Title Evaluation of Douglas-fir progeny test FR508/1 and FR508/2

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EXECUTIVE SUMMARY

Scion’s Douglas-fir breeding program is continuing in genetic improvement of traits related to productivity and stem form by establishment of new generation of progeny trial. The latest generation of progeny test was established in 2011 and recently measured for standard traits at age of 10 years on two sites (Kaingaroa and Gowan Hill). Kaingaroa shows higher level of plant survival compared to Gowan Hill site. Due to extreme weather in 2016 (heavy snowstorm), it has more stem form issues, such as multiple stems. We assume this extreme weather event enhanced stress at this site, reducing additive genetic variance and heritability. California (including Fort Bragg) and Washington had the most affected provenances, whereas NZ Ashley had the least.

Gowan Hill has greater mean diameter at breast height (DBH), stem straightness (STR), stem malformation (MAL), and acceptability (ACC) but also branching quality (BRH) which is undesirable, compared to Kaingaroa. The ability to estimate larger additive genetic variation and heritability allowed for more accurate breeding value, which can lead to more precise expected genetic gain. Surprisingly, spatial analysis by first-order autoregression did not increase genetic parameters, and we may infer that the experimental design is adequate to capture environmental variability at this time (age of 10 years).

Phenotypic data correlation analysis showed two clusters of connected traits: DBH, HT, and BRH, and STR, MAL, and ACC. The patterns in genetic corelations verified these groups. Due of limited genetic components in Kaingaroa, this validation was only done for Gowan Hill trials. STR and DBH are connected with separate clusters, although they can be improved simultaneously due to a 0.27 genetic corelation.

The most productive families at Gowan Hill were from California, Ashly, and Fort Bragg. The unfavourable genetic correlation between DBH and BRH will require selection of correlation breakers to select individuals with above-average DBH and below-average BRH. In stem straightness and malformation, the top families were from Washington and Oregon. Best-performing families in Kaingaroa were from California, NZ Ashley, and Fort Bragg. Again, search for correlation breakers will be required to make genetic improvement in both DBH and BRH simultaneously. Stem straightness was highest in Fort Bragg, Washington, and Oregon, whereas malformation was best in California.

INTRODUCTION

Douglas-fir is the second most significant species of conifer plantation in New Zealand (i.e., after the radiata pine), and it now has a planted area of around 104,000 hectares. However, the economic viability of Douglas-fir plantations is highly dependent on genetic improvement (Magalska and Howe, 2014). Productivity and stem defects are considered to be the two most significant features, followed by resistance to Swiss needle cast (Dungey et al., 2012). It is very necessary to incorporate breeding programmes into the management of genetic resources for future climates if robust genetic progress is to be maintained in adaptive as well as non-adaptive yet economically relevant traits (Borralho and Dutkowski, 1998).

During the 1950s, Coastal Douglas-fir was first planted in New Zealand as a provenance test that included genetic material from the Washington and Oregon, in addition to a small amount of representation from California (Sweet 1965). Because the early study revealed that provenances from Oregon and California had greater growing performance in New Zealand, the focus of the selection of new breeding material was placed on these geographical regions. In 1996, a new provenance/progeny test was created in New Zealand from a collection of seeds taken from trees that had been found in the original wild stands on the west coast of US (Shelbourne et al., 2007). In 1996, the material that was used to plant at three different locations in New Zealand (Kaingaroa, Golden Downs, and Gowan Hill) was collected from populations in California and Oregon across the range of latitude from 36 to 48 North.

The measurements that were acquired at these sites made it possible for a number of forward selections as well as grafting. Because 2009 was a favourable flowering year, it was possible to harvest seed from selections made in 1988, from commercial stands, from the 1996 progeny experiments, and from commercial seed orchards. This seed was used for the establishment of a new generation of progeny trials in 2011. At the age of 10, the purpose of this investigation is to carry out an early review of the experiment in terms for growth and form.

METHODS

Fresh seed was collected from the following selections in PROSEED's Waikuku archive, two commercial stands and from across the three progeny trials at Kaingaroa, Gowan Hills and Golden Downs. All seedlots were sent to the Scion Nursery in 2009, and following stratification sown into plugs, and then in 2010 the plugs were lined out in the nursery beds for growing on. Two sites were established:

- FR508/1 – Kaingaroa Timberlands provided space the first experiment at cpt898 Kaingaroa forest. It is a windrowed Pinus radiata cutover site with a nominal 3x3m spacing.
- FR508/2 – Ernslaw One provided space for the second experiment, a windrowed Pinus radiata cutover site with a nominal spacing 3x3m, at Gowan Hills forest.

The plant material included in these two sites was measured at age of 10 for traits such as diameter at breast height (DBH [mm]), stem straightness (STR scored on scale 1 [crooked] – 9 [straight]), malformation (MAL scored on scale 1 [multileaded] – 9 [no defects]) and branching quality (BRH scored on scale 1 [fine branching] – 5 [bigger heavy branching]).

Genetic parameters such as variance components, narrow-sense heritability, breeding values and their accuracy were estimated using mixed linear models implemented in "breedR" package (Munoz and Sanchez 2020) as follows:

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Zu} + \boldsymbol{e}$$

Where $\boldsymbol{y}$ is a vector of measurements, $\boldsymbol{\beta}$ is a vector of fixed effects including intercept and provenance effect, $\boldsymbol{u}$ is vector of random effects such as breeding values (additive genetic effects) following ~N(0,$\boldsymbol{A}\sigma_g^2$) where $\boldsymbol{A}$ is average numerator relationship matrix (Wright 1922) and σ_g^2 is additive genetic variance, and block effects following ~N(0,$\boldsymbol{I}\sigma_b^2$) where $\boldsymbol{I}$ is identity matrix and σ_b^2 is block variance, $\boldsymbol{e}$ is a vector of residuals errors following ~N(0,$\boldsymbol{I}\sigma_e^2$) where σ_e^2 is error variance. The model was extended for first order autoregression structure (AR1) to fit spatial patterns in residuals. The $\boldsymbol{X}$ and $\boldsymbol{Z}$ are incidence matrices associating fixed effects from a vector $\boldsymbol{\beta}$ and random effects from a vector $\boldsymbol{u}$ to measurements in vector $\boldsymbol{y}$. The narrow-sense heritability was estimated as follows:

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

The accuracy of breeding values was estimating as follows:

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

Where PEV is prediction error variance (Mrode 2007) and F_i is inbreeding coefficient of ith individual.

The genetic correlations were estimated as follows:

$$r_g = \frac{\sigma_{xy}}{\sqrt{\sigma_x^2 \sigma_y^2}}$$

where σ_{xy} is additive genetic covariance between trait x and y estimated from bivariate mixed linear model using phenotypes adjusted for design and/or spatial terms.

Similarly, σ_x^2 and σ_y^2 are additive genetic variances for x^th and y^th trait estimated in bivariate mixed linear model.

RESULTS

The survival was 75% at Gowan Hill and 88% at Kaingaroa. However, the Kaingaroa suffered significantly from occurrence of trees with multiple stems showing 7 cases of 4 stems, 90 cases of 3 stems and 473 cases of 2 stems trees compared to 7 cases of 3 stems and 143 cases of 2 stems trees in Gowan Hill. This was most likely caused by a severe snow event in 2016 at Kaingaroa site. The most affected provenances to produce multiple stems were from Washington and California (including Fort Bragg provenance) and NZ_Ashley while the least affected provenances were from Myrtle point (Oregon) and Swanton (California) at both sites.

Gowan hill site shows higher productivity compared to Kaingaroa according to mean DBH and similarly slightly higher scores in STR, MAL and ACC. On the other hand, the same site shows higher mean in BRH which is undesirable (Table 1 and Table 2).

Table 1: Description of phenotypic data in Gowan Hill site

Gowan Hill	Multistem	Stem	DBH	STR	BRH	MAL	ACC
nbr.val	3043.00	3043.00	3043.00	3044.00	3036.00	3039.00	3034.00
nbr.null	2642.00	2642.00	0.00	0.00	0.00	0.00	1407.00
nbr.na	4362.00	4362.00	4362.00	4361.00	4369.00	4366.00	4371.00
min	0.00	0.00	8.00	1.00	1.00	1.00	0.00
max	1.00	3.00	265.00	9.00	5.00	9.00	1.00
range	1.00	3.00	257.00	8.00	4.00	8.00	1.00
sum	401.00	615.00	457171.00	18718.00	8277.00	23602.00	1627.00
median	0.00	0.00	153.00	6.00	3.00	9.00	1.00
mean	0.13	0.20	150.24	6.15	2.73	7.77	0.54
SE.mean	0.006	0.010	0.583	0.027	0.015	0.043	0.009
CI.mean.0.95	0.012	0.020	1.143	0.052	0.029	0.083	0.018
var	0.114	0.308	1034.833	2.143	0.687	5.496	0.249
std.dev	0.338	0.555	32.169	1.464	0.829	2.344	0.499
coef.var	2.567	2.746	0.214	0.238	0.304	0.302	0.930

Table 2: Description of phenotypic data in Kaingaroa site

Kaingaroa	Multistem	Stem	DBH	HT	STR	BRH	MAL	ACC
nbr.val	4713.00	4713.00	4643.00	607.00	4650.00	4650.00	4650.00	4650.00
nbr.null	3119.00	3119.00	0.00	0.00	0.00	0.00	0.00	2939.00
nbr.na	3484.00	3484.00	3554.00	7590.00	3547.00	3547.00	3547.00	3547.00
min	0.00	0.00	10.00	5.10	1.00	1.00	1.00	0.00
max	1.00	4.00	250.00	19.10	9.00	5.00	9.00	1.00
range	1.00	4.00	240.00	14.00	8.00	4.00	8.00	1.00
sum	1594.00	2616.00	648839.00	4941.70	27748.00	12129.00	29747.00	1711.00
median	0.00	0.00	145.00	8.10	6.00	3.00	8.00	0.00
mean	0.34	0.56	139.75	8.14	5.97	2.61	6.40	0.37
SE.mean	0.007	0.013	0.534	0.046	0.020	0.011	0.042	0.007
CI.mean.0.95	0.014	0.025	1.047	0.091	0.039	0.021	0.083	0.014
var	0.224	0.750	1324.852	1.306	1.881	0.543	8.318	0.233
std.dev	0.473	0.866	36.399	1.143	1.372	0.737	2.884	0.482
coef.var	1.399	1.560	0.260	0.140	0.230	0.282	0.451	1.311

The analysis of phenotypic data through mixed linear model found heritability at each investigated trait. However, Kaingaroa site showed almost unusually low level of heritability with their maximum at 0.07. Although, this site shows higher phenotypic variance in the DBH (Table 4) compared to Gowan Hill (Table 3), the estimated additive genetic variance in Kaingaroa is around 23% of that estimated in Gowan Hill site. We are speculating that the higher frequency of trees with multiple stems as a results of severe weather conditions in 2016 might be the reason for such low level of heritability at this site. Gowan Hill site found heritability around 0.18 for DBH and BRH while 0.11 for STR and 0.03 for MAL.

Table 3: Variance components, heritability and accuracy of breeding values in Gowan Hill site

Model	Parameter	DBH	STR	BRH	MAL
Design	**Add. Gen. var.**	141.9 (37.90)	0.23 (0.098)	0.12 (0.033)	0.14 (0.179)
	Block var.	114.9 (19.60)	0.04 (0.017)	0.02 (0.006)	0.10 (0.043)
	Res. Var.	638.0 (31.72)	1.83 (0.099)	0.60 (0.028)	5.16 (0.197)
	h2	0.182 (0.0476)	0.11 (0.056)	0.17 (0.046)	0.03 (0.037)
	AIC	21615.9	4999.787	1985.312	7648.61
	r	0.548	0.349	0.343	0.227
AR1	**Add. Gen. var.**	130.9 (36.61)	0.23 (0.098)	0.12 (0.033)	0.14 (0.178)
	Block var.	21.7 (11.03)	0.03 (0.017)	0.01 (0.007)	0.08 (0.053)
	Spat. var.	119.9 (30.35)	1.83 (0.100)	0.02 (0.011)	0.26 (0.393)
	Res. Var.	617.4 (31.57)	0.00 (NA)	0.59 (0.029)	4.95 (0.414)
	AR1 row	0.97 (0.015)	0.05 (0.025)	0.96 (0.038)	0.46 (0.552)
	AR1 col	0.85 (0.044)	0.03 (0.025)	0.22 (0.311)	0.37 (0.549)
	h2	0.18 (0.046)	0.99 (0.000)	0.17 (0.044)	0.03 (0.035)
	AIC	21557.99	9435.605	1981.731	7652.938
	r	0.544	0.344	0.371	0.189

Table 4: Variance components, heritability and accuracy of breeding values in Kaingaroa site

Model	Parameter	DBH	HT	STR	BRH	MAL
Design	**Add. Gen. var.**	49.5 (24.25)	0.52 (0.345)	0.03 (0.045)	0.02 (0.016)	0.42 (0.261)
	Block var.	19.6 (5.39)	0.15 (0.061)	0.05 (0.014)	0.02 (0.005)	0.06 (0.042)
	Res. Var.	624.8 (26.28)	0.73 (0.319)	1.78 (0.054)	0.49 (0.016)	7.52 (0.295)
	h2	0.074 (1.819)	0.42 (0.342)	0.017 (0.025)	0.038 (0.031)	0.053 (0.046)
	AIC	28324.1	662.4577	6184.445	1519.309	11670.7
	r	0.318	0.277	0.112	0.267	0.261
AR1	**Add. Gen. var.**	54.9 (24.12)	0.56 (0.341)	0.02 (0.046)	0.02 (0.015)	0.42 (0.258)
	Block var.	0.00 (NA)	0.01 (0.038)	0.00 (0.009)	0.00 (NA)	0.00 (NA)
	Spatial var.	98.6 (17.77)	0.26 (0.114)	0.13 (0.033)	0.07 (0.012)	0.14 (0.065)
	Res. Var.	555.5 (25.39)	0.60 (0.314)	1.74 (0.0597)	0.45 (0.017)	7.46 (0.296)
	AR1 row	0.98 (NA)	0.93 (0.068)	0.98 (NA)	0.98 (NA)	0.80 (0.150)
	AR1 col	0.60 (0.074)	0.86 (0.095)	0.69 (0.082)	0.47 (0.089)	0.96 (0.042)
	h2	0.089 (0.039)	0.49 (0.280)	0.009 (0.026)	0.045 (0.032)	0.053 (0.033)
	AIC	28112.54	655.0431	6136.868	1287.083	11664.14
	r	0.342	0.288	0.467	0.594	0.231

The spatial modelling to remove environmental heterogeneity within site did not improve results significantly (Table 3 and 4). Therefore, the experimental design was sufficient to remove all significant environmental variability within field experiment (Figures 1 and 2). The accuracy of breeding values followed pattern in heritability and reached values from 0.227 in MAL to 0.548 in DBH in Gowan Hill (Table 3). The additional spatial modelling rather decreased the accuracy in breeding values (Table 3). Although the narrow-sense heritability was low in Kaingaroa, the accuracies of breeding values were equivalent to those estimated in Gowan Hill. Again, spatial modelling of environmental heterogeneity resulted in rather decrease in accuracy of breeding values.

Figure 1: Environmental heterogeneity captured by design or first order autoregression for DBH (as an example) in Gowan Hill site

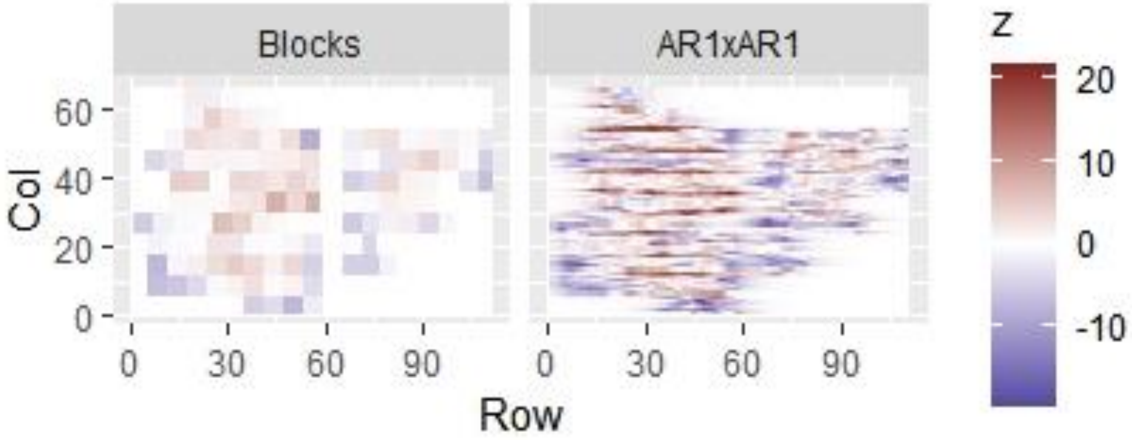

Figure 2: Environmental heterogeneity captured by design or first order autoregression for DBH (as an example) in Kaingaroa site

The genetic correlations between traits were obtained only for Gowan Hill site due to inability to get model convergence for data from Kaingaroa site. The most likely reason for difficulty of model convergence is generally low level of heritability at this site. We used cluster analysis to present relationships between traits at phenotypic level and genetic level (only at Gowan Hill site).

We found that at the phenotypic level, the acceptance, stem malformation and stem straightness clustered together wile DBH and branching quality created separate cluster (Figure 3). This pattern was confirmed in genetic level when DBH clustered with BRH while MAL clustered with STR (Figure 4). The strong positive genetic correlations were observed between DBH and BRH (0.78) and between MAL and STR (0.52) while low negative to low positive genetic correlations were observed between traits from different clusters reaching from -0.28 to 0.28. The cluster analysis of phenotypic correlations between traits measured in Kaingaroa followed the same pattern observed in Gowan Hill. As expected, tree height measured only on the subset of trees in Kaingaroa clustered with DBH and BRH (Figure 5).

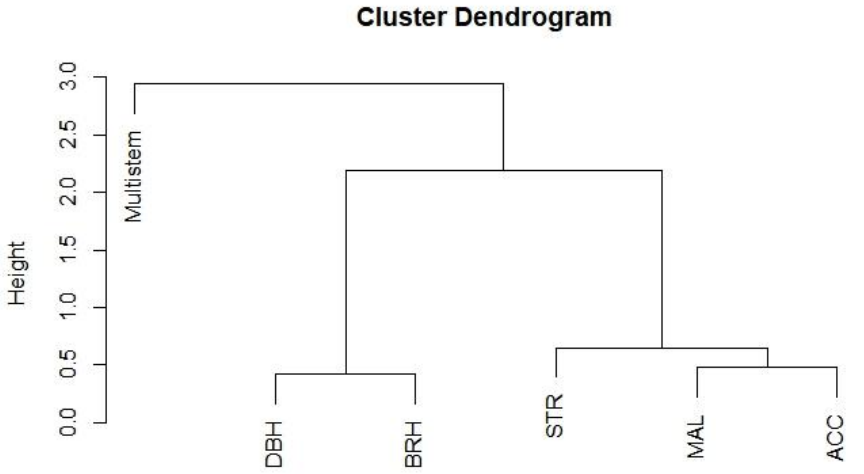

Figure 3: Dendrogram showing relationship between traits based on phenotypic correlations in Gowan Hill site.

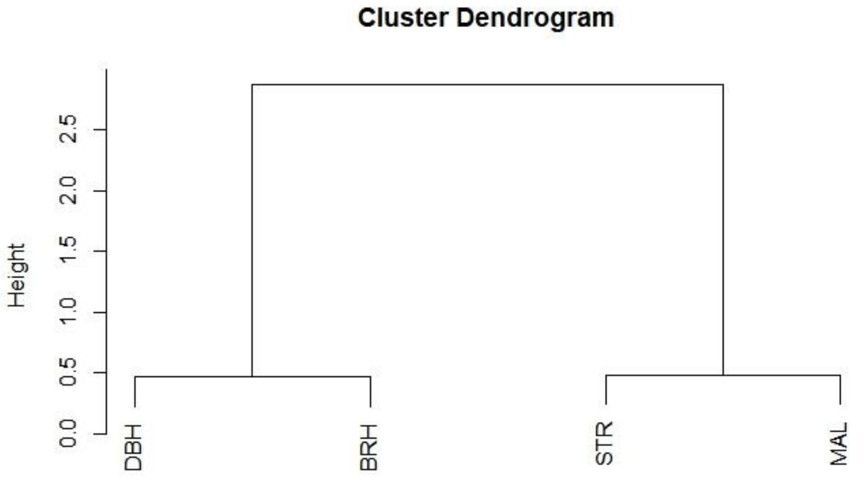

Figure 4: Dendrogram showing relationship between traits based on genetic correlations in Gowan Hill.

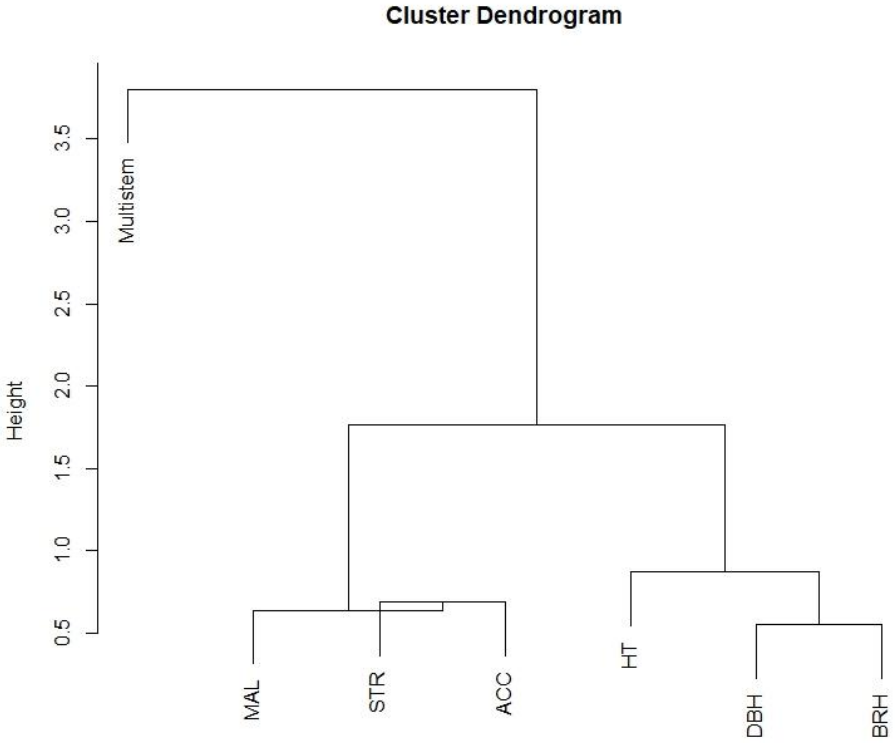

Figure 5: Dendrogram showing relationship between traits based on phenotypic correlations in Kaingaroa site.

The best families in productivity in Gowan Hill site were mostly from California provenance (family 2005928, 2005868 and 2005854), NZ Ashley (family 889633) and Fort Bragg (family 888434 and 888445). On the other hand, similar families performed poor in BRH due to high positive genetic correlation with DBH which is undesirable relationship. The poorest performance in productivity at this site showed similar provenances but different families such as family 2005884 in California provenance, family 889561 in NZ Ashley and family 888431 in Fort Bragg provenance (Figure 6).

The full list of individual breeding values is included in Appendix 1.

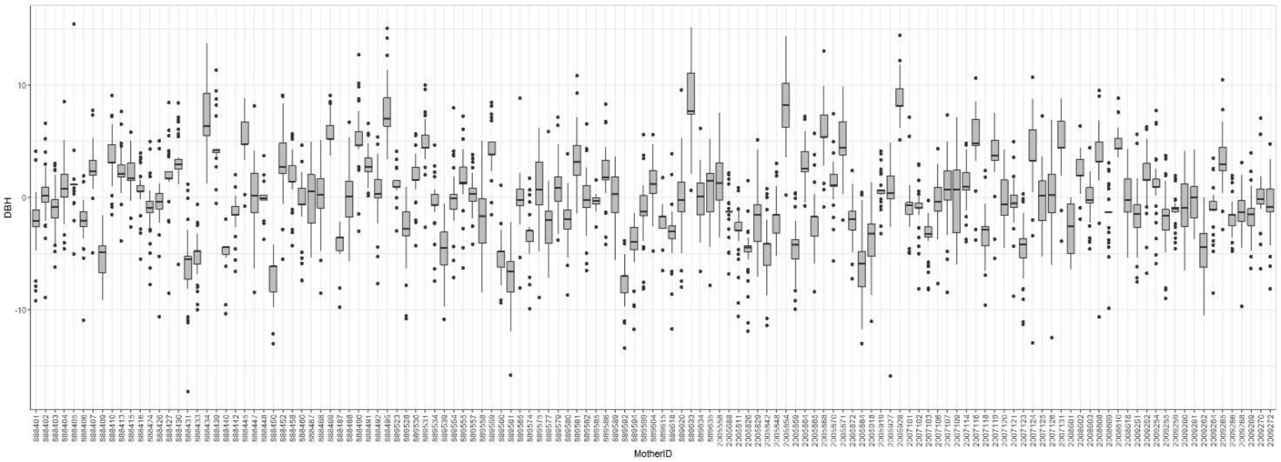

Figure 6: Family-wise boxplots of estimated individual breeding values for DBH at Gowan Hill site

The best families for stem form traits such as straightness were from Washington provenance (family 889594) and Oregon provenances (families 2007119, 2007123 and 2009255) while the poorest families were from California (families 88433 and 888442) and Oregon (families 2009251 and 2008603). In malformation, the best families were from Oregon provenance (family 889590) and California provenances (families 889528, 2009268 and 2005864) while the poorest families were from Oregon provenances (families 888405 and 2009251) and California (families 2008609, 2005826 and 889586) (Figure 7).

The full list of individual breeding values is included in Appendix 1.

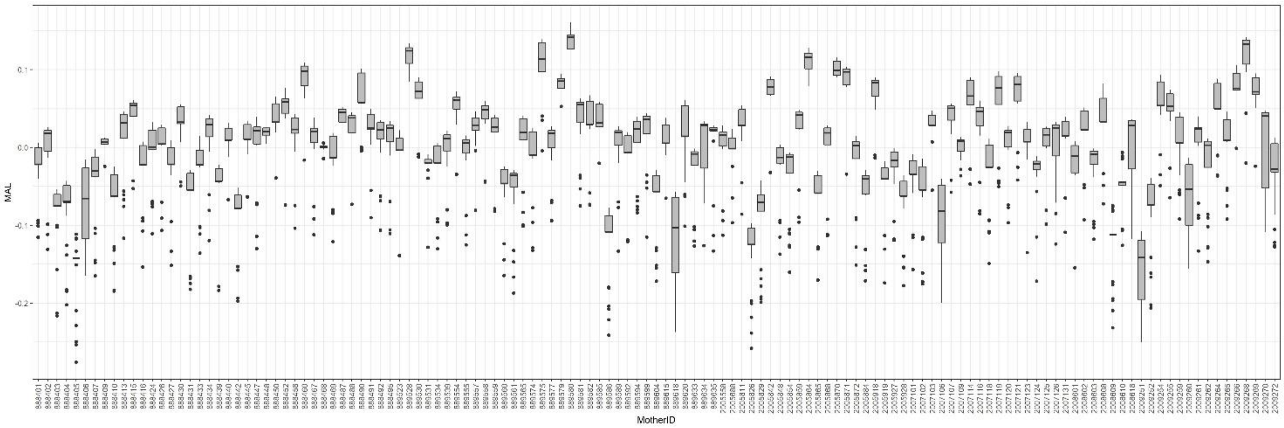

Figure 7: Family-wise boxplots of estimated individual breeding values for MAL at Gowan Hill site

The best families in productivity in Kaingaroa site were mostly from California provenance (family 888401,2005928, 2005868 and 2009262), NZ Ashley (family 889555) and Fort Bragg (family 888433). Again, similar families performed poor in BRH due to high genetic correlation with DBH. The poorest performance in productivity at this site showed similar provenances but different families such as family 2007118 and 888491 in California provenance, family 889557 in NZ Ashley provenance and family 2009266 in Oregon provenance (Figure 8).

The full list of individual breeding values is included in Appendix 1.

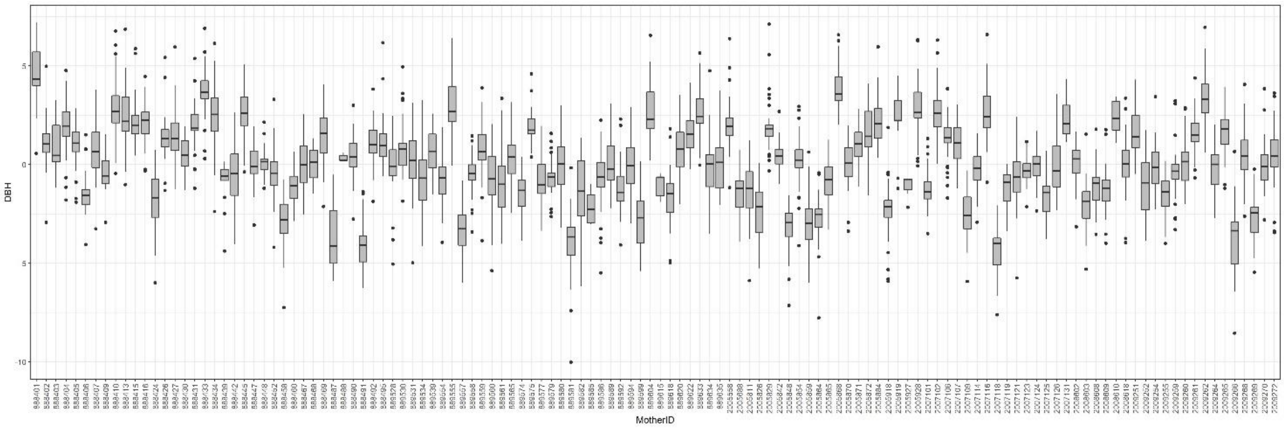

Figure 8: Family-wise boxplots of estimated individual breeding values for DBH at Kaingaroa site

The best families for stem form traits such as straightness were from Fort Bragg provenance (family 889539), Washington provenance (family 889594) and Oregon provenances (family 88405) while the poorest families were from California (families 2009259 and 2005829) and Oregon (family 889577). In malformation, the best families were from California provenances (family 889539, 888490, 88407 and 2005864) while the poorest families were also from California provenances (families 888430, 88410, 2005826 and 888433) (Figure 9).

The full list of individual breeding values is included in Appendix 1.

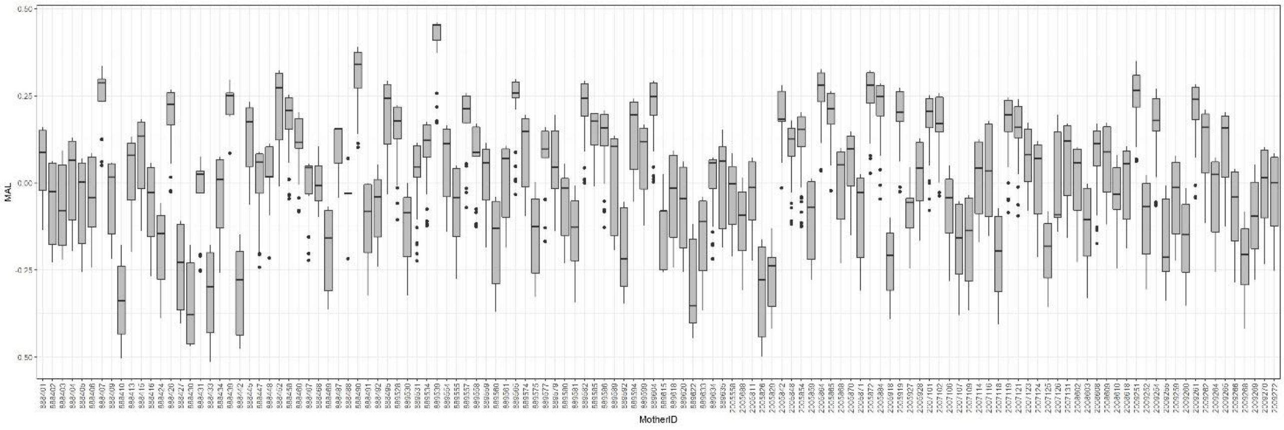

Figure 9: Family-wise boxplots of estimated individual breeding values for MAL at Kaingaroa site

CONCLUSION

In comparison to the Gowan Hill site, the Kaingaroa site has a far larger percentage of plants that have survived. On the other hand, it has a greater incidence of stem defects, such as having multiple stems, which is most likely attributable to the extreme weather (heavy snowstorm) that occurred in 2016. We have a suspicion that this extreme weather event contributed to the increased variation, which in turn resulted in a significantly lower amount of recoverable additive genetic variance and heritability. The provenances from California (including the Fort Bragg provenance) and Washington were the ones that were influenced the most, while the families that came from the New Zealand Ashley selections were the ones that were damaged the least.

When compared to Kaingaroa, the Gowan Hill site exhibits significantly greater levels of productivity as measured by mean diameter at breast height (DBH), as well as somewhat higher scores in stem straightness (STR), stem malformation (MAL), and acceptability (ACC) but also higher mean score in branch quality (BRH) which is undesirable case. In addition, the capability of estimating higher additive genetic variance and, consequently, heritability enabled for greater accuracy of breeding value, which in turn can result in greater precision of expected genetic gain. Surprisingly, the incorporation of spatial analysis using first-order autoregression did not result in an improvement of genetic parameters, and we may draw the conclusion that the experimental design is effective enough to capture environmental variation within the trials at this time (age of 10 years).

The correlation analysis performed on the phenotypic data revealed the existence of two distinct groups of connected characteristics. The first group consists of DBH, HT, and BRH, while the second group consists of STR, MAL, and ACC. The study of genetic relationships also provided additional evidence that these clusters were reflecting the impact of genetic factors. However, this validation was only carried out for the Gowan Hill experiment since the multi-trait model convergence could not be achieved for the data from Kaingaroa site. This was probably because of the low number of additive genetic variance components that were retrieved at this location. As a result, a search for correlation breakers is required to enhance both the production and the quality of the branching at the same time. However, despite the fact that STR and DBH are linked to separate clusters, there is the possibility to improving both of these characteristics simultaneously due to the positive genetic correlation of 0.27 that exists between them.

Based on the findings of the investigation of estimated breeding values, it was determined that the most productive families at the Gowan Hill location originated mostly from of California, Ashley and Fort Bragg provenances. Because of the strong unfavourable positive genetic association with DBH, the same families did poor in BRH. In relation to stem form features, the best families came from provenances in the states of Washington and Oregon for stem straightness, and provenances in the states of Oregon and California for malformation. The most productive families at the Kaingaroa site were most commonly from the Ashly, Fort Bragg and California provenances. Again, because of the strong undesirable genetic association with DBH, the same families did poor in BRH. In stem form features, the best families came from the provenances of Fort Bragg, Washington, and Oregon in terms of stem straightness, and the best families came from the provenances of California in terms of malformation.

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APPENDICES

Appendix: List of individual breeding values, their standard errors and accuracies

Please contact FGR for a copy of “Appendix 1 - Estimated breeding values.xls”