Evaluation of the Ernslaw One Douglas-fir progeny tests

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EXECUTIVE SUMMARY

This project evaluates a Douglas-fir open-pollinated progeny trial established on two New Zealand sites (Gowan Hill and Tramway), using seedlots from three Oregon (US) seed zones. The material was measured for diameter at breast height (DBH) and scored for forking (FRK), branching pattern (BR), straightness (STR), malformation (MAL) and acceptance (AC). A low level of plant survival was identified at the Gowan Hill site which prevented us from obtaining statistically significant estimates of genetic parameters. Results from this site should be considered with caution. Descriptive summary statistics found slightly better performance for straightness and forking in the interior seed zone compared with both coastal zones at the Tramway site.

Analysis of data from the Tramway site resulted in statistically significant estimates of heritability, indicating the possibility for genetic improvement in the assessed traits. Therefore, genetic improvement through breeding and selection can be achieved. However, it should be noted that open-pollinated experiments can suffer from over-estimated genetic parameters due to unrecognized relatedness from the paternal parent, and it is expected that the real genetic parameters may be lower.

Correlation analysis discovered two clusters of traits:
-   Acceptability (AC), malformation (MAL) and straightness (STR) – indicating a strong focus on stem form rather than productivity in acceptance evaluation; it also uncovered a strong negative correlation of this cluster of traits with forking (FRK), which is a favourable situation that supports the opportunity for simultaneous improvement across all the traits.
-   DBH, FRK and BR were moderately and negatively correlated with MAL – indicating the negative impact of fast growth on stem defects such as forks and ramicorns. Therefore, the selection of fast growing individuals will result in an increased incidence of stem defects and the trade-off between productivity and stem form should be considered.

The unexpected positive correlations between DBH and BR found in our analysis can be explained by the unreliable scoring of the BR at an early age, and we would recommend re-evaluating this trait in a later age when the crown is better developed.

Potential response to selection was generally higher in Tramway due to the higher heritability at this site. The highest improvement in DBH and FRK is achieved in Counties coastal zone. However, the unfavourable relationship between these traits prevents the simultaneous improvement in both traits. The highest response to selection in STR and BR is achievable in the Coastal interior zone and MAL in the Coastal zone.

INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the second most important conifer plantation species in New Zealand after radiata pine with a current planted area approaching 104,000 ha. The genetic improvement of the reproductive material through a breeding programme is the major tool ensuring Douglas-fir plantation forestry is an economically viable alternative of land use. Productivity and stem defects are the two most important groups of traits considered in Douglas-fir breeding (Magalska and Howe, 2014), followed by resistance to Swiss needle cast (Dungey *et al*, 2012; Suontama, 2014). The provenance tests performed on the broad geographical scale and using a representative sample of populations, found the local populations to be the best performers with decreasing performance of populations with increasing distance between the tested site and population origin beyond 435 km in latitude and 370 m in elevation (Ye and Jayawickrama, 2014). However, it is not always the case, and in some instances, the geographically distant provenances perform as well as the local one (Krakowski Stoehr 2009). Stem defects (such as ramicorn branches and forks) are identified mostly on fertile sites (Temel and Adams, 2000) and represent a source of decreased stability, grade and strength of the lumber (Schermann *et al*, 1997; Temel and Adams, 2000).

Previous analyses have identified positive correlations between forking and ramicorn branching in Douglas-fir (genetic correlation of 0.54) (Schermann *et al*, 1997) as well as in loblolly pine (Xiong *et al*, 2014) and thus the selection can efficiently reach improvement in both traits simultaneously. Schermann et al. (1997) also found a moderate positive genetic correlation between the forking defects and budburst timing. The earlier budburst is connected to early bud set and thus early maturity of new buds. This may result in a second flushing when favourable weather and soil moisture conditions occur. Moreover, the early flushing in spring increases the chance of late frost damage, which can further increase the frequency of forking (Schermann *et al*, 1997).

Our analysis was focused on the initial evaluation of open-pollinated material originating from three seed zones located at mid-southern Oregon and planted on two sites within the South Island of New Zealand. Genetic parameters, such as additive genetic variance, heritability, genetic correlations and accuracy of breeding values were estimated and reported.

METHODS

The investigated progeny trial was established on two sites located at Gowan Hill and Tramway during 2004 and measured in 2017 (13 years after planting). Each location was divided into three fairly separated trials representing different seed sources originating from the middle to the south of Oregon (US) (Figure 1).
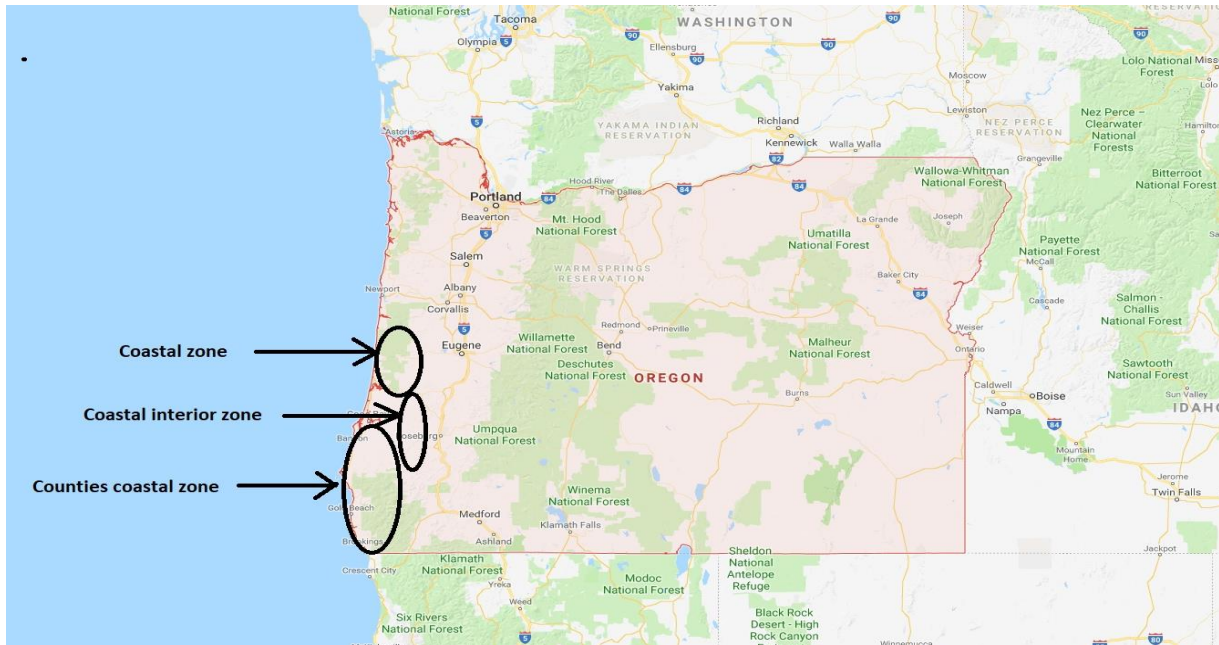

Figure 1: Map of seed zones.

The Gowan Hill site was designed as a seed orchard with 8 replications and trees grouped into clumps or 3 trees, allowing for potential future genetic thinning. The site suffered, however, from high mortality and large areas failed early after planting (personal communication Charlie Low) with each clump containing mostly only one or no trees. Therefore, clumps were not considered in the statistical analysis due to potential overlap with residual structure causing a model singularity. However, by testing row and column effects in the model as a random term, the column effect was found to be significant and was therefore included in the final model for this site. The Tramway site was a standard progeny test layout, established as incomplete block design with four replications. Survival rate was higher at this site compared with the Gowan Hill site.

Table 1: Description of assessed traits.

Trait	Description	Type	Units
DBH	Diameter at breast height	Quantitative	millimetres
BR	Branching pattern	Scalar	- score 1 represents a case of one whorl per year with one set of branches,
			- score 2 represents a case of one whorl per year with two sets of branches,
			- score 3 represents a case of one whorl per year with multiple sets of branches
			- score 4 represents a case of short internode with multiple sets of branches per whorl
			- scores 6 to 9 represent cases multimodal trees with increasing score as the frequency of nodes increased
STR	Stem Straightness	Scalar	scored on a 9-degree scale from 1 (crooked stem) to 9 (straight stem),
MAL	Malformation	Scalar	- score 1 represents a case of the tree with multiple leaders
			score 2 represents a case of the tree with two leaders,
			score 3 represents the case where the main stem was shifted for more than one half of its diameter,
			- score 4 represents the case where the main stem was shifted for less than one half of its diameter
			- score 5 represents the case where multiple ramicorns took the place of the main leader,
			- score 6 represents the case where the tree has three and more distinctive ramicorns
			- score 7 represents the case where the tree has two distinctive ramicorns,
			- score 8 represents the case where the tree has one distinctive ramicorn,
			- score 9 represents the case where the tree has no shift in stem, multiple leaders or distinctive ramicorns,
FRK	Forking	Scalar	the number of ramicorns scored on 10-degree scale from 0 (no visible ramicorns) to 9 (the tree has more than nine ramicorns)
AC	Acceptability	Binary	scored as 1 (generally acceptable) or 0 (unacceptable)

The investigated traits are listed and described in Table 1. The phenotypes (traits) developed on the basis of multiple-degree scale (MAL, STR and BR) were transformed to a normal score following (Gianola and Norton, 1981).

The mixed linear model used at Gowan Hill was implemented in the ASReml-R package (Butler *et al*, 2009) as follows:

$$y = X\beta + Zg + Zr + Zc + e$$

where **y** is a vector of measurements, **β** is a vector of fixed effects (overall mean), **g** is the vector of random breeding values following $var(g) \sim N(0, A\sigma_g^2)$, where **A** is average numerator relationship matrix (Wright, 1922) and σ_g^2 is additive genetic variance, **r** is the vector of random replication effects following $var(r) \sim N(0, I\sigma_r^2)$, where **I** is identity matrix and σ_r^2 is replication variance, **c** is the vector of random column effects following $var(c) \sim N(0, I\sigma_c^2)$, where σ_c^2 is column variance, **e** is the vector of random residual effects following $var(e) \sim N(0, I\sigma_e^2)$, where σ_e^2 is residual variance.

The mixed linear model used for Tramway was implemented as follows:

$$y = X\beta + Zg + Zr + Zb + Zp + e$$

where **b** is the vector of random block nested within replication following $var(b) \sim N(0, I\sigma_b^2)$, where σ_b^2 is block nested within replication variance, **p** is the vector of random plot nested within block nested within replication effects following $var(p) \sim N(0, I\sigma_p^2)$, where σ_p^2 is plot nested within block nested within replication variance.

Variance and co-variance estimates were obtained for the estimation of genetic correlations using the equivalent bivariate mixed linear model including heterogeneous variance-covariance structure $\begin{bmatrix} \sigma_{g_1}^2 & \sigma_{g_1 g_2} \\ \sigma_{g_2 g_1} & \sigma_{g_2}^2 \end{bmatrix}$ for the additive genetic term and heterogeneous variance structures for replications $\begin{bmatrix} \sigma_{r_1}^2 & 0 \\ 0 & \sigma_{r_2}^2 \end{bmatrix}$ and columns $\begin{bmatrix} \sigma_{c_1}^2 & 0 \\ 0 & \sigma_{c_2}^2 \end{bmatrix}$ representing the design terms. The heterogeneous variance-covariance structure was also considered in residuals.

The narrow-sense heritability for continuous traits and transformed traits were estimated follows:

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

and for the binary trait (acceptability):

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

where ϕ is the over/under dispersion coefficient.

Genetic correlations were estimated by using Pearson's moment product correlation as follows:

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

where $\sigma_{g_1 g_2}$ is the additive genetic covariance between trait 1 and 2, $\sigma_{g_1}^2$ and $\sigma_{g_2}^2$ are additive genetic variances for trait 1 and 2.

The theoretical accuracy of breeding values 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. Genetic gains are reported as average breeding values.

RESULTS

The exploration of data showed that the Gowan Hill experimental site suffered from low survival rate, resulting in only 1865 to 2908 (seed zone dependent) individuals being analysed compared with 3993 to 5211 (seed zone dependent) at the Tramway experimental site. The basic descriptive statistics showed generally higher productivity at the Gowan Hill site, ranging from 197 to 209 mm, compared with 179 to 188 mm at Tramway. The higher productivity was most likely the result of the decreased competition effect due to higher mortality at Gowan Hill. All other assessed traits showed similar values across seed zones and sites with the exception of forking, which showed higher values at Tramway for coastal and counties coastal zones (Table 2).

Table 2: Descriptive statistics of investigated traits.

Site	Trait	Coastal zone				Counties coastal zone				Coastal interior zone			
		Mean	Min	Max	Std. dev	Mean	Min	Max	Std. dev	Mean	Min	Max	Std. dev
Gowan Hill	DBH	197.1	102	321	32.87	206.5	52	320	33.92	209.3	20	332	34.02
	STR	5.204	1	9	1.767	5.279	1	9	1.723	5.345	1	9	1.736
	BR	2.028	1	6	0.645	2.107	1	6	0.608	2.139	1	8	0.548
	MAL	4.183	1	9	1.662	4.247	1	9	1.605	4.220	1	9	1.492
	FRK	2.030	0	9	1.023	2.024	0	6	1.061	2.181	0	9	1.094
	AC	0.093	0	1	0.290	0.095	0	1	0.294	0.095	0	1	0.293
Tramway	DBH	179.6	100	322	37.13	188.8	21	336	35.32	182.4	29	283	29.81
	STR	5.064	1	9	2.063	5.336	1	9	1.896	5.488	1	9	1.814
	BR	2.240	0	8	0.798	2.264	0	7	0.646	2.191	0	8	0.665
	MAL	4.464	1	9	1.907	4.215	1	9	1.638	4.431	1	9	1.744
	FRK	2.515	0	9	1.268	2.437	0	9	1.168	2.085	0	9	1.066
	AC	0.113	0	1	0.317	0.102	0	1	0.303	0.110	0	1	0.313

Genetic parameters were estimated for each seed zone within each site separately. Results generally showed lower and mostly statistically non-significant heritability estimates at Gowan Hill compared with Tramway, probably due to a reduced number of observations and a wider variability in micro-environmental (micro-climatic) conditions as a result of the high level of mortality. In the coastal zone population, the lowest heritabilities were observed for acceptability (0.064), DBH (0.080) and straightness (0.092), while the highest was obtained for forking (0.174). A similar pattern was observed for the accuracy of breeding values, with lowest values for acceptability (0.110), DBH (0.266) and straightness (0.287) while the highest was observed for forking (0.364). In the counties coastal zone population, the lowest heritabilities were observed for branching pattern (0.057), forking (0.063) and DBH (0.094) while the highest was observed for straightness (0.176). In the coastal interior zone population, the lowest heritabilities were observed for malformation (0.043), acceptability (0.089) and DBH (0.91) while the highest was observed for straightness (0.182) (Table 3).

The analysis of each seed zone population at the Tramway site obtained moderate and mostly statistically significant (in terms of standard errors) estimates of heritability, which is a result of the more complete data available for the analysis. In the coastal zone, the lowest heritabilities were observed for acceptability (0.024), forking (0.159) and malformation (0.166) while the highest was observed for branching pattern (0.451). In the counties coastal zone, the lowest heritabilities were observed for acceptability (0.213), malformation (0.220) and branching pattern (0.223) while the highest was observed for DBH (0.586). In the coastal interior zone, the lowest heritabilities were observed for malformation (0.079), forking (0.144) and acceptability (0.231) while the highest was observed for straightness (0.536). The accuracies of breeding values estimated at Tramway were

also higher compared with those estimated at Gowan Hill and followed a similar pattern as heritability estimates. In the coastal zone population, the lowest accuracy was observed for acceptability (0.131) and the highest for straightness (0.569). In the counties coastal zone, the lowest accuracy of breeding values was observed for acceptability (0.327) while the highest was observed for DBH (0.728). In the coastal interior zone, the lowest accuracy of breeding values was observed for acceptability (0.388) while the highest was observed for straightness (0.722) (Table 4).

Table 3: Variance components, heritability, theoretical accuracy of breeding values and log-likelihood (model fit parameter) for populations planted at Gowan Hill site.

Population	Trait	Additive genetic variance	Rep. variance	Column variance	Residual (error) variance	Heritability (h^2)	Accuracy (r)	log likeli-hood
Coastal zone	**DBH**	74.01 (45.04)	90.98 (52.26)	73.17 (21.45)	855.6 (53.28)	0.080 (0.048)	0.266	-7373.6
	STR	0.017 (0.011)	0.015 (0.009)	0.006 (0.005)	0.246 (0.014)	0.064 (0.043)	0.246	283.1
	BR	0.011 (0.005)	0.042 (0.023)	0.011 (0.002)	0.078 (0.005)	0.125 (0.053)	0.318	1223.5
	MAL	0.012 (0.006)	0.043 (0.024)	0.002 (0.002)	0.114 (0.007)	0.092 (0.047)	0.288	975.9
	FRK	0.012 (0.006)	0.043 (0.024)	0.005 (0.002)	0.101 (0.006)	0.105 (0.050)	0.302	1048.1
	AC	0.133 (0.302)	0.011 (0.037)	0.029 (0.170)	1 (NA)	0.064 (0.136)	0.11	-3148.8
Counties coastal zone	**DBH**	98.71 (46.45)	49.51 (29.38)	46.03 (20.19)	954.5 (55.69)	0.094 (0.044)	0.308	-7598.9
	STR	0.047 (0.017)	0.092 (0.050)	0.021 (0.007)	0.260 (0.018)	0.153 (0.054)	0.365	107.4
	BR	0.002 (0.003)	0.028 (0.015)	0.017 (0.002)	0.077 (0.004)	0.024 (0.039)	0.168	1306.6
	MAL	0.026 (0.010)	0.025 (0.014)	0.000 (0.000)	0.164 (0.010)	0.137 (0.051)	0.359	618.7
	FRK	0.006 (0.004)	0.028 (0.015)	0.010 (0.002)	0.096 (0.005)	0.059 (0.043)	0.254	1126.1
	AC	0.268 (0.265)	0.125 (0.097)	0.000 (0.000)	1 (NA)	0.124 (0.108)	0.17	-3164.7
Coastal interior zone	**DBH**	96.77 (34.99)	74.47 (41.99)	38.53 (14.21)	965.6 (41.97)	0.091 (0.033)	0.376	-11635.4
	STR	0.038 (0.010)	0.019 (0.011)	0.005 (0.03)	0.187 (0.010)	0.168 (0.042)	0.457	694.2
	BR	0.003 (0.002)	0.015 (0.008)	0.012 (0.002)	0.083 (0.003)	0.034 (0.026)	0.255	1966.9
	MAL	0.002 (0.004)	0.012 (0.007)	0.002 (0.004)	0.162 (0.006)	0.012 (0.021)	0.164	1145.7
	FRK	0.018 (0.005)	0.014 (0.008)	0.014 (0.002)	0.096 (0.005)	0.157 (0.042)	0.442	1579.5
	AC	0.189 (0.191)	0.063 (0.050)	0.000 (0.000)	1 (NA)	0.089 (0.082)	0.188	-4893.2

Table 4: Variance components, heritability, theoretical accuracy of breeding values and log-likelihood for populations planted at Tramway site.

Population	Trait	Additive genetic variance	Replicate variance	Block variance	Plot variance	Residual (error) variance.	Heritability (h^2)	Accuracy (r)	Log likeli-hood
Coastal zone	DBH	368.7 (84.95)	105.7 (95.46)	49.71 (20.57)	71.26 (16.18)	839.8 (69.25)	0.305 (0.065)	0.548	-16186.8
	STR	0.095 (0.021)	0.012 (0.011)	0.007 (0.003)	0.023 (0.004)	0.167 (0.017)	0.363 (0.074)	0.569	652.7
	BR	0.014 (0.005)	0.108 (0.088)	0.001 (0.001)	0.007 (0.002)	0.089 (0.004)	0.139 (0.046)	0.434	2447.1
	MAL	0.042 (0.012)	0.020 (0.017)	0.004 (0.002)	0.007 (0.003)	0.214 (0.011)	0.164 (0.044)	0.471	694.9
	FRK	0.037 (0.013)	0.021 (0.018)	0.007 (0.003)	0.024 (0.004)	0.177 (0.011)	0.172 (0.058)	0.446	954.2
	AC	0.050 (0.177)	0.092 (0.094)	0.035 (0.037)	0.413 (0.123)	1 (NA)	0.024 (0.084)	0.131	-6364.8
Counties coastal zone	DBH	649.9 (113.7)	26.74 (28.28)	41.62 (15.56)	66.40 (12.17)	459.5 (87.67)	0.586 (0.088)	0.728	-19724.5
	STR	0.113 (0.023)	0.012 (0.012)	0.011 (0.004)	0.025 (0.004)	0.171 (0.018)	0.398 (0.074)	0.632	640.2
	BR	0.042 (0.012)	0.012 (0.010)	0.004 (0.002)	0.023 (0.003)	0.188 (0.010)	0.183 (0.051)	0.492	1049.5
	MAL	0.057 (0.013)	0.012 (0.011)	0.006 (0.003)	0.009 (0.003)	0.203 (0.011)	0.217 (0.047)	0.542	852.9
	FRK	0.069 (0.018)	0.011 (0.010)	0.004 (0.002)	0.034 (0.004)	0.204 (0.014)	0.251 (0.061)	0.536	627.8
	AC	0.470 (0.160)	0.000 (0.000)	0.055 (0.040)	0.275 (0.105)	1 (NA)	0.213 (0.057)	0.327	-7881.2
Coastal interior zone	DBH	305.4 (63.86)	7.047 (9.208)	18.16 (7.994)	38.06 (8.333)	537.4 (50.51)	0.362 (0.069)	0.636	-20098.5
	STR	0.156 (0.029)	0.009 (0.003)	0.004 (0.002)	0.015 (0.029)	0.130 (0.022)	0.546 (0.088)	0.722	809.7
	BR	0.027 (0.008)	0.106 (0.087)	0.001 (0.001)	0.019 (0.002)	0.097 (0.007)	0.221 (0.062)	0.521	2669.8
	MAL	0.021 (0.007)	0.010 (0.009)	0.001 (0.001)	0.006 (0.002)	0.223 (0.007)	0.085 (0.028)	0.437	1026.4
	FRK	0.032 (0.010)	0.010 (0.009)	0.004 (0.002)	0.016 (0.003)	0.210 (0.009)	0.130 (0.039)	0.470	992.5
	AC	0.570 (0.154)	0.022 (0.030)	0.029 (0.028)	0.035 (0.078)	1 (NA)	0.231 (0.048)	0.388	-8180.4

Genetic correlations followed the same pattern as the heritability estimates, with most of the correlations estimated at Gowan Hill not differing greatly from their standard error estimates (Table 5). The correlation networks estimated at this site differs slightly between seed zone populations (Figure 2). The most obvious is a difference in the correlation between DBH and acceptance. While this correlation is strongly negative in coastal zone population, it becomes positive in two other populations. Similarly, the genetic correlation between acceptance and branching pattern is positive in the coastal interior zone but negative in the others. Another interesting change in correlation is between DBH and branching pattern. While this correlation is negative in counties coastal zone, it becomes positive in the other two zones. On the other hand, there are correlations that are stable across seed zone populations, between acceptance and malformation (positive), acceptance and straightness (positive), malformation and branching pattern (positive).

In contrary, the majority of genetic correlations estimated at Tramway site were statistically significant (regarding their standard errors), and relatively stable across tested seed zone populations. However, there are few observable trends with respect to changes in the strength of correlations. For example, the correlation between acceptance and forking and between forking and straightness were the strongest at the coastal zone population and decreased toward to coastal interior zone population. The opposite pattern was found in the correlation between malformation and branching and between branching and straightness.

Table 5: Pair-wise genetic correlations estimated at each seed zone within each site.

| Trait combination	Gowan Hill			Tramway		
	Coastal zone	Counties coastal zone	Coastal interior zone	Coastal zone	Counties coastal zone	Coastal interior zone
DBH – STR	-0.852 (0.474)	0.315 (0.298)	0.047 (0.216)	-0.370 (0.140)	-0.245 (0.124)	-0.154 (0.134)
DBH – BR	0.143 (0.348)	-0.686 (0.706)	0.223 (0.347)	0.611 (0.156)	0.450 (0.128)	0.611 (0.130)
DBH – MAL	-0.337 (0.410)	-0.070 (0.298)	-0.677 (0.664)	-0.334 (0.161)	-0.208 (0.132)	-0.543 (0.149)
DBH – FRK	0.719 (0.347)	0.232 (0.390)	0.357 (0.204)	0.502 (0.165)	0.481 (0.117)	0.585 (0.137)
DBH – AC	-0.950 (0.838)	0.537 (0.416)	0.331 (0.370)	0.026 (0.245)	0.235 (0.147)	0.051 (0.168)
STR – BR	-0.166 (0.383)	0.042 (0.530)	-0.557 (0.339)	-0.130 (0.187)	-0.291 (0.160)	-0.367 (0.145)
STR – MAL	-0.065 (0.427)	0.029 (0.263)	0.998 (0.902)	0.881 (0.080)	0.664 (0.093)	0.712 (0.114)
STR – FRK	-0.076 (0.397)	0.194 (0.371)	-0.238 (0.182)	-0.616 (0.150)	-0.486 (0.124)	-0.413 (0.141)
STR – AC	0.941 (0.707)	0.524 (0.306)	0.812 (0.276)	0.999 (NA)	0.783 (0.085)	0.812 (0.075)
BR – MAL	0.031 (0.331)	0.613 (0.674)	-0.831 (0.925)	-0.163 (0.208)	-0.284 (0.170)	-0.589 (0.181)
BR – FRK	0.181 (0.309)	-0.982 (1.001)	0.670 (0.319)	0.258 (0.225)	0.664 (0.135)	0.752 (0.145)
BR – AC	-0.537 (0.589)	-0.121 (0.757)	0.564 (0.562)	0.009 (0.297)	-0.187 (0.190)	-0.339 (0.184)
MAL – FRK	-0.326 (0.318)	-0.667 (0.286)	-0.834 (0.224)	-0.832 (0.112)	-0.793 (0.087)	-0.926 (0.119)
MAL – AC	0.780 (0.119)	0.994 (0.397)	0.941 (0.770)	0.947 (0.152)	0.781 (0.084)	0.772 (0.115)
FRK – AC	-0.559 (0.565)	-0.329 (0.470)	-0.699 (0.322)	-0.999 (0.270)	-0.632 (0.128)	-0.458 (0.167)
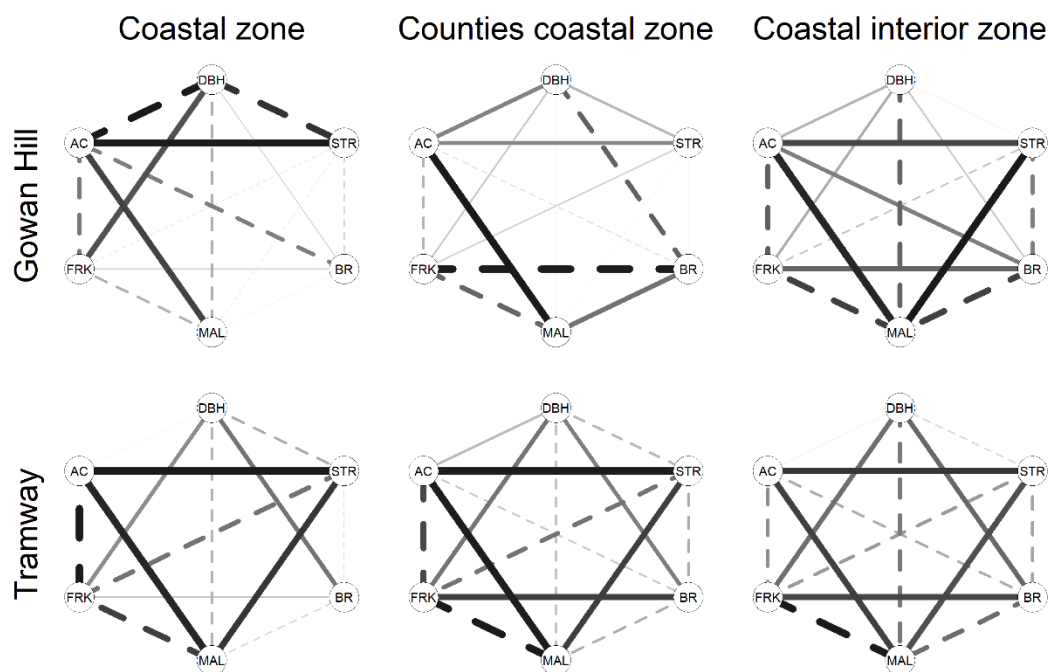
Figure 2: Correlation networks between investigated traits at each studied population; solid line represents positive while dashed line represent negative genetic correlation, the thickness of line represent strength. The darkest, thickest lines are close to 1.0, or strongly positively correlated, where as the thinner lines are close to zero, or not correlated.

The potential response to selection was examined for each zone and each site (Figures 3-8). The potential response to selection was relatively lower in Gowan Hill compared with Tramway due to lower heritability estimates caused by higher mortality and micro-site variability. The response to selection in DBH was between 10 – 15 millimetres at Gowan Hill across all tested zones and between 40 (Coastal and Coastal interior zone) and 80 (Counties coastal zone) millimetres at Tramway. Potential response to selection in STR was between 0.2 (Coastal zone) and 0.4 of the 1-9 assessment score used (Counties coastal and Coastal interior zone) at Gowan Hill and between 0.4 (Counties coastal zone) and 0.8 score (Coastal interior zone) at Tramway.

The potential response to selection in BR was between 0.03 (Counties coastal zone) and 0.22 score (Coastal zone) at Gowan Hill and between 0.18 (Coastal zone) and 0.34 score (Coastal interior zone) at Tramway. The potential response to selection in MAL was between 0.04 (Coastal interior zone) and 0.4 score (Counties coastal zone) at Gowan Hill and between 0.23 (Coastal interior zone) and 0.34 score (Coastal zone) at Tramway. The potential response to selection in FRK was between -0.13 (Counties coastal zone) and -0.29 score (Coastal interior zone) at Gowan Hill and between -0.29 (Coastal interior zone) and -0.52 score (Counties coastal zone) in Tramway (Figures 3 - 8).
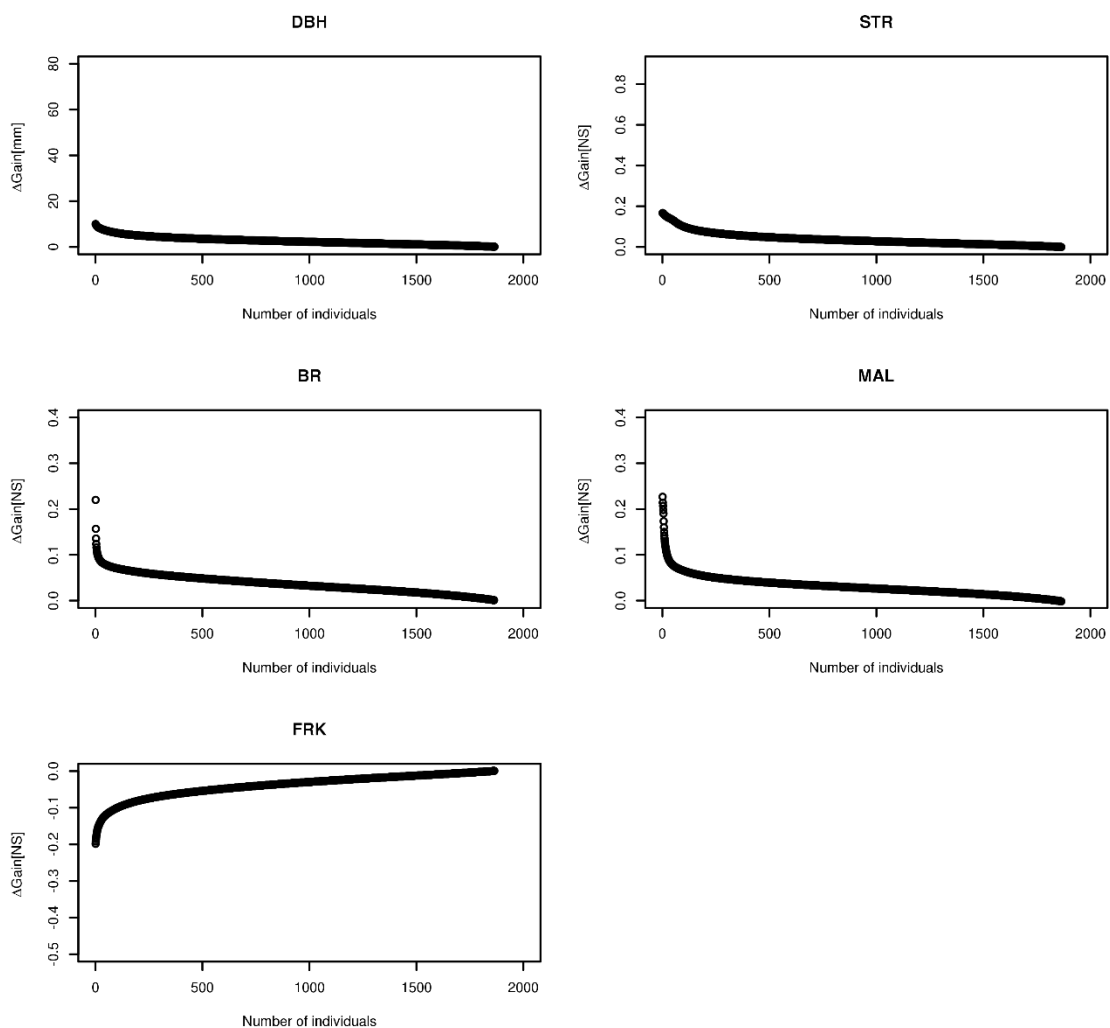

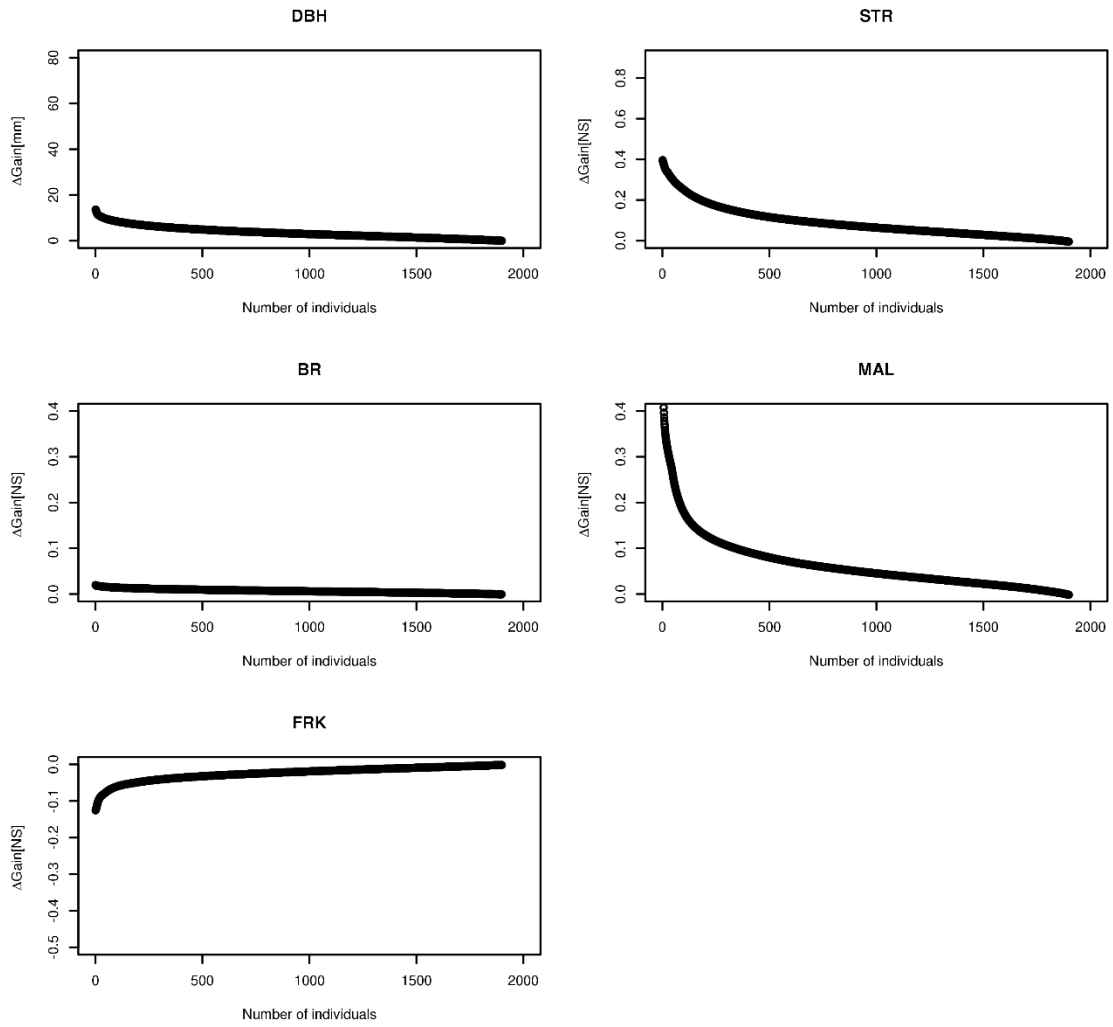**Figure 3:** Potential response to selection in Coastal zone population planted at Gowan Hill.

Figure 4: Potential response to selection in Counties coastal zone population planted at Gowan Hill.
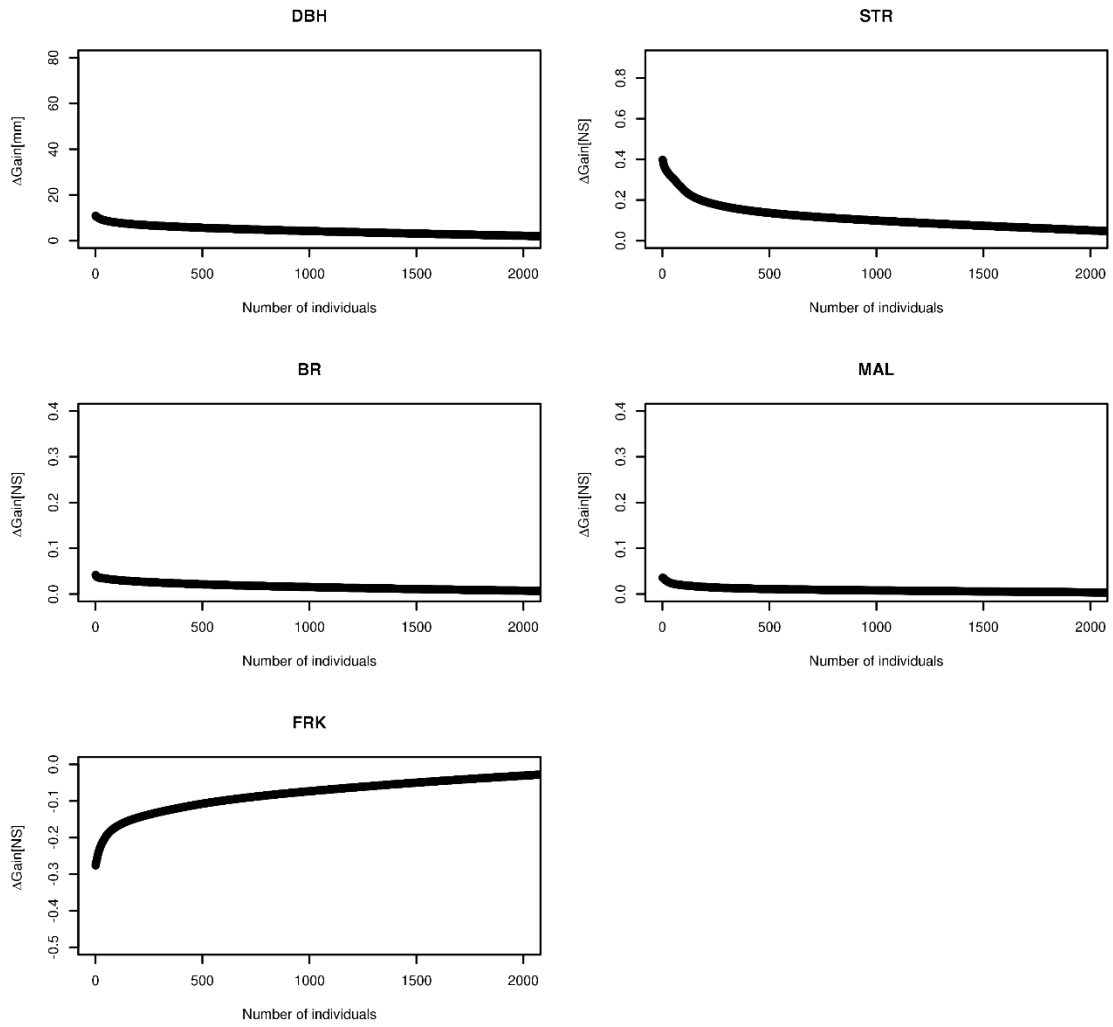
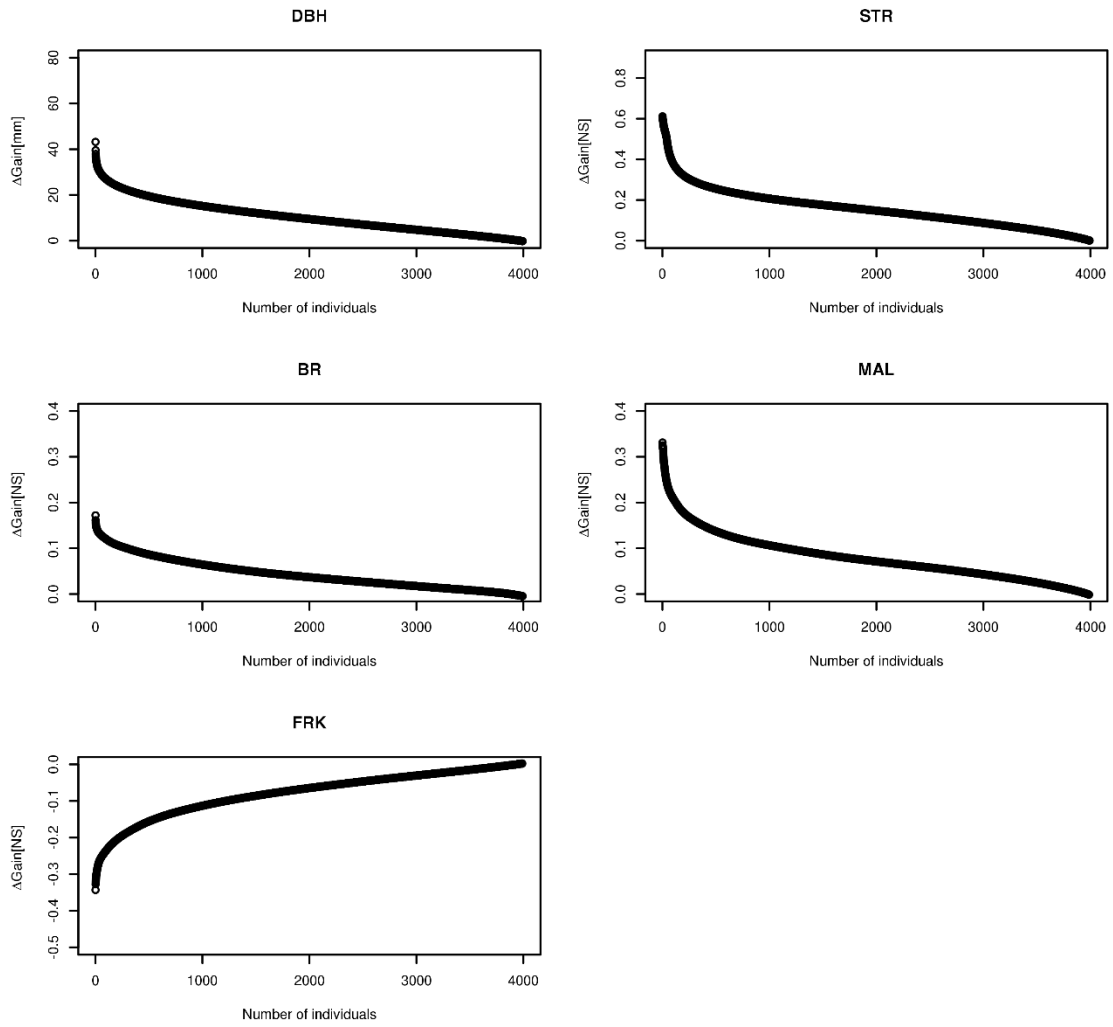**Figure 5:** Potential response to selection in Coastal interior zone population planted at Gowan Hill.

Figure 6: Potential response to selection in Coastal zone population planted at Tramway.
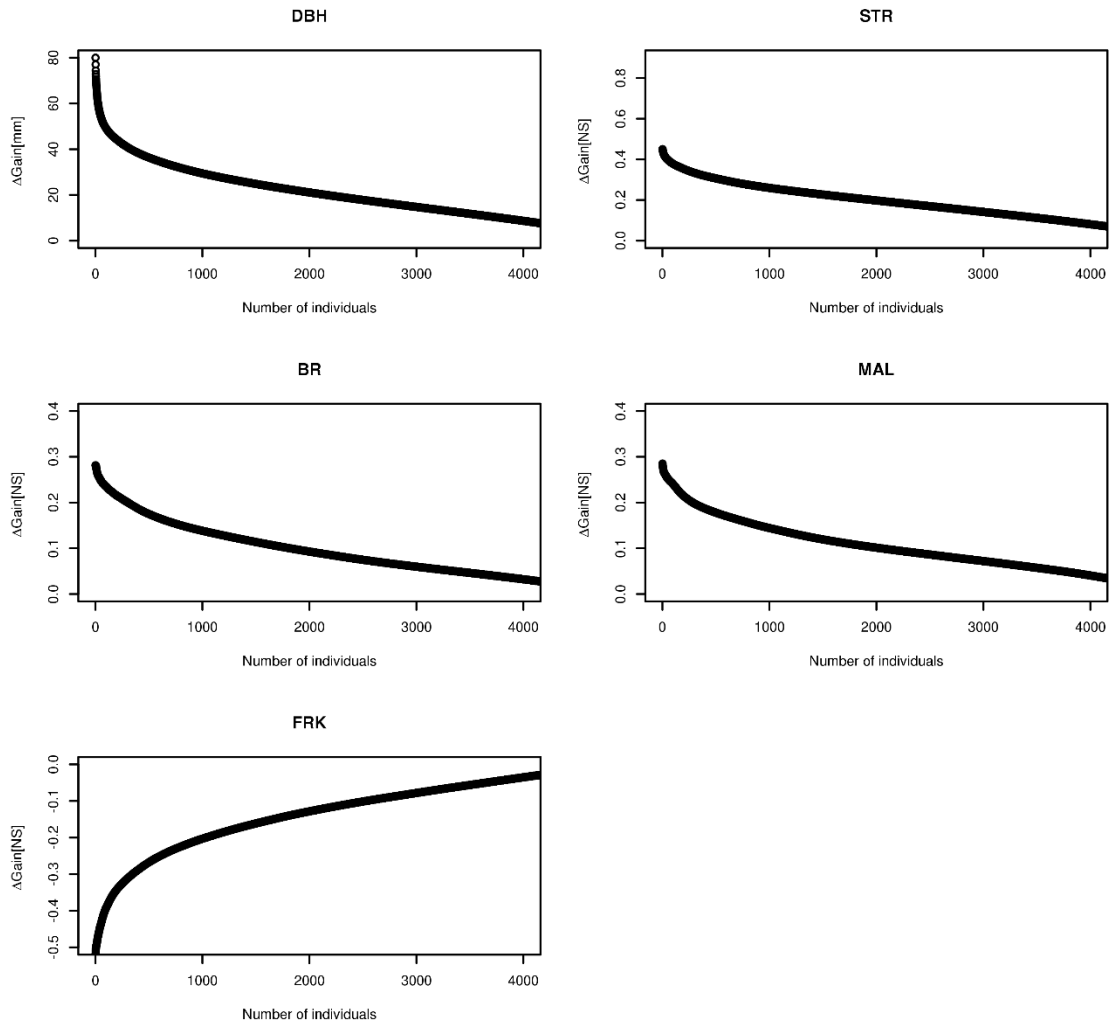
Figure 7: Potential response to selection in Counties coastal zone population planted at Tramway.
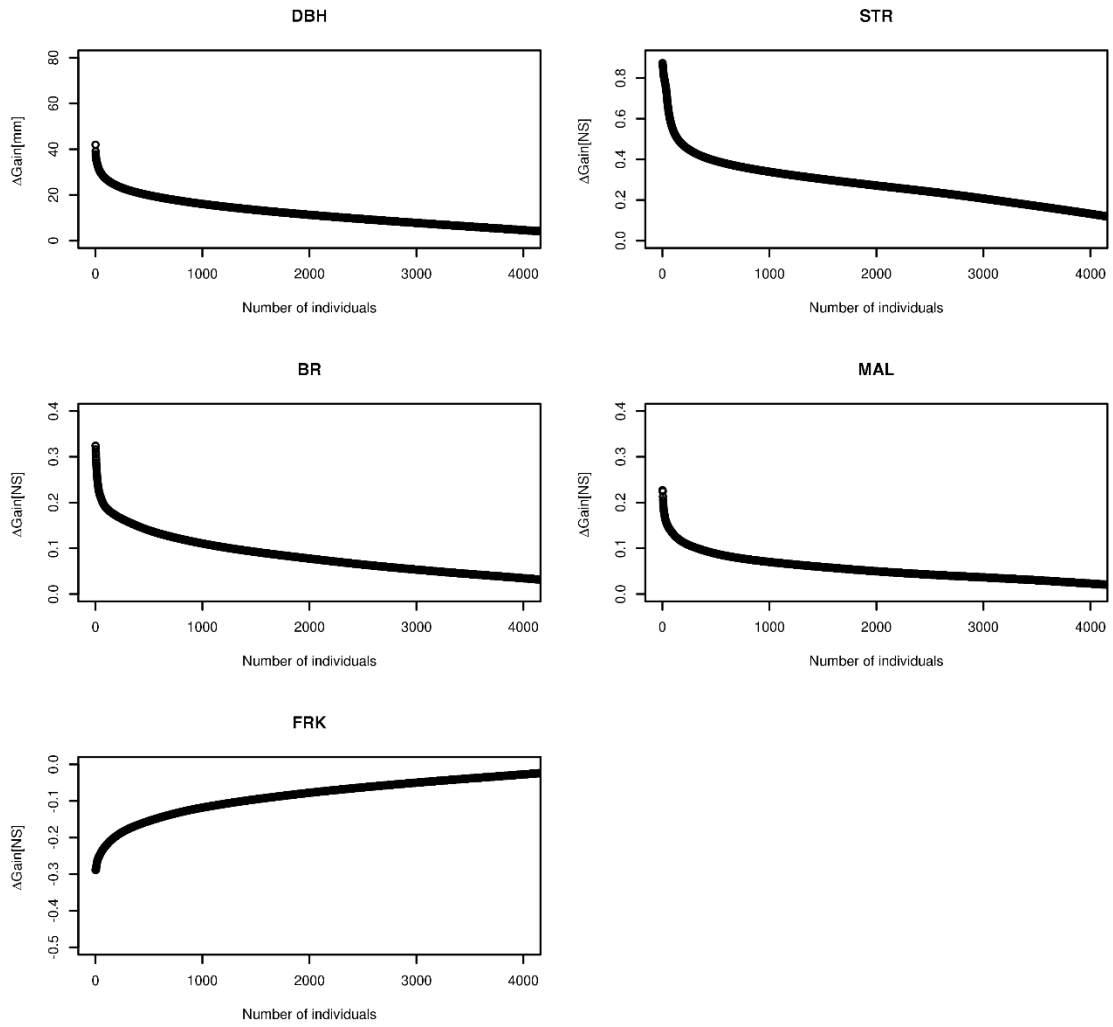
Figure 8: Potential response to selection in Coastal interior zone population planted in Tramway.

CONCLUSION

The average productivity was found to be higher at Gowan Hill compared with Tramway across all tested seed zones (Table 2). This would indicate Gowan Hill is a higher productivity site, a consequence of which usually means that the site will also suffer from a higher proportion of stem defects (Schermann *et al*, 1997). However, we did not observed a higher average occurrence of stem defects in terms of FRK and MAL at Gowan Hill. We suggest that this could be explained by the higher mortality at this site giving the remaining individuals greater growing space, representing release from competition rather than direct site productivity. The higher mortality at Gowan Hill generally resulted in lower estimates of additive genetic variance, heritability and accuracy of breeding values (Table 3). Therefore, results from this site should be considered with caution.

The Tramway site showed moderate estimates of heritability across all traits with the exception of acceptance in the coastal seed zone. This would indicate the possibility of achieving a response to selection through breeding and selection in all investigated traits. The accuracy of breeding values was moderate to high, indicating highly precise selection of high merit candidates at an early age. However, open-pollinated experiments usually suffer from upwardly biased estimates of genetic parameters due to hidden relatedness (El-Kassaby *et al*, 2011). Therefore, these breeding values are likely to be at least a little inflated. A lower level of heritability would be expected after pedigree reconstruction and re-analysis.

While the age : age correlation for productivity traits has been found to be high in previous studies (height at the age of 12 and 35 showed correlation of 0.71 (Thistlethwaite *et al*, 2017); DBH at the age of 12 and 24 showed correlation of 0.84 (Temel and Adams, 2000)), age:age correlations for stem defects can change with time. Temel and Adams (2000) found a change in the proportion of trees having ramicorns and forks, for example. While the proportion of trees with only ramicorns increased from 24.5% in the age of 12 to 30.2% at age 24, the proportion of trees having only forks decreased from 5% to 1.5%. Therefore, more than 50% of trees originally scored as having forks were later scored as having only ramicorns (Temel and Adams, 2000). Nevertheless, both traits seem to be highly correlated (Schermann *et al*, 1997) and therefore considering only one of them in the selection decision procedure should be sufficient.

The analysis of genetic correlations discovered 2 groups of traits connected by positive correlations (Figure 2 – bottom row; Table 5): 1) acceptability, malformation and straightness; 2) DBH, forking and branching pattern. The first group of traits showed that acceptability scores tended to focus mainly on stem quality rather than productivity in the South Island, corresponding with findings in the previous analysis performed on provenance/progeny test established in 1996 (Klapste *et al*, 2017). In addition, a negative correlation between forking and acceptance only confirmed the observed trend. The strong correlation determined between forking and malformation (partially representing ramicorns) would also indicate a useful and efficient response to the simultaneous selection in both traits.

The second group of traits reveals the tendency highly performing individuals to be more likely to suffer from stem defects such as forks or ramicorns than other slower growing trees. In this case, there is a clear and positive correlation between DBH and forking and a weak to moderate negative correlation between DBH and malformation. A negative correlation is due to the direction of the developed scale (higher is better). A positive association between productivity and the number ramicorns was therefore found in this study, a feature that is highlights the complextiy of the observed phenotype in Douglas-fir. The positive relationship between productivity and stem defects has also been identified in previous studies (Magalska and Howe, 2014; Schermann *et al*, 1997; Temel and Adams, 2000). The only unexpected relationship was a positive correlation between DBH and branching pattern, which could be explained by an under-developed crown structure at the time of measurement, or the crown length was still high, with needles able to hide the underlying branch habit, revealed post canopy closure. In order to make a reliable judgement on branching we therefore recommend that the scoring of branching habit should be performed at later age when the crown is already well developed and/or branches are clearly visible.

In summary, the current analysis has provided insight into the inheritance of the investigated traits at a young age. We would highly recommend that any selection decisions are focussed on the Tramway experiment due to higher survival rate and higher statistical confidence in estimated genetic parameters compared with Gowan Hill. The descriptive statistics found slightly better average straightness and lower average number of forks in the Coastal Interior zone compared with the other provenance groups. It was unclear what the exact cause was, but the difference could be explained by delayed bud break and budset of interior provenances.

The heritability estimates obtained in this study indicate the potential for genetic improvement through selection and breeding. We found most of the stem defect traits well expressed in the early age to obtain statistically significant genetic parameters. However, the branching pattern (BR) showed an unexpected relationship with the productivity trait (DBH), which could be caused by the immaturity of this trait to be reliably scored. We recommend evaluating this trait at a later age when the crown structure is more developed.

Generally lower response to selection was achievable in Gowan Hill compared to Tramway due to lower heritability estimates caused by increased micro-environmental heterogeneity. The response to selection of 80 millimetres achievable in DBH was found in Counties coastal zone while only 40 millimetres were found in other two seed zones (following trends observed in heritability). Similarly, the highest response to selection in FRK was found in the same zone but the unfavourable correlation prevent to improve these traits simultaneously. Coastal interior zone was able to reach maximum response to selection in STR and BR while Coastal zone reached maximum response to selection in MAL.

Selections should now be made for inclusion into the testing and deployment programmes. We recommend this is undertaken using the breeding values supplied to Ernslaw One with this report, based on the desired traits from the Douglas-fir breeding workshop, and in consultation with Forest Growers.

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