Hill may be linked to poorer tree form (particularly stem straightness and wood stiffness) at this site than at Kaingaroa.

Diameter at breast height (DBH) and stem straightness at age 21 years were moderately heritable at both sites, which indicated that these traits could be improved by breeding. In contrast, branching, malformation and acceptability traits had low heritability. Malformation and acceptability had very low heritability at Kaingaroa; much lower than at Gowan Hill. These results show that branching, malformation and acceptability are mainly affected by non-additive genetic effects and environmental factors, so genetic gains would be small.

Age correlations were determined for DBH, malformation and stem straightness, as these three traits were assessed at age 11 years and again at age 21 years. These genetic correlations were high for all three traits both at provenance and tree levels. The traits at both ages are genetically very similar, i.e. affected by the same genetic effects so little new information would be obtained by conducting any further assessments.

Genetic correlations between the traits within the sites showed that DBH at age 11 years was negatively (i.e. unfavourably) correlated with most other traits at both sites, except with stem straightness and wood stiffness at Kaingaroa. At age 21 years, there was still a negative genetic correlation between DBH and either stem straightness or branching at the provenance level and with branching at the tree level at Gowan Hill, and with malformation at the provenance level and branching at the tree level at Kaingaroa. A number of genetic correlations between DBH and form traits were insignificant. In general, selection for increased diameter does not favour good tree form in Douglas-fir at these sites. Genetic correlations between NR and DBH indicated that DBH can be used as a surrogate trait for selecting for improved needle retention. Also, branching and acceptability were highly positively associated with needle retention.

A provenance effect similar to the genetic effect was also observed, i.e. tree material originating from Californian provenances had larger diameters than those from Oregon or Washington but had poorer tree form. The effect of provenance on various traits demonstrates that there is considerable variability in the suitability of Douglas-fir provenances to New Zealand environments, and these differences can be utilised in selection.

Genotype by environment interaction (GxE) was strongest for stem straightness at age 11 years but only at provenance level, and for DBH at ages 11 and 21 years at both levels. It was interesting that stem straightness at age 21 years was stable across both sites, and a stronger GxE was estimated for DBH at age 21 years than at age 11 years. These results indicate that selections should be conducted cautiously, at least for DBH and stem straightness, when deploying tree material at different sites across New Zealand. Also, further information for a breeding strategy is required to address GxE and this information is expected to be available after the next generation progeny testing material has been investigated.

CONCLUSIONS

Considerable genetic gains could be achieved for DBH and stem straightness at Gowan Hill based on good heritability. Selection at age 21 years for stem straightness would result in particularly good genetics gains (heritability of the trait, 0.46). Heritability for DBH and straightness at Kaingaroa also promise good genetic gains. Nevertheless, genomic selection is expected to increase the accuracy of breeding values and more targeted selections would result in higher genetic gains compared to pedigree based breeding value selections. If further selections from these sites are necessary then our recommendation is to apply genomic breeding values when they become available in the breeding programme.

The previously performed selection was focused primarily on productivity which resulted in a less-than-favourable selection of tree form due to the traits' adverse genetic correlations. It is more important at Gowan Hill site to simultaneously select for both productivity and tree form since the acceptance is more correlated to tree form rather than productivity which is in opposite to Kaingaroa site. This can be reached by careful selection at the provenance level, with provenances towards the north showing greater productivity while maintaining above average and acceptable stem form.

Those populations provide a broad source of genetic variability which is needed to successfully implement genomic selection. We believe that capturing broad genetic variability will provide a robust source of information to train the genomic selection prediction model and provide a good framework to connect in to other sources of material being deployed in the New Zealand forest industry.

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