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Evaluation of wood stiffness in Douglas-fir progeny test FR280_2 and FR280_3

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FOREST GROWERS RESEARCH

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EXECUTIVE SUMMARY

The key outcome from this research is that wood stiffness was found to be moderately heritable, had low genotype by environment interaction and good potential still exists for improvement in this trait in the New Zealand Douglas-fir breeding programme.

An evaluation of acoustic wave velocity was performed at two sites of a Douglas-fir open-pollinated experiment, which includes a geographically broad representation of the species natural distribution. Our quantitative genetic analysis found statistically significant genetic variance and a moderate heritability. This confirms that genetic improvement of wood fibre quality continues to have potential.

Our analysis also found considerable trait stability across environments and age, making cost-effective phenotyping strategies and genomic prediction feasible for forward selection. However, silvicultural treatments are likely to cause structural changes and attenuate genetic variation. Therefore, the implementation of models accounting for spatial competition could amplify the genetic signal and consequently increase the precision of genetic parameters.

Detailed laboratory-based phenotyping of wood fibre attributes and their relationship with acoustic velocity would be beneficial. While not essential, this data would help to understand the wood structure changes associated with changes in acoustic velocity, helping tree breeders fully utilise acoustic velocity or alternative phenotyping methods in the selection process.

INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the second most important conifer plantation species in New Zealand after radiata pine (Shelbourne et al., 2007; Miller and Knowles, 1994). The current planted area is approximately 104,000 ha. Douglas-fir breeding programme in New Zealand was initiated in 1955 with extensive provenance test including material from Washington, Oregon and California (Sweet, 1965) with additional provenance test established in 70'. Initial genetic evaluations identified material from Oregon and California as the best for growing conditions in New Zealand and was followed by establishment of multi-site provenance/progeny test with material coming from the preferred provenances (Dungey et al., 2012). Genetic improvement is a major tool for ensuring that Douglas-fir plantations remain economically viable. In addition to growth parameters, breeding should be focused on the quality of wood fibre in genetically improved materials. Wood density and stiffness are the most important wood quality attributes (physical properties) that are measured on an operational scale. Lausberg (1996) found decent variation between individuals within provenances rather than between provenances which provided evidence for reasonable improvement of wood quality in Douglas-fir through breeding and selection.

Acoustic wave velocity (AWV) has been proved to be a viable alternative of more sophisticated and expensive types of measurements, such as those obtained by the SilviScan technology (Wang et al. 2002; Leg and Bradley 2016; Newton 2018). Measurements of AWV are derived as a function of the density-weighted velocity of a longitudinal stress wave (km/s) that propagates through the xylem tissue. The heritability of AWV has been estimated for several tree species, with values ranging from 0.20 in Douglas-fir (El-Kassaby et al. 2011) to 0.38 in white spruce (Lenz et al. 2013) and 0.60 in radiata pine (Wielinga et al. 2009). Strong phenotypic correlations with wood quality traits were estimated in black spruce, red pine and jack pine, especially with wood density (0.67 – 0.78), microfibril angle (MFA) (-0.71 – -0.90), tracheid wall thickness (0.67 – 0.69), and specific surface area (-0.58 – 0.64). Therefore, there is potential for indirect genetic improvement in wood fibre characteristics associated with AWV. Lenz et al. (2013) found improvement of 4% in MFA, 5.5% in wood density, 9% in ring width, and 13% in late wood width as an indirect response on selection for AWV (improvement of 9.9%).

This study is focused on the evaluation of AWV in a population of Douglas-fir with geographically broad representation (Oregon and Northern California). Genetic parameters, such as heritability and genetic correlations, were estimated to compare the stability of AWV across environments and ages.

METHODS

Wood stiffness was measured through AWV (time of flight between two probes placed on the tree around breast height) using the Hitman ST300 (Fibre-gen, Christchurch, New Zealand). Measurements were taken for 241 families at Kaingaroa Cpt 1322 in August and September 2018 and 246 families at Gowan Hill in May 2018. These field experiments were previously measured and analyses for productivity, stem form and acoustic wave velocity at age of 11 years (Dungey et al. 2012). Because genomic information was available for a subset of the population included in the genomic selection project, marker data were used for sib-ship reconstruction. Results from these analyses were used to update the pedigree information. For individuals with missing paternal information, genetic groups were assigned to account for genetic differences between provenances and improve the precision of genetic parameters (Klapste et al. 2019).

Variance components were estimated using a mixed linear model implemented in the ASReml-R package (Butler et al. 2009) as follows:

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Zg} + \boldsymbol{Zr} + \boldsymbol{Zr}(\boldsymbol{s}) + \boldsymbol{e}$$

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 $var(\boldsymbol{g}) \sim N(0, \boldsymbol{A}\sigma_g^2)$, where ***A*** is average numerator relationship matrix (Wright 1922) and σ_g^2 is additive genetic variance. The vector ***r*** contains the replication effects following $var(\boldsymbol{r}) \sim N(0, \boldsymbol{I}\sigma_r^2)$, where ***I*** is identity matrix and σ_r^2 is replication variance and ***r(s)*** is the vector of random set within replication effects following $var(\boldsymbol{r}(\boldsymbol{s})) \sim N(0, \boldsymbol{I}\sigma_c^2)$, where $\sigma_{r(s)}^2$ is the set within replicate variance. The vector ***e*** contains random residual effects and follows $var(\boldsymbol{e}) \sim N(0, \boldsymbol{I}\sigma_e^2)$, where σ_e^2 is residual variance.

The narrow-sense heritability of continuous traits and traits transformed into normal scores was estimated as:

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

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

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

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

The theoretical accuracy of breeding values was estimated as follows:

$$r = \sqrt{1 - \frac{PEV}{\sigma_g^2}}$$

where PEV is the prediction error variance (Mrode 2014) estimated as the squared standard errors of the breeding value estimates.

RESULTS

The measurements of acoustic wave velocity taken at both sites followed an approximately normal distribution (Figure 1), with a higher mean observed at Kaingaroa (4.97) compared with Gowan Hill (3.85). However, the phenotypic variances were similar at both sites (0.162 versus 0.155). The narrow sense heritability was statistically significant at both sites (i.e. based on standard errors) and was higher at Gowan Hill (0.369 ± 0.050) than at Kaingaroa (0.255 ± 0.053). Similarly, the accuracy of estimated breeding values was higher at Gowan Hill (0.530) than at Kaingaroa (0.393) (Table 1).

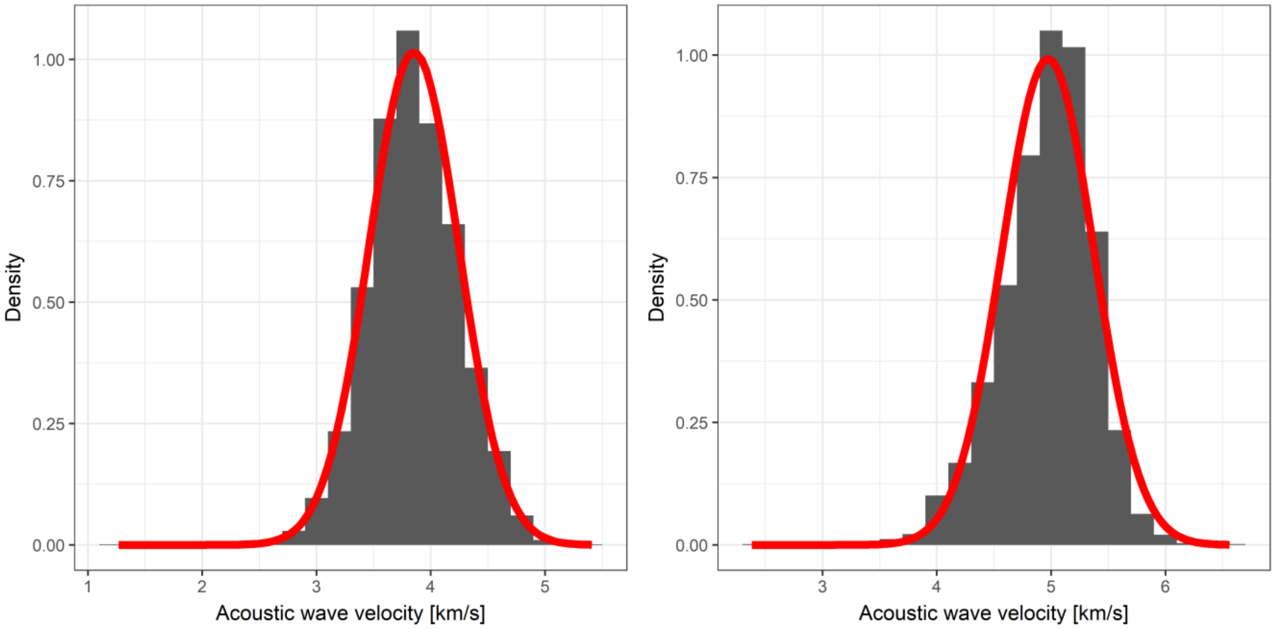

Figure 1: Distribution of acoustic wave velocity measurements from Gowan Hill (left) and Kaingaroa (right).

Table 1: Variance components, narrow-sense heritability, log likelihood and accuracy of breeding values estimated at each investigated site.

Parameter	Gowan Hill	Kaingaroa
Additive genetic var.	0.039 (0.0058)	0.033 (0.0072)
Replicate var.	0.041 (0.0110)	0.017 (0.0054)
Replicate(set) var.	0.002 (0.0001)	0.015 (0.0025)
Residual var.	0.067 (0.0049)	0.097 (0.0067)
h^2	**0.369 (0.0504)**	**0.255 (0.0528)**
logL	2770.3	2900
r	0.53	0.393

The genetic correlation of AWV measured at Kaingaroa versus at Gowan Hill was 0.81 ± 0.097, indicating a low impact of environmental variation (North Island versus South Island) and only a weak genotype by environment interaction (GxE). Similarly, the genetic correlation between AWV measured at different ages (11 versus 23) was very strong (0.98 ± 0.023) at Gowan Hill, suggesting that trends were highly consistent across ages and the screening tools were reliable. The age-age correlation was lower at Kaingaroa (0.67 ± 0.171), presumably due to thinning that occurred between the two different ages of assessment.

The nearly perfect genetic correlation (0.98) obtained at Gowan Hill between measurements at different ages (10 versus 22) indicates high reliability of the phenotyping screening process and lack of major wood quality changes between these ontogenetic stages. On the other hand, the lower heritability (0.26) and age-age correlation (0.67) at Kaingaroa was probably caused by silvicultural treatments performed between age 10 and the age 22 assessment. This is very likely to have changed the competition dynamics in the stand, potentially also affecting wood quality. Additionally, the number of early-age observations was much lower at this site, which might have further affected our genetic correlation estimate. The implementation of models accounting for changes in the dynamics of competition could potentially improve the estimates of genetic parameters.

The response to selection found the limits of genetic improvement at 0.7 above the population mean at Gowan Hill and at 0.4 above population mean at Kaingaroa which corresponds to differences in heritability estimates obtained at each site. Nevertheless, when DBH is considered only 0.2 at Gowan Hill and 0.1 at Kaingaroa can be considered as limit for improvement without decrease in productivity. However, the analysis identified several individuals that were superior at both investigated traits coming mostly from the Willamette forest, Umpqa river and Point Reyes provenances (Figure 2).

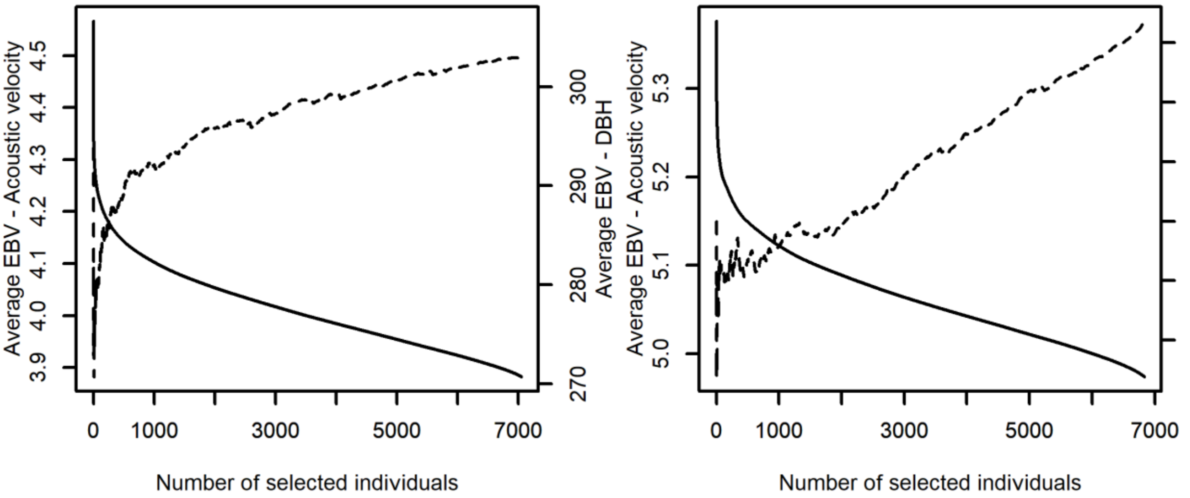

Figure 2: Response to selection in acoustic velocity (solid line) and DBH (dash line) in terms of average breeding values when n best individuals in acoustic velocity are selected at Gowan Hill (left plot) and Kaingaroa (right plot). Average EBV is equivalent to the genetic gain that would be achieved should these individuals be selected.

CONCLUSION

Acoustic wave velocity was found to be moderately heritable in Douglas-fir, with values ranging from 0.26 to 0.37. These results are consistent with previous results obtained at an early age by Dungey et al. (2012) where heritability reached values from 0.34 to 0.75. Moderate heritabilities such as these demonstrate good potential for genetic improvement and selection for wood stiffness, and its constituent fibre attributes such as microfibril angle, cell wall thickness and wood density. The heritability reached at the current age allowed for genetic improvement of 0.4 – 0.7 km/s when the top 10 individuals were selected. However, selection for acoustic velocity only would result in decreased productivity. Nevertheless, we identified several individuals having superior genetic quality for both traits.

In contrast with other conifer species, El-Kassaby et al. (2011) found a poor relationship between AWV and X-ray-based estimates of wood density in a Douglas-fir full-sib progeny test. Based on this result, they recommended using a resistograph for field-based measurements of wood density. While AWV is already being used for selection in the Douglas-fir breeding programme, the results from El-Kassaby et al. (2011) suggest that New Zealand should test the association further. Validation of AWV measured on a number of trees followed by lab-based measurements of wood stiffness and/or fibre traits would help bring assurance that this is the right tool for this species. This could be pursued through inventory studies or in progeny tests.

The strong genetic correlation of 0.81 between AWV measured at different sites indicates high stability and weak genotype-by-environment interactions. This is in an agreement with previous results from an early age evaluation (Dungey et al., 2012) which found genetic correlation of 0.97 between investigated sites. This is favourable as it potentially allows measurements to be taken at a single site. Since the prediction of non-phenotyped individuals based on pedigree information only allows the prediction of the family mean, a genomic prediction model would be necessary to capture Mendelian segregation (within-family variation), as well as allowing more effective forward selection. In the meantime, breeding values from progeny tests using a quantitative approach will remain appropriate. The currently adopted approach reflects the reasonable deployment of available investments into Douglas-fir breeding in New Zealand. However, the relationship between acoustic wave velocity and x-ray based wood density should be investigated for further improvement in selection efficiency. Even sparse x-ray wood density phenotyping with implementation of genetic correlations with intensive phenotyping for acoustic velocity in the context of genomic selection could be a reasonable strategy to increase precision of the selection decisions.

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APPENDIX

Breeding values estimated for each individual at each population/site