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Analysis of Growth and Wood Traits at Age 5.5-year from *Eucalyptus nitens* Progeny Test at Fortification Road

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EXECUTIVE SUMMARY

Eucalyptus nitens plantations totalling 12,000 ha and growing at above 20 m^3/ha/year MAI are grown on short rotations in Southland. These plantations are harvested to produce export woodchips for kraft pulping. The firm involved seeks to increase the profitability of the enterprise by creating a breeding population composed of individuals that will increase the amount of kraft pulp produced per hectare. This is a function of three traits: growth rate, wood basic density and pulp yield of each tree.

The potential of *E. nitens* as a source of pulp wood in New Zealand has given the impetus to several cycles of breeding, starting with the testing of native provenances, Australian seed orchard material and selections from provenance/progeny trials. The resulting selected genotypes have been maintained in clonal archives that are also managed as seed production areas. The current breeding programme aims to

(i) confirm the breeding value of selections in the archive, and
(ii) confirm the breeding value of forwards selections from a trial of these offspring.

This interim report details the results of the age 5.5 year measurement of the FR481 *Eucalyptus nitens* progeny test at Fortification Road in Southland. Selections from this trial will be used to form part of the third generation of *E. nitens* to be tested in New Zealand, while providing further information of the genetic value of the parents.

Four *E. nitens* seed orchards in New Zealand supply the current seed requirements of *E. nitens* growers. The current breeding strategy requires progeny testing of selections made within these orchards. The present progeny test was established in 2005, and 2160 trees were measured for diameter, straightness, and stem malformation in February 2011. Height and volume were derived from regression equations on DBH. Basic density was measured from increment cores that were collected at the time growth and form traits were assessed. Data were analysed for genetic parameters, and breeding values were estimated for all traits. Several selection scenarios were explored to provide provisional selections pending availability of predicted pulp yield data.

There were significant differences among seed orchard sources for all traits, while region was significant for all traits except straightness and malformation. Waikuku and Alexandra sources tended to be superior for growth and form traits, while Tinkers was best for density. The Forestry Tasmania source and ATSC control generally performed poorly in this trial.

The analysis demonstrated significant and exploitable genetic variation in all traits. Heritability was moderate to high for density (0.48), moderate for straightness (0.20), but low (≤ 0.10) for all other traits. The only significant genetic correlations were observed between the three growth traits. The genetic correlations between growth and form traits (or density) were generally low and adverse (negative), but not statistically significant.

A rolling front selection scheme allows selection of the best performing genotypes regardless of generation based on breeding values. The selection scenario where we make selections from only those individuals with positive breeding values for both volume and density is one alternative to advance and make genetic improvements for both traits in the *E. nitens* breeding population. The trade-off between maximising genetic gain and maximising genetic diversity will need to be considered. Individual selection with no restriction on relatedness results in a loss of genetic diversity. The alternative of maximising the number of families retained reduces genetic gain but retains genetic diversity.

Management decisions that involve culling of parents from existing seed orchards, or changing germplasm supply arrangements should be delayed until pulp yield has been assayed. While this report provides preliminary selections for growth, form and density, the final selections for deployment in orchards and for turnover of the breeding population will be based on selection for pulp productivity, and on resistance to browsing by *Paropsis charybdis*.

INTRODUCTION

This project sits in the eucalypt section of Diversified Species Theme in Future Forests Research (FFR). The project aims to identify growth, form and density selections that will contribute to the selection of the next generation of *E. nitens* in New Zealand. Final selections will be made once NIR-predicted pulp yield data become available.

The initial breeding strategy for New Zealand *E. nitens* (Cannon and Shelbourne 1991) established an open-pollinated breeding population with 305 families divided into 10 sublines. The first meeting of the technical steering committee of FFR (2008) voted that

- the status of *E. nitens breeding* trials, selections, orchards and archives in New Zealand be documented, and
- a draft formal breeding plan (Stovold *et al*. unpublished) for the species be produced.

This breeding plan provides direction, goals and a measure of progress for future genetic improvement. Current goals of the programme are to:

- maintain long-term viability of the breeding population (using parental reconstruction),
- select families with elevated pulp production, and
- identify selections for use in improved commercial seed production (including health traits).

Eucalyptus nitens plantations totalling 12,000 ha are grown in southern New Zealand for pulpwood export. At present, the genetic material deployed in these stands is open-pollinated (OP) seed collected from second generation seed orchards located in the central and southern South Island of New Zealand. These include the Tinkers, Waikuku, Alexandra and Drumfern sites. Forestry Tasmania also operates *E. nitens* seed orchards in Tasmania. OP seeds collected from outstanding individuals in all of these orchards were established in new progeny tests in southern New Zealand in 2005. The purpose of these tests was to confirm the genetic worth of the parents in the seed orchards as a basis for their retention in the breeding population (backwards selection) and to provide selections from within the new trials (forwards selection).

The owner of the land on which the trial grows is the major grower of *E. nitens* in New Zealand, and also owns and operates pulping operations offshore. Harvested trees are chipped at the dockside and exported to kraft pulping facilities. This business structure is vertically integrated from the growing of trees through to their processing to pulp. Traits relevant to this owner's objective are volume, wood density and pulp yield. Each of these traits has a significant impact on the profitability of a breeding programme that aims to maximise profit per hectare of land (Greaves *et al*. 1997).

[1] Profit ($) = *a* volume +*b* basic density + *c* pulp yield

The breeding value for each individual is the Profit, which is estimated as a linear function of the breeding value for each profit trait multiplied by their economic weight, obtained via the Smith Hazel index $\mathbf{b} = \mathbf{P}^{-1}\mathbf{Aa}$; where **b** is an n x 1 vector of index coefficients, **P** and **A** are the n x n matrices of the phenotypic and additive genetic variance-covariance matrix, and **a** is an n x 1 vector of index weights.

Estimating **b** is relatively straightforward provided that all traits have been measured in a genetic trial of appropriate scale. Stem diameter and volume are readily obtained from field measurement (as are form and malformation which are non-key culling traits more suited to sawlog profit objectives). Wood property traits are more rarely measured due to the cost of processing large samples. While wood density (fresh volume/Oven dry weight of a wood specimen) is readily obtained from a basal cambium-to-cambium wood core, predicted pulp yield is best obtained through methods that model the near infrared (NIR) spectra of powdered wood specimens to those spectra for which laboratory values of pulp yield are available.

The FFR *E. nitens* breeding population is to be managed as a rolling front cycle, whereby forwards and backwards selection from progeny tests are made as each progeny test matures. The present report describes the genetic material in the FR481 trial at Fortification Road, eastern Southland.

This interim report details the results of the age 6 measurements (growth, form, density) of the FR481 *Eucalyptus nitens* progeny test at Fortification Road. Selections from this trial will be used to form part of the third generation of *E. nitens* selections to be tested in New Zealand, while providing further information of the genetic value of the parents. Data were analysed for genetic parameters and breeding values were estimated for all traits. Several selection scenarios were explored to provide provisional selections pending availability of NIR-predicted pulp yield data.

NIR chemo-metric techniques have been developed to acquire larger samples of wood chemical values for a given measurement cost. Data sets with larger numbers of families for which density and pulp yield are available allow reasonably reliable estimation of unbiased heritabilities and genetic correlations. High sampling intensity helps identify the significance of correlations, which is essential to evaluating the value of a low correlation between two potentially important traits. The genetic correlations between growth rate and density (often assumed to be negative) and between density and pulpwood (often wishfully assumed to be positive) are not necessarily so, and for any population the relationship needs to be established prior to making critical selection decisions.

METHODS

Genetic Material

Fifty-eight outstanding mother trees were selected from four second-generation New Zealand seed orchards, from which OP seed was collected (Table 1).This New Zealand material could be traced back to the original Australian collection regions (Toorongo, Macalister and Rubicon) in central-east Victoria, Australia (Appendix 1). Twelve seedlots were obtained from the Forestry Tasmania breeding programme, for which the pedigree was unavailable. One Australian Tree Seed Centre (ATSC) bulk collection from OP parent trees (Blue Range provenance) was nominated as the control.

Table 1: Seed orchard origin of mother trees used in FR 481

Alexandra (9)	ATSC – Control (1 bulked seedlot)	Drumfern (12)	Forestry Tas. (12 with unknown pedigree)	Tinkers (29)	Waikuku (8)
P800	P999	P49	P5009	P101	P874
P804		P693	P5010	P109	P1110
P807		P820	P5015	P110	P1865
P810		P836	P5016	P113	P1870
P811		P854	P5018	P119	P1875
P815		P865	P5019	P124	P1888
P822		P867	P5028	P129	P1893
P828		P870	P5031	P134	P1899
P829		P875	P5044	P135	
		P888	P5049	P141	
		P893	P5058	P142	
		P899	P5138	P143	
				P144	
				P145	
				P148	
				P150	
				P153	
				P155	
				P156	
				P158	
				P161	
				P163	
				P164	
				P168	
				P169	
				P173	
				P177	
				P408	
				P423	

Trial Design

The trial comprised 30 replicates, each made up of two sets-within-replicates, of 36 planting spaces. The sets were used to simplify trial preparation, while equal numbers of families from each seed orchard were allocated to each set-within-replicate to minimise the likelihood of a set effect. The trial was raised and planted out according to McConnochie (2005, 2006); location was 46°30'S 168°58'E; elevation ranges between 80-100 m above sea level, while aspect was 5 degrees to the south. Following a previous rotation, slash was windrowed in north-south lines, approximately 20 m apart. Containerised *E. nitens* planting stock (Figure 1) were planted in August 2005 at 3.0 x 2.8-metre spacing. Each replicate spanned two windrows, with one set planted in six rows across one windrow. A line of edge trees around the entire trial was planted later, but not consistently at 2.8 metres between the trial trees; nor did they consistently establish with the same vigour as the trial trees.

Figure 1: Picture of containerised *Eucalyptus nitens* planting stock at the time of planting.

Trial Measurements

A total of 2160 trees were measured for diameter (DBH, mm), stem straightness (on a scale of 1 worst to 9 best; Figure 2), and stem malformation (Figure 3**Error! Reference source not found.**) in February 2011 (Figure 4). Height (m) was derived by measuring a select number of trees from each orchard to form regression equations based on diameter (Appendix 3); and volume was calculated based on diameter and derived heights. Where two stems were encountered at breast height, both diameters were obtained. For analysis, the average of the two stems was used. Cambium-to-cambium wood cores 6 mm diameter were obtained from all trees of >6 cm DBH in those replicates numbered 1, 3, 5, 7, 10, 11, 15, 15, 18, 20, 21, 24, 25, 28 and 30, and then frozen. Density of wood cores was measured. NIR will also be measured on wood cores to derive pulp yield, but is not included in this report.

Statistical Analyses

See Appendix 2.

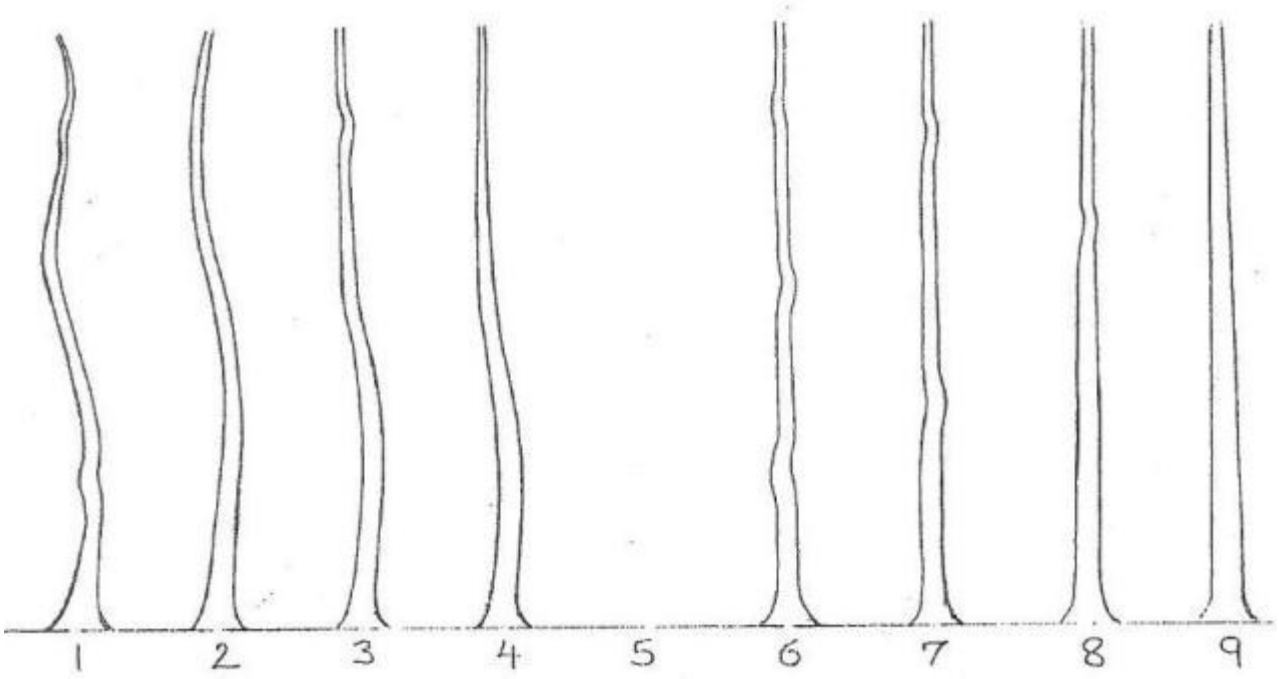

Figure 2:Stem straightness score for *Pinus radiata* stem quality (NZRPBC 1997) as applied in the 2011 Fortification Road *E. nitens* assessment. Class 5 is not scored to avoid central bias.

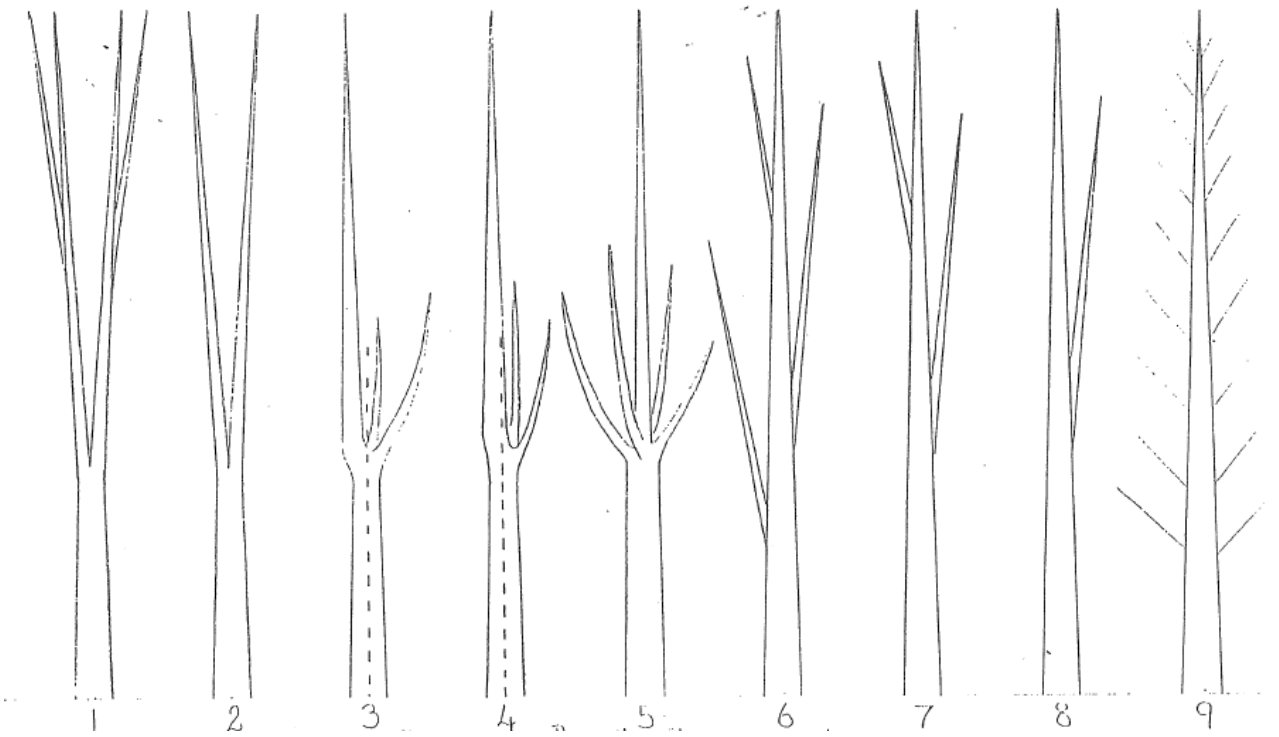

Figure 3: Malformation score for *Pinus radiata* stem quality (NZRPBC 1997) as applied in the 2011 Fortification Road *E.nitens* assessment.

Figure 4: *Eucalyptus nitens* progeny trial at time of assessment.

Rolling Front Selection, Genetic Gain and Diversity

The FFR *E. nitens* breeding population is to be managed as a rolling front cycle, whereby forwards and backwards selections from progeny tests are made as each progeny test matures. The breeding values for all individuals and parents (= family) for diameter, height, volume, straightness, malformation and density were predicted. A number of selection scenarios were explored in order to estimate the genetic gain.

First, a backwards selection scenario was simulated in which families were sorted from highest to lowest based on the BVs for each trait. The genetic gain (%) compared with the population mean was estimated from direct selection of each trait. Statistics obtained were: average of 10 top families, average of 20 top families, average of 30 top families, average of 40 top families, average of 50 top families, average of 60 top families, and average of all 70 families (ATSC control was excluded).

Second, two different rolling front selection scenarios were considered. One selection scenario looked to maximize genetic diversity (MGD) by selecting the single best individual in each of 70 families (70 selections), top two individuals in each family (140 selections), top three individuals in each family (210 selections), and top four individuals in each family (280 selections). As a comparison, selection was made to maximize genetic gain (MGG) ignoring relatedness among selections by selecting the top 70, 140, 210 and 280 individuals with the best breeding values for each trait. The corresponding genetic response was also tallied for the remaining five traits. Genetic diversity here is measured as a count of the number of families represented in selections.

Third, in order to explore the relationship between genetic gain and genetic diversity further, the genetic gain versus genetic diversity was plotted at selection intensities from 1-60% of the total population. Genetic gain (%) was plotted on one axis, while the number of families represented in the selected population was plotted on a secondary axis.

Fourth, the final selection scheme aimed at selection of individuals with positive breeding values for both density and volume. Similarly to approach three above, genetic gain versus genetic

by direct selection of either density or volume, the genetic gain from indirect selection of the alternative trait was estimated. In this scenario, population advancement would be possible for both traits.

In all cases of predicting genetic gain,

$$\text{Gain} = \frac{\bar{x}_{BV\_SEL}}{\bar{x}_{Pred}} \times 100\%$$

where $\bar{x}_{BV\_SEL}$ is the mean predicted breeding value of selected population and

$\bar{x}_{Pred}$ is the predicted mean using fixed-effect solutions from the model and

$= \text{mu} + \frac{\sum \text{Source}_i}{m} + \frac{\sum \text{region}_j}{n}$, where m and n are the number of Sources and Regions, respectively.

RESULTS AND DISCUSSION

Trial Statistics

At age 5.5 years, the FR481 field trial had an overall phenotypic mean for DBH of 145.3 mm, height of 13.0 m, volume of 0.24 m^3, straightness of 6.4, malformation of 7.6 and density of 467.9 kg m^{-3} (

Table 2). Mean survival was 94.8% (data not shown).

Comparison between Seed Orchard Source and Region

Seed orchard source was statistically significant for all traits (

Table 2). The mean DBH for the offspring of the Waikuku (152.86 mm), Alexandra (151.73 mm), and Drumfern (148.69 mm) orchards was significantly higher ($p < 0.05$) than the mean values of those trees from the Tinkers orchard (141.82 mm), the Forestry Tasmania source (141.12 mm) and the ATSC control (140.78 mm) genotypes (

Table 2a). A similar trend was observed for height and volume, and Forestry Tasmania material had significantly lower height and volume than the other sources (Table 2b; 2c). The range in mean straightness was 0.9, Waikuku and Alexandra seed orchards having significantly higher straightness than other sources, while mean straightness of ATSC control had significantly lower straightness scores ($p < 0.05$) (Table 2d). Alexandra ranked highest for malformation (8.2) although not significantly better than Waikuku (7.8)or the ATSC control (7.7) (Table 2e). For density, Tinkers source (479.1 kg m^{-3}) was significantly higher than all other sources, and the ATSC control (437.3 kg m^{-3}) had significantly lower density than all other sources ($p < 0.05$) (Table 2f).

The effect of region was significant for DBH ($p < 0.05$), height ($p < 0.0001$), volume ($p < 0.001$) and density ($p < 0.05$), while not significant for straightness and malformation (Table 3). Rubicon region ranked highest for DBH (Table 3a), and means of height and volume of Rubicon region were significantly greater than all other regions (Table 3b; 3c). Region N was confounded with the Forestry Tasmania seed orchard source. However, Forestry Tasmania (Region N) ranked lowest for all traits (Table 3), and was significantly lower than all other regions for DBH, height, volume and malformation. Macalister and Toorongo had significantly greater density than Rubicon and Forestry Tasmania Region ($p < 0.01$) (Table 3f).

Table 2: Trial statistics for Seed Orchard Source: Means followed by different letters are statistically different (p < 0.05) based on pairwise-comparisons of means (t-statistics). A significant Wald F-stat or (p-value) suggests that seed orchard source is a significant source of variation for that trait. Height and volume was not derived for ATSC control.

a) DBH (mm)

Source	Mean	StDev	Minimum	Maximum	n
Waikuku	152.86a	24.37	60	209	235
Alexandra	151.73ab	27.53	29	221	262
Drumfern	148.69b	25.71	46	201	355
Tinkers	141.82c	26.85	25	219	843
ForestryTas	141.12c	27.74	29	198	349
ATSC	140.78c	25.39	51	199	58
OVERALL	145.31	26.97	25	221	2102
Wald F-Stat (p-value)	7.01 (< 0.001)				

b) Height (m)

Source	Mean	StDev	Minimum	Maximum	n
Drumfern	13.24a	0.25	12.21	13.75	355
Waikuku	13.23a	0.37	11.82	14.09	235
Tinkers	13.09b	0.44	11.17	14.35	843
Alexandra	13.05b	0.42	11.17	14.11	262
ForestryTas	12.48c	0.50	10.41	13.52	349
ATSC	---	---	---	---	---
OVERALL	13.02	0.49	10.41	14.35	2044
Wald F-Stat (p-value)	8.79 (< 0.0001)				

c) Volume

Source	Mean	StDev	Minimum	Maximum	n
Waikuku	0.2665a	0.085	0.04	0.51	235
Alexandra	0.2511ab	0.091	0.01	0.57	262
Drumfern	0.2524b	0.082	0.02	0.46	355
Tinkers	0.2300c	0.083	0.01	0.57	843
ForestryTas	0.2183d	0.082	0.01	0.44	349
ATSC	---	---	---	---	---
OVERALL	0.2401	0.085	0.01	0.57	2044
Wald F-Stat (p-value)	8.63 (<0.0001)				

d) Straightness (1-9 with no 5)

Source	Mean	StDev	Minimum	Maximum	n
Alexandra	6.98a	1.43	3	9	261
Waikuku	6.98a	1.38	3	9	234
Tinkers	6.33b	1.63	2	9	831
Drumfern	6.30bc	1.65	1	9	355
ForestryTas	6.09c	1.71	2	9	346
ATSC	5.45d	1.84	1	9	58
OVERALL	6.42	1.64	1	9	2085
Wald F-Stat (p-value)	5.82 (< 0.001)				

e) Malformation (1-9)

Source	Mean	StDev	Minimum	Maximum	n
Alexandra	8.20a	1.88	2	9	261
Waikuku	7.84ab	2.25	1	9	234
Drumfern	7.74b	2.36	1	9	355
ATSC	7.72abc	2.17	2	9	58
Tinkers	7.45bc	2.63	1	9	831
ForestryTas	7.31c	2.64	1	9	346
OVERALL	7.62	2.46	1	9	2085
Wald F-Stat (p-value)	3.42 (< 0.05)				

f) Density (kg m^{-3})

Source	Mean	StDev	Minimum	Maximum	n
Tinkers	479.13a	28.76	409	577	419
Waikuku	467.87b	26.24	405	541	115
Drumfern	461.54bc	27.61	396	540	172
ForestryTas	460.24c	29.28	394	542	173
Alexandra	456.93c	24.39	384	517	115
ATSC	437.29d	25.79	390	496	28
OVERALL	467.91	29.62	384.0	577.0	1035
Wald F-Stat (p-value)	7.46 (< 0.0001)				

Table 3: Trial statistics for Region of origin: Means followed by different letters are statistically different (p < 0.05) based on pairwise-comparisons of means (t-statistics). Note: Region = N is confounded with Seed Orchard Source = Forestry Tasmania

a) DBH (mm)

Region	Mean	StDev	Minimum	Maximum	n
Rubicon	149.73a	24.34	47	219	290
Macalister	146.38ab	27.16	45	208	409
Toorongo	145.06b	27.14	25	221	1054
N = ForestryTas	141.12c	27.74	29	198	349
Wald F-Stat (p-value)	3.08 (< 0.05)				

b) Height (m)

Region	Mean	StDev	Minimum	Maximum	n
Rubicon	13.22a	0.34	11.97	14.35	232
Macalister	13.13b	0.42	11.46	14.17	409
Toorongo	13.11b	0.40	11.17	14.11	1054
N = ForestryTas	12.48c	0.50	10.41	13.52	349
Wald F-Stat (p-value)	122.57 (< 0.0001)				

c) Volume (m^3)

Region	Mean	StDev	Minimum	Maximum	n
Rubicon	0.2628a	0.082	0.02	0.57	232
Macalister	0.2450b	0.087	0.02	0.51	409
Toorongo	0.2404b	0.085	0.01	0.57	1054
N = ForestryTas	0.2183c	0.082	0.01	0.44	349
Wald F-Stat (p-value)	6.75 (< 0.001)				

d) Straightness (1-9 with no 5)

Region	Mean	StDev	Minimum	Maximum	n
Macalister	6.66a	1.63	3	9	403
Toorongo	6.48a	1.60	1	9	1046
Rubicon	6.25b	1.64	1	9	290

N = ForestryTas	6.09b	1.71	2	9	346
Wald F-Stat (p-value)	2.72 (< 0.1)				

e) Malformation (1-9)

Region	Mean	StDev	Minimum	Maximum	n
Rubicon	7.76a	2.32	1	9	290
Toorongo	7.67a	2.43	1	9	1046
Macalister	7.65a	2.46	1	9	403
N = ForestryTas	7.31b	2.64	1	9	346
Wald F-Stat (p-value)	1.61 (< 0.2)				

f) Density (kg m^{-3})

Region	Mean	StDev	Minimum	Maximum	n
Macalister	474.32a	29.1	384	577	203
Toorongo	469.87a	28.7	396	557	517
Rubicon	461.02b	31.2	390	541	142
N = ForestryTas	460.24b	29.3	394	542	173
Wald F-Stat (p-value)	2.81 (< 0.05)				

Variance Components, Heritability and Genetic Correlations

Generally, observed variance components for each trait were significantly different from zero (Table 4). The variance associated with individual trees ($\hat{\sigma}^2_{\mathrm{TREE}}$) was always significant ($p < 0.01$ to $p < 0.001$). Narrow-sense heritability was greatest for density (0.48 ± 0.09), followed by straightness (0.20 ± 0.05). Height and volume (0.10 ± 0.03), DBH (0.09 ± 0.03), and malformation (0.06 ± 0.03) had low heritability (Table 4). Heritability for diameter and stem volume were typical for those of *E. nitens* from other trials (Hamilton and Potts 2005). Heritability for straightness and malformation (were comparable to those previously reported ($h^2 = 0.28$, number of studies = 5; and $h^2 = 0.05$, number of studies = 1, respectively) (Hamilton and Potts 2005).

Family mean repeatability followed a similar trend with $\hat{\mathrm{h}}^2_{\mathrm{HS}}$ greatest for density and straightness (Table 4). Coefficient of additive genetic variation ($\mathrm{CV}_{\hat{\mathrm{A}}}$) followed a slightly different trend (Table 4). $\mathrm{CV}_{\hat{\mathrm{A}}}$ was greatest for straightness, malformation and volume, indicating that greatest gain could be achieved in these traits, while $\mathrm{CV}_{\hat{\mathrm{A}}}$ for height was less than 1%, indicating low genetic variation relative to the other traits (Table 4). Caution is needed in that $\mathrm{CV}_{\hat{\mathrm{A}}}$ for volume was estimated at the individual-tree level and probably differs than $\mathrm{CV}_{\hat{\mathrm{A}}}$ at the per-hectare crop level (Stranger *et al.* 2011).

Genetic correlations of diameter with volume and height were high, as expected for these growth traits (~unity, $p < 0.0001$) (Table 5). Such high genetic correlations indicate that the same genotypes would be selected regardless of selection trait. These high genetic correlations for

growth traits may be upwardly biased due to the derivation of height and low sampling intensity. On the other hand, all other genetic correlations of growth traits with form traits and density were relatively low and adverse (i.e. negative), but not significantly different from zero (Table 5). Negative correlations indicate that selection for one trait would likely result in genetic loss in the other trait, while correlations near zero indicate that traits are independent.

Table 4: Estimates of observed variance components ± approximate standard error (SE), causal variances (V_A and V_P), narrow-sense heritability ($\hat{h}^2$), family mean heritability ($\hat{h}^2_{HS}$), and coefficient of additive genetic variation (CVA). Significance of observed variances was tested with Likelihood Ratio Tests, where: [NS] Non-significant, [1] p < 0.1, [2] p < 0.05, [3] p < 0.01, and [4] p < 0.001.

	DBH	Height	Volume	Straightness	Malformation	Density
Estimate	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
$\hat{\sigma}^2_X$	55.02[4] ± 13.1	0.012[4] ± 0.003	0.0006[4] ± 0.0001	0.111[3] ± 0.04	0[NS]	29.23[2] ± 16.3
$\hat{\sigma}^2_Y$	15.56[2] ± 8.3	0.004[2] ± 0.002	0.0002[2] ± 0.0001	0.023[NS] ± 0.03	0.05[NS] ± 0.07	0[NS]
$\hat{\sigma}^2_{REP}$	7.02[1] ± 6.3	0.002[1] ± 0.002	0.0001[2] ± 0.0001	0.015[NS] ± 0.02	0.091[3] ± 0.05	13.16[2] ± 9.4
$\hat{\sigma}^2_{TREE}$	93.36[4] ± 33.5	0.025[4] ± 0.009	0.001[4] ± 0.0003	0.789[4] ± 0.20	0.519[3] ± 0.24	576.57[4] ± 135.0
$\hat{\sigma}^2_{ERR}$	539.41 ± 34.7	0.130 ± 0.009	0.005 ± 0.0003	1.657 ± 0.18	5.353 ± 0.27	172.73 ± 107.5
$\hat{V}_A$	58.35 ± 20.9	0.015 ± 0.005	0.0006 ± 0.0002	0.493 ± 0.13	0.324 ± 0.15	360.36 ± 84.4
$\hat{V}_P$	632.77 ± 22.8	0.155 ± 0.006	0.006 ± 0.0003	2.446 ± 0.09	5.872 ± 0.19	749.30 ± 44.0
$\hat{h}^2$	0.09 ± 0.03	0.10 ± 0.03	0.10 ± 0.03	0.20 ± 0.05	0.06 ± 0.03	0.48 ± 0.09
$\hat{h}^2_{HS}$	0.53 ± 0.09	0.55 ± 0.09	0.55 ± 0.09	0.72 ± 0.05	0.40 ± 0.11	0.77 ± 0.04
$CV_{\hat{A}}$	5.26%	0.96%	10.35%	18.78%	18.83%	4.06%

Table 5: Estimated additive genetic (upper diagonal) and phenotypic correlations (below diagonal) among DBH, Height, Volume, Straightness, Malformation, and Density at trial FR481. Statistical significance of genetic correlations was tested with 2-tail LRT. Note: only genetic correlations among DBH, Height and Volume were significant ($p < 0.0001$). All other genetic correlations were non-significant (NS, $p > 0.1$).

	DBH	Height	Volume	Straightness	Malformation	Density
DBH		0.99	0.99	-0.12	-0.32	-0.21
Height	0.98		0.98	-0.14	-0.41	-0.14
Volume	0.98	0.96		-0.12	-0.39	-0.21
Straightness	0.07	0.07	0.06		0.30	0.003
Malformation	0.01	-0.01	-0.01	0.30		0.14
Density	0.07	0.07	0.07	0.02	-0.01	

BackwardsSelection and Genetic Gain

Although the FFR *Eucalyptus nitens* breeding population is to be managed as a rolling front cycle, a selection scenario of backwards selection of parents is useful for making culling decisions in seed orchards. The greatest gain over the predicted population mean for a trait occurred where the selection intensity was greatest, and steadily declined as the number of families selected increased. In other words there is a trade-off between achieving gain and maintaining genetic diversity. The greatest gain was demonstrated for straightness (17.7%), followed by volume (13.9%), malformation (9.4%), density (7.3%), DBH (6.7%) and height (1.3%) when selecting the top 10 families out of 70 (not including the ATSC bulk seedlot) (Figure 5).

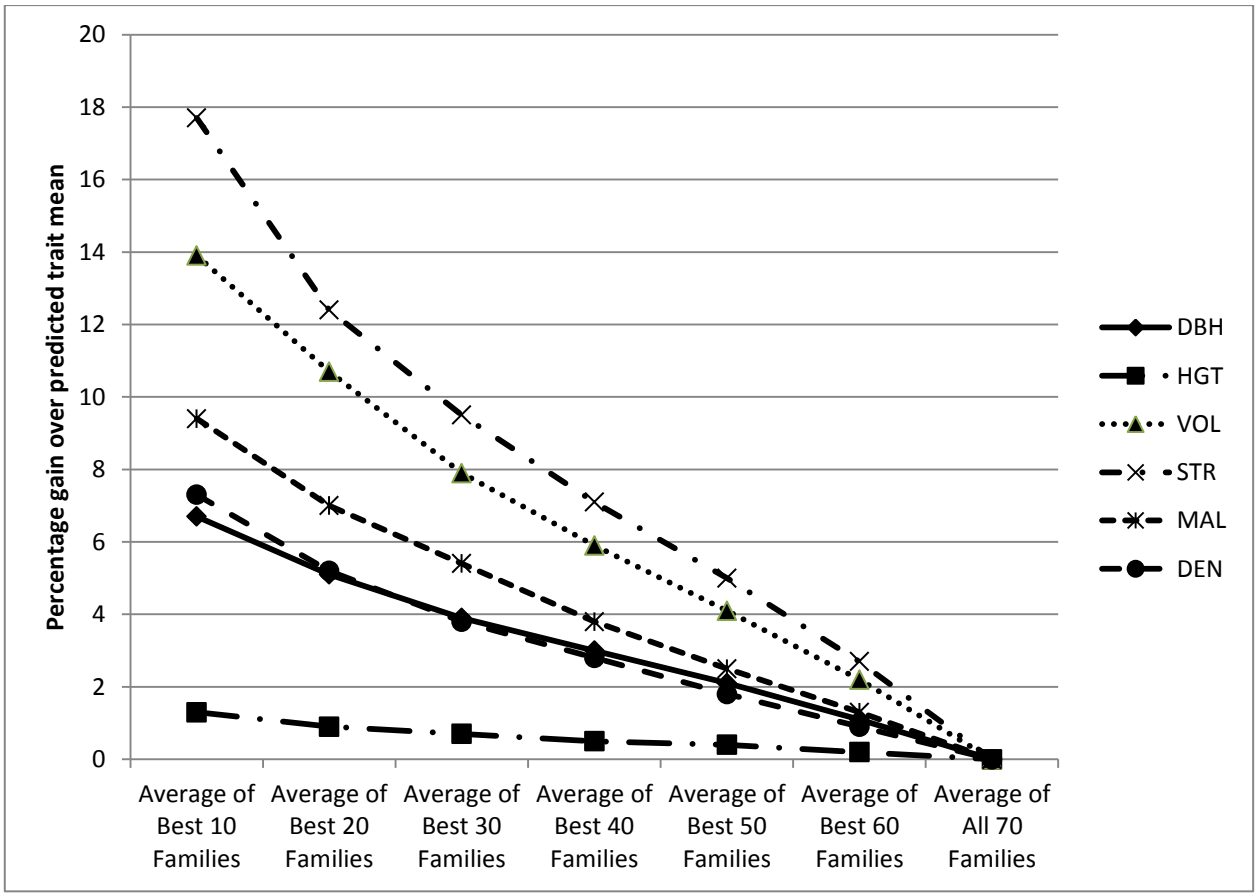

Figure 5: Relative gain when selecting best families in increments of ten relative to the predicted trial mean.

Rolling Front Selection Scenarios

The trade-off between maximising genetic gain (MGG) or maximising genetic diversity (MGD) was explored through two rolling front selection scenarios. The selection of one individual (regardless of generation) from each of all 70 families (MGD) on the basis of largest individual diameter gave a gain over the predicted trial mean of 3.05%, which reduced to 2.77%, 2.58%, and 2.42% when the best two, three, and then four individuals were required to be included (

Table 6). When selecting on diameter from individuals regardless of family (MGG), the mean of the largest 70, 140, 210 and 280 individuals gave a gain of 6.18%, 5.44%, 4.97% and 4.60%, respectively. Tables 7-11 show gains from MGD versus MGG strategies for height, volume, straightness, malformation, and density, respectively. For example, a genetic gain of 13.75% in volume was simulated by selecting the very best 70 individuals from the population, while only 7.52% genetic gain was obtained by managing the family structure of the selected population by selecting the single best individual in each family for volume (Table 8). Similarly, genetic gain was maximised for density by ignoring relatedness of selections compared with a MGD strategy: 9.12% from MGG versus 6.41% from MGD (Table 11). However, this selection strategy (MGG) restricted the number of families included, thereby increasing relatedness and reducing genetic variability in the selected population.

Figure 6 demonstrates the trade-off between maximising genetic gain and maximising genetic diversity of the selected population using volume and density as selection traits. For example, genetic gain in volume over the predicted population mean was 16.8% by selecting 1% of the population. Although 22 individuals were selected at 1% selection rate, only nine families were represented. For volume, 1,302 individuals (60% selection rate) would have to be selected to have all 70 families represented in the selected population (Figure 6). However this would result in only 3.9% genetic gain in volume. For density, a maximum gain of 11.6% when the top 22 individuals were selected corresponded with 10 families being represented. A total of 806 individuals (37% selection rate) would have to be selected for density in order to include all 70 families in the selection population, and corresponded to a genetic gain of 3.3% in density (Figure 6).

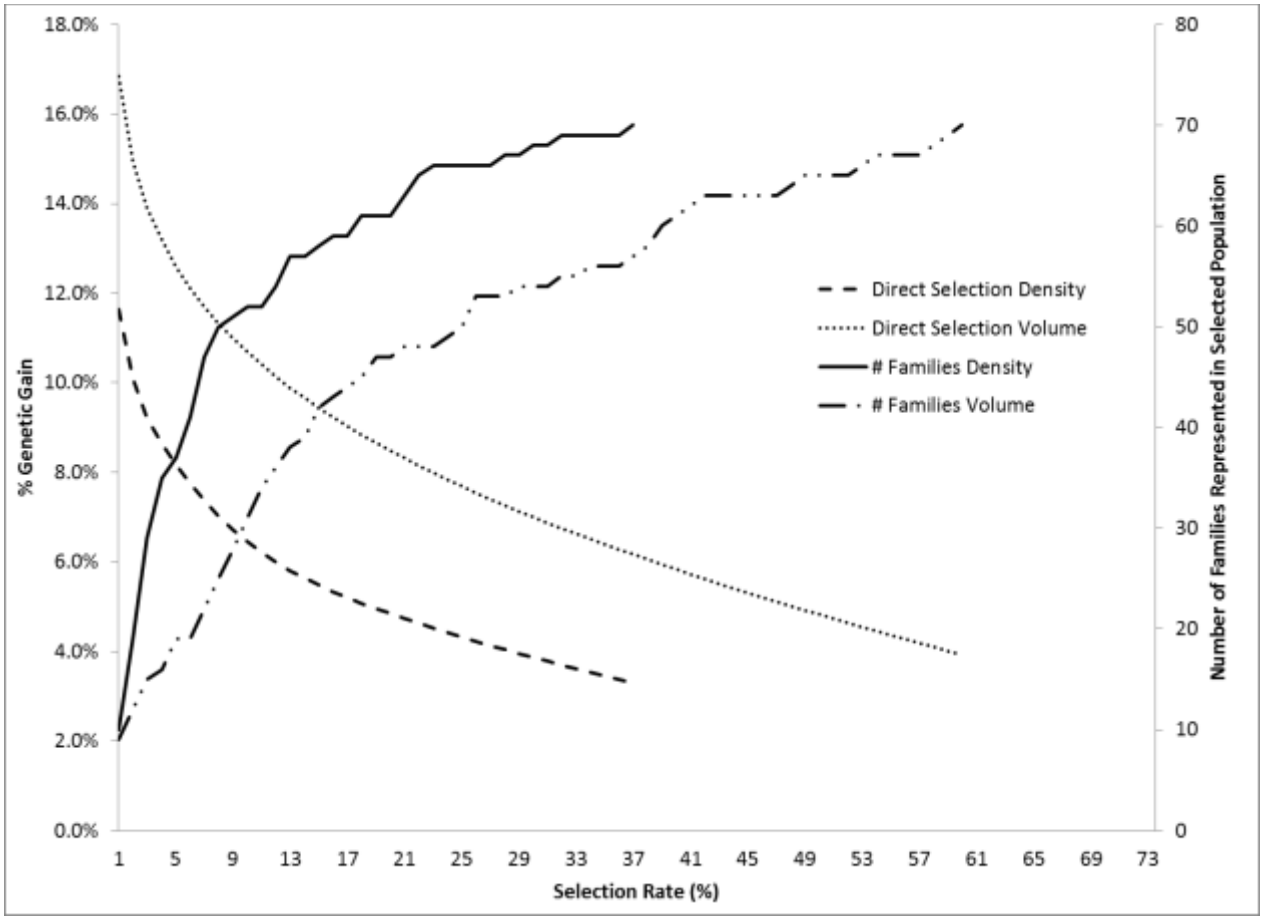

Figure 6: Trade-off between genetic gain and genetic diversity in direct selection of volume or density from rolling front selection strategy.

Table 6: One generation of rolling front selection scenarios for direct selection for DBH: a) Maximising Genetic Diversity, b) Maximising Genetic Gain. The genetic response in other traits is also shown.

a) Maximising Genetic Diversity: direct selection for DBH

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 1 in each family	4.4736	0.0736	0.0181	0.0076	-0.0161	-1.4807
Best 2 in each family	4.0705	0.0672	0.0163	0.0007	-0.0097	0.1395
Best 3 in each family	3.7844	0.0624	0.0150	0.0005	-0.0226	1.2232
Best 4 in each family	3.5470	0.0585	0.0139	0.0016	-0.0147	0.9426
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain1	3.05%	0.57%	7.36%	0.12%	-0.21%	-0.32%
%gain2	2.77%	0.52%	6.65%	0.01%	-0.13%	0.03%
%gain3	2.58%	0.48%	6.09%	0.01%	-0.29%	0.26%
%gain4	2.42%	0.45%	5.65%	0.03%	-0.19%	0.20%

b) Maximising Genetic Gain: direct selection for DBH

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 70 individuals	9.0657	0.1501	0.0336	-0.0760	-0.1224	-2.3404
Best 140 individuals	7.9808	0.1314	0.0290	0.0159	-0.0401	0.3028
Best 210 individuals	7.2922	0.1188	0.0262	0.0274	-0.0381	1.2205
Best 280 individuals	6.7489	0.1099	0.0241	0.0103	-0.0390	0.9256
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain70	6.18%	1.15%	13.66%	-1.18%	-1.59%	-0.51%
%gain140	5.44%	1.01%	11.79%	0.25%	-0.52%	0.07%
%gain210	4.97%	0.91%	10.66%	0.43%	-0.50%	0.26%
%gain280	4.60%	0.85%	9.81%	0.16%	-0.51%	0.20%

Table 7: Rolling front selection scenarios for direct selection for Height: a) Maximising Genetic Diversity, b) Maximising Genetic Gain. The genetic response in other traits is also shown.

a) Maximising Genetic Diversity: direct selection for Height

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 1 in each family	4.4723	0.0744	0.0182	0.0182	-0.0071	-0.0192
Best 2 in each family	4.0725	0.0677	0.0163	-0.0120	-0.0177	0.2740
Best 3 in each family	3.7866	0.0628	0.0150	0.0067	-0.0230	1.1088
Best 4 in each family	3.5406	0.0589	0.0139	0.0060	-0.0155	1.2066
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain1	3.05%	0.57%	7.40%	0.28%	-0.09%	0.00%
%gain2	2.77%	0.52%	6.63%	-0.19%	-0.23%	0.06%
%gain3	2.58%	0.48%	6.10%	0.10%	-0.30%	0.24%
%gain4	2.41%	0.45%	5.65%	0.09%	-0.20%	0.26%

b) Maximising Genetic Gain: direct selection for Height

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 70 individuals	8.9301	0.1536	0.0331	-0.0257	-0.1070	-0.1677
Best 140 individuals	7.8619	0.1351	0.0285	0.0591	-0.0535	2.2207
Best 210 individuals	7.1152	0.1227	0.0255	0.0458	-0.0606	1.4141
Best 280 individuals	6.5710	0.1132	0.0234	0.0293	-0.0675	0.7753
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain70	6.08%	1.18%	13.46%	-0.40%	-1.39%	-0.04%
%gain140	5.36%	1.04%	11.58%	0.92%	-0.70%	0.48%
%gain210	4.85%	0.94%	10.38%	0.71%	-0.79%	0.31%
%gain280	4.48%	0.87%	9.52%	0.46%	-0.88%	0.17%

Table 8:Rolling front selection scenarios for direct selection for Volume: a) Maximising Genetic Diversity, b) Maximising Genetic Gain. The genetic response in other traits is also shown.

a) Maximising Genetic Diversity: direct selection for Volume

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 1 in each family	4.4657	0.0740	0.0185	0.0172	-0.0098	-0.6119
Best 2 in each family	4.0716	0.0674	0.0165	-0.0357	-0.0239	0.0327
Best 3 in each family	3.7842	0.0625	0.0151	0.0018	-0.0253	1.2440
Best 4 in each family	3.5455	0.0585	0.0140	-0.0051	-0.0197	1.1204
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain1	3.04%	0.57%	7.52%	0.27%	-0.13%	-0.13%
%gain2	2.77%	0.52%	6.70%	-0.56%	-0.31%	0.01%
%gain3	2.58%	0.48%	6.13%	0.03%	-0.33%	0.27%
%gain4	2.42%	0.45%	5.69%	-0.08%	-0.26%	0.24%

b) Maximising Genetic Gain: direct selection for Volume

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 70 individuals	9.0068	0.1475	0.0338	-0.0641	-0.1051	-1.5263
Best 140 individuals	7.9229	0.1294	0.0293	-0.0157	-0.0660	-0.6770
Best 210 individuals	7.2272	0.1172	0.0265	0.0250	-0.0600	-0.1803
Best 280 individuals	6.7002	0.1093	0.0244	0.0318	-0.0527	0.2227
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain70	6.14%	1.13%	13.75%	-1.00%	-1.37%	-0.33%
%gain140	5.40%	1.00%	11.92%	-0.24%	-0.86%	-0.15%
%gain210	4.92%	0.90%	10.79%	0.39%	-0.78%	-0.04%
%gain280	4.56%	0.84%	9.92%	0.49%	-0.69%	0.05%

Table 9. Rolling front selection scenarios for direct selection for Straightness: a) Maximising Genetic Diversity, b) Maximising Genetic Gain. The genetic response in other traits is also shown.

a) Maximising Genetic Diversity: direct selection for Straightness

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 1 in each family	0.3570	0.0040	0.0011	0.5653	0.0914	-0.0319
Best 2 in each family	0.3113	0.0036	0.0007	0.5245	0.0898	0.1668
Best 3 in each family	0.3433	0.0043	0.0009	0.4879	0.0803	0.5725
Best 4 in each family	0.2628	0.0030	0.0006	0.4597	0.0781	0.3157
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain1	0.24%	0.03%	0.43%	8.81%	1.19%	-0.01%
%gain2	0.21%	0.03%	0.29%	8.17%	1.17%	0.04%
%gain3	0.23%	0.03%	0.38%	7.60%	1.05%	0.12%
%gain4	0.18%	0.02%	0.26%	7.16%	1.02%	0.07%

b) Maximising Genetic Gain: direct selection for Straightness

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 70 individuals	-1.1517	-0.0207	-0.0043	1.0261	0.2668	0.7137
Best 140 individuals	-1.7433	-0.0317	-0.0059	0.9167	0.2359	0.4667
Best 210 individuals	-1.1141	-0.0202	-0.0039	0.8446	0.1878	0.2637
Best 280 individuals	-0.9291	-0.0173	-0.0032	0.7892	0.1764	1.7356
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain70	-0.78%	-0.16%	-1.74%	15.99%	3.48%	0.15%
%gain140	-1.19%	-0.24%	-2.42%	14.28%	3.07%	0.10%
%gain210	-0.76%	-0.16%	-1.60%	13.16%	2.45%	0.06%
%gain280	-0.63%	-0.13%	-1.32%	12.30%	2.30%	0.37%

Table 10:Rolling front selection scenarios for direct selection for Malformation: a) Maximising Genetic Diversity, b) Maximizing Genetic Gain. The genetic response in other traits is also shown.

a) Maximising Genetic Diversity: direct selection for Malformation

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 1 in each family	-0.5622	-0.0109	-0.0021	0.1085	0.1706	-1.8105
Best 2 in each family	0.2013	0.0025	0.0006	0.1129	0.1441	0.0901
Best 3 in each family	0.1244	0.0014	0.0003	0.0964	0.1316	0.0138
Best 4 in each family	0.1442	0.0019	0.0004	0.1104	0.1244	-0.2595
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain1	-0.38%	-0.08%	-0.84%	1.69%	2.22%	-0.39%
%gain2	0.14%	0.02%	0.26%	1.76%	1.88%	0.02%
%gain3	0.08%	0.01%	0.14%	1.50%	1.71%	0.00%
%gain4	0.10%	0.01%	0.16%	1.72%	1.62%	-0.06%

b) Maximising Genetic Gain: direct selection for Malformation

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 70 individuals	-1.9545	-0.0355	-0.0065	0.2620	0.5394	12.9778
Best 140 individuals	-0.9155	-0.0182	-0.0035	0.2901	0.5024	9.0177
Best 210 individuals	-1.3696	-0.0258	-0.0048	0.1998	0.4743	5.3956
Best 280 individuals	-1.8216	-0.0328	-0.0060	0.2182	0.4439	3.3781
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain70	-1.33%	-0.27%	-2.65%	4.08%	7.03%	2.80%
%gain140	-0.62%	-0.14%	-1.44%	4.52%	6.55%	1.95%
%gain210	-0.93%	-0.20%	-1.95%	3.11%	6.18%	1.17%
%gain280	-1.24%	-0.25%	-2.44%	3.40%	5.78%	0.73%

Table 11:Rolling front selection scenarios for direct selection for Density: a) Maximising Genetic Diversity, b) Maximising Genetic Gain. The genetic response in other traits is also shown.

a) Maximising Genetic Diversity: direct selection for Density

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 1 in each family	0.2753	0.0045	0.0011	0.0639	-0.0070	29.6900
Best 2 in each family	0.2088	0.0035	0.0007	-0.0119	-0.0140	25.4834
Best 3 in each family	0.1833	0.0037	0.0007	-0.0063	-0.0138	22.3917
Best 4 in each family	0.2191	0.0036	0.0008	0.0076	-0.0070	19.5086
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain1	0.19%	0.03%	0.46%	1.00%	-0.09%	6.41%
%gain2	0.14%	0.03%	0.29%	-0.19%	-0.18%	5.50%
%gain3	0.12%	0.03%	0.29%	-0.10%	-0.18%	4.84%
%gain4	0.15%	0.03%	0.34%	0.12%	-0.09%	4.21%

b) Maximising Genetic Gain: direct selection for Density

	Average of Breeding Values from Selected Population					
	DBH	**Height**	**Volume**	**Straightness**	**Malformation**	**Density**
Best 70 individuals	-1.1917	-0.0143	-0.0040	0.0200	-0.0547	42.2207
Best 140 individuals	-1.3838	-0.0162	-0.0049	-0.0321	-0.0418	35.3081
Best 210 individuals	-1.3735	-0.0183	-0.0048	-0.0531	-0.0253	30.4727
Best 280 individuals	-0.7062	-0.0086	-0.0027	0.0184	0.0267	27.2072
Predicted Trait Mean	**146.7833**	**13.0030**	**0.2458**	**6.4186**	**7.6753**	**463.0833**
%gain70	-0.81%	-0.11%	-1.62%	0.31%	-0.71%	9.12%
%gain140	-0.94%	-0.12%	-2.00%	-0.50%	-0.54%	7.62%
%gain210	-0.94%	-0.14%	-1.96%	-0.83%	-0.33%	6.58%
%gain280	-0.48%	-0.07%	-1.08%	0.29%	0.35%	5.88%

Although the genetic correlation between density and volume was not statistically significant in this population, it was adverse (-0.21) (Table 5). Selecting for volume would result in a negative genetic response (genetic loss) for density (Table 8b), and vice versa (Table 11b). Therefore an alternative selection approach was simulated by considering only individuals with positive breeding values for both volume and density (Figure 7).

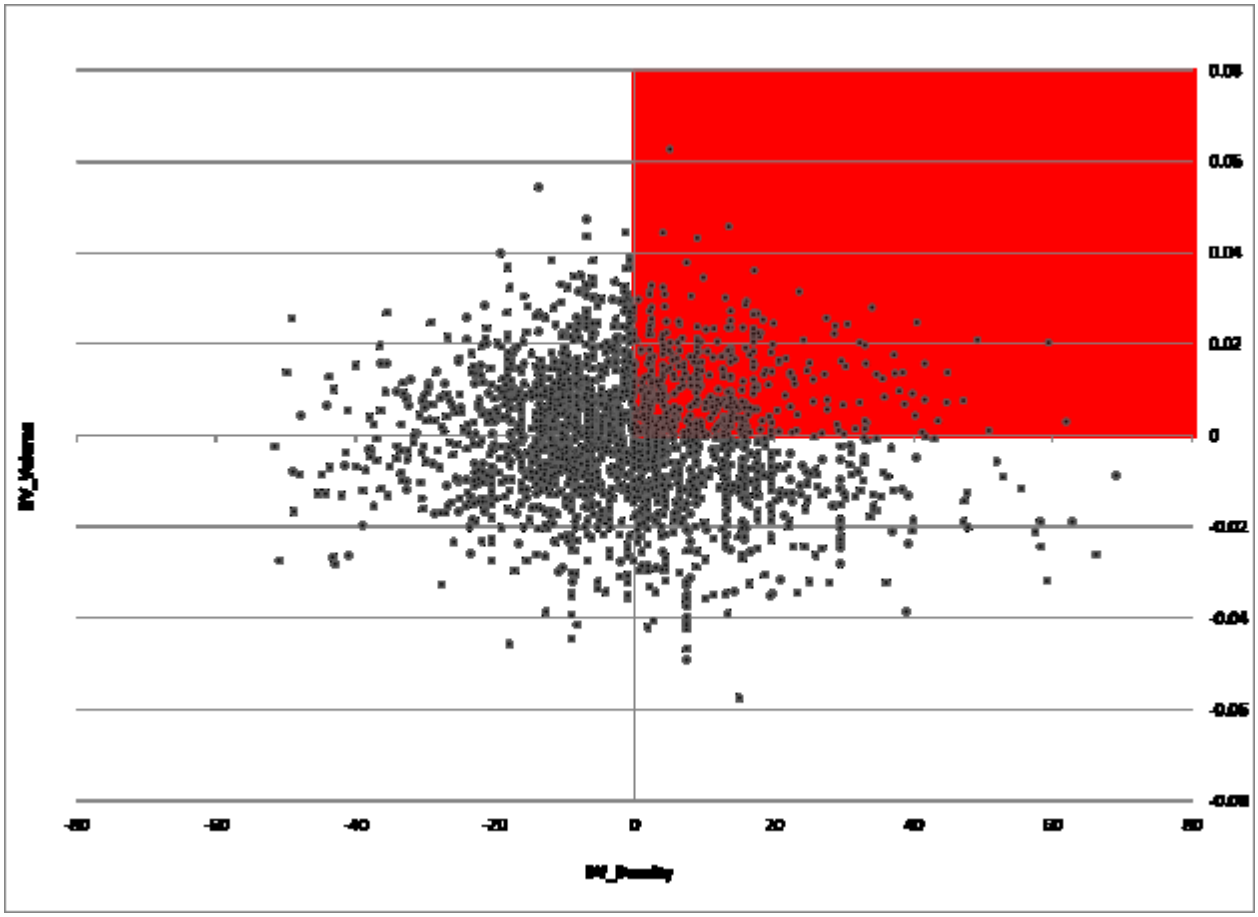

Figure 7: Estimated breeding values (parents and offspring) for density versus breeding values for volume. Upper shaded quadrant represents individuals with positive breeding values for both traits.

By restricting selection to only those genotypes with positive breeding values for both traits, direct selection for volume ranged from 13.9% to 4.9% depending on selection rate (Figure 8). This would also result in positive gains in density (Figure 8). In fact, the indirect genetic response in density was relatively stable regardless of selection rate for volume, ~ 2.5% (Figure 8). Similar trends were observed when density was the selection trait. For example, genetic gains from selection for density ranged from 9.3% to 2.7%, while the indirect genetic response for volume was approximately 4.7% across all selection rates for density (Figure 8). Decisions still would need to be made regarding maximising diversity with potential genetic gain. For example, as selection rate increases, genetic gain increases but genetic diversity decreases (Figure 8).

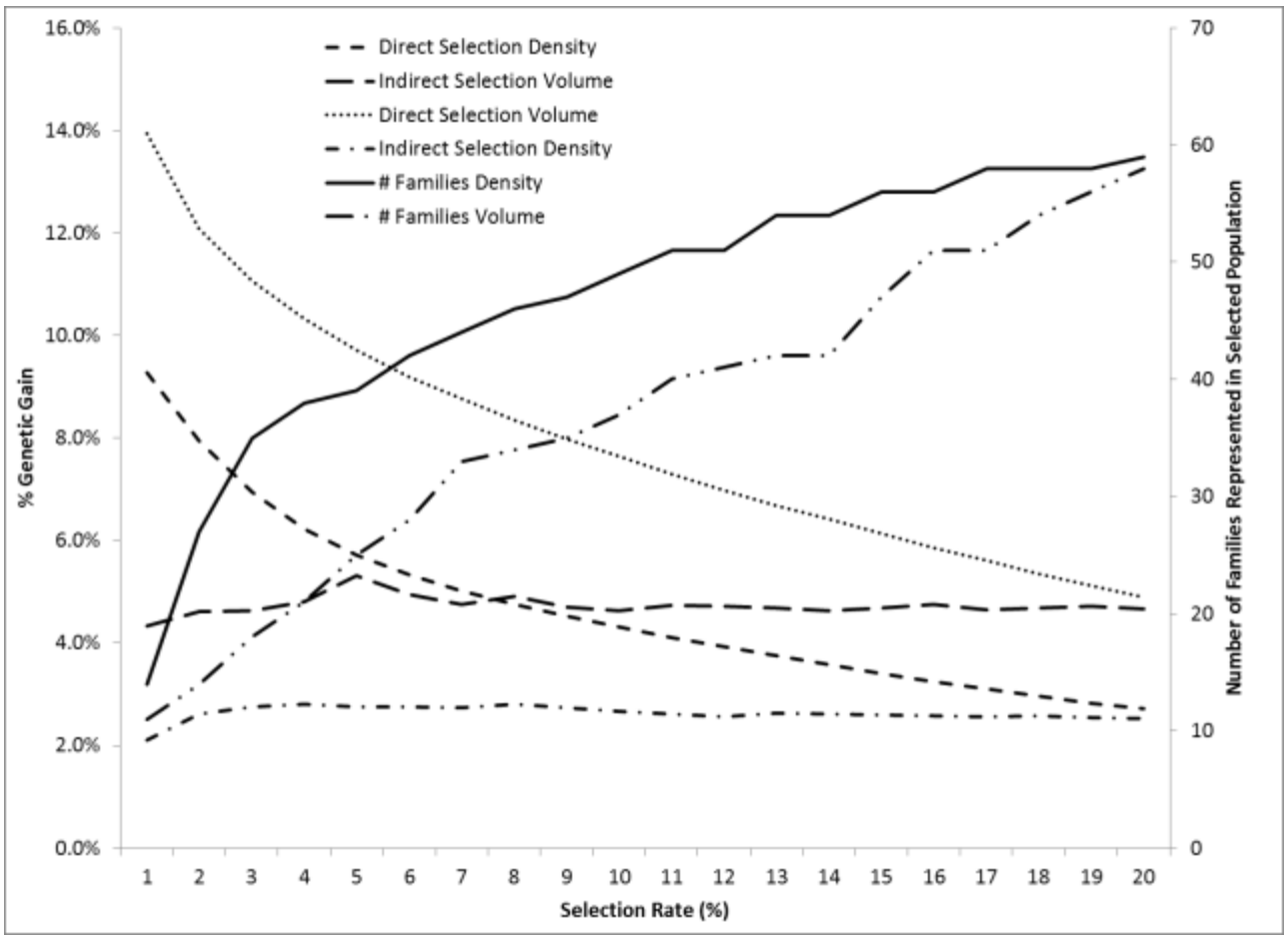

Figure 8: Genetic gains from direct selection for volume or density and the corresponding indirect genetic response of the alternative trait from a truncated population with positive breeding values for both traits (Figure 5).

CONCLUSION

There were significant differences among seed orchard sources for all traits, while region of origin was significant for all traits except straightness and malformation. Waikuku and Alexandra sources tended to be the better sources for growth and form traits, while Tinkers was best for density. The Forestry Tasmania source and ATSC control generally performed poorly in this trial.

The analysis demonstrated significant and exploitable genetic variation in all traits. Heritability was moderate to high for density (0.48), moderate for straightness (0.20), and low (≤ 0.10) for all other traits. The only significant genetic correlations were observed between the three growth traits. The genetic correlations between growth and form traits (or density) were generally low and adverse (negative), but not statistically significant.

Backwards selection of families would be used as a basis for culling existing seed orchards or for marshalling clones into a new seed orchard. The greatest gains came from selecting families based on straightness, volume and malformation. While growth gains are often expressed as diameter, gain based on estimated volume was at least double that indicated by DBH.

A rolling front selection scheme allows selection of the best-performing genotypes, regardless of generation, based on breeding values. The selection scenario where we make selections from only those individuals with positive breeding values for both volume and density is one alternative to advance and make genetic improvements for both traits in the *E. nitens* breeding population.

The trade-off between maximising genetic gain and maximising genetic diversity was demonstrated. Individual selection with no restriction on relatedness results in a loss of genetic diversity. The alternative of maximising the number of families retained reduces genetic gain but retains genetic diversity. The situations where (i) excessive uncompetitive families are retained in the name of maintaining genetic diversity, or (ii) where excessive diversity is lost through the emphasis on gain, are normally readily detected in operational breeding programs, and an intermediate strategy can be implemented. Forwards selection within the current trial would require pedigree reconstruction to separate maternally or paternally related individuals within the selections (Lambeth *et al*. 2001). Pedigree reconstruction is feasible for *E. nitens* in New Zealand as most of the parental DNA lineages are available from previous studies (Gea *et al.* 2007). Pedigree reconstruction would also be required whether propagation is via collection of open-pollinated seed, or in possible scenarios that clones or grafts can be taken from the field material.

The field measurement in February 2011 included the sampling of 6-mm diameter, cambium-to-cambium cores from 15 replicates on all live trees above 7 cm diameter in the trial. Processing of these for NIR-predicted pulp yield would enable constructing the kraft pulp production index for each tree, thus enabling the definitive selection from the trial, as suited to the kraft pulp breeding objective. Such a project also provides the impetus for development of New Zealand-based NIR models, and the capacity to predict wood chemical properties. Before turning over the next generation, the breeding population will also be tested for resistance to browsing by *Paropsis charybdis.* This, as well as the kraft pulp yield index, will determine the final selections for turning over the next generation of *E. nitens* in New Zealand.

ACKNOWLEDGEMENTS

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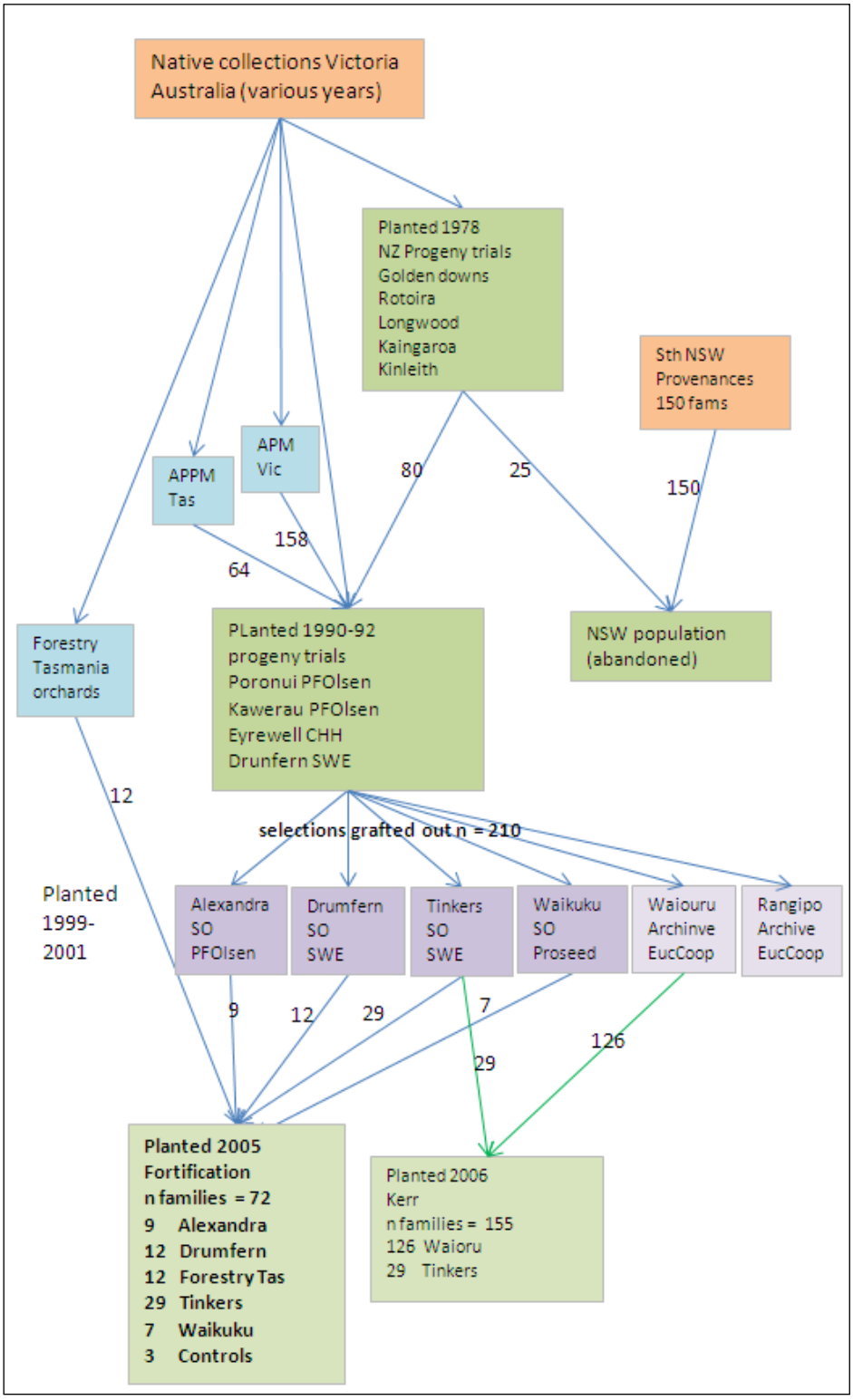
APPENDICES

Appendix 1. Outline of the populations involved in the history of breeding *Eucalyptus nitens* in New Zealand (after Stovold *et al*. 2008).

Native Australian sources are shown in Orange; Australian seed orchards (SO) in blue; New Zealand progeny tests in green, New Zealand clonal archives (some used for seed production) in purple. Known numbers of families carried forwards (usually OP) shown on the connecting arrows



Appendix 2. Statistical Analyses

DBH, height, volume, straightness, malformation and density data were converted from the x-y field coordinates and set into a data array for analysis. The x-y coordinates were incorporated into the analysis as a basis for spatial analysis, i.e., equivalent to row and column. A simple model using set as a fixed factor and family as a random effect to establish that set was not a significant determinant of these traits. The set effect was subsequently excluded from all analysis.

A series of analyses were conducted in ASReml (Gilmour *et al.* 2009) in order to estimate the variance components and derive the associated genetic parameters and breeding values for DBH, height, volume, straightness, malformation and density. First, a univariate mixed-effects individual-tree model was used.

[2] $$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_1 m} + \mathbf{Z_2 n} + \mathbf{Z_3 r} + \mathbf{Z_4 a} + \mathbf{e}$$

where, $\mathbf{y}$ is a vector of observations on a trait, $\mathbf{b}$ is the vector of fixed effects (mean, region, seed orchard source), $\mathbf{X}$ is the known incidence matrix relating observations in $\mathbf{y}$ to the fixed effects in $\mathbf{b}$,

$\mathbf{m}$ is the vector of random effects of X within replicate (eg., row) ~N(0, $\hat{\sigma}^2_{\mathrm{X}}$),

$\mathbf{n}$ is the vector of random effects of Y within replicate (eg., column) ~N(0, $\hat{\sigma}^2_{\mathrm{Y}}$),

$\mathbf{r}$ is the vector of random effects of replicate ~N(0, $\hat{\sigma}^2_{\mathrm{REP}}$),

$\mathbf{a}$ is the vector of random effects of individual tree ~N(0, $\hat{\sigma}^2_{\mathrm{TREE}}$) based on the numerator relationship matrix in ASReml,

$\mathbf{e}$ is the vector of random residual terms ~N(0,$\hat{\sigma}^2_{\mathrm{ERR}}$),

$\mathbf{Z_1}$, $\mathbf{Z_2}$, $\mathbf{Z_3}$, $\mathbf{Z_4}$ are the known incidence matrices relating the observations in $\mathbf{y}$ to effects in $\mathbf{m}$, $\mathbf{n}$, $\mathbf{r}$, and $\mathbf{a}$, respectively.

The significance of fixed effects, Region and Source, was tested with Wald-type F-statistics (Kenward and Roger 1997) in ASReml. Statistical significance from pairwise comparisons of means for both Region and Source was tested with t-statistics in Microsoft Excel. The significance of random effects was tested using one-tail likelihood ratio tests (LRT) (Stram and Lee 1994).

Observed variance components were used to estimate causal components of variance:

$\hat{\mathrm{V}}_{\mathrm{A}} = 0.625 \times \hat{\sigma}^2_{\mathrm{TREE}}$ = additive genetic variance, and

$\hat{\mathrm{V}}_{\mathrm{P}} = \hat{\sigma}^2_{\mathrm{TREE}} + \hat{\sigma}^2_{\mathrm{ERR}}$ = phenotypic variance.

Individual-tree narrow-sense heritability was estimated:

$$\hat{\mathrm{h}}^2 = \frac{\hat{\mathrm{V}}_{\mathrm{A}}}{\hat{\mathrm{V}}_{\mathrm{P}}}$$

In addition family mean repeatability was estimated as

$$\hat{\mathrm{h}}^2_{\mathrm{HS}} = \frac{\hat{\sigma}^2_{\mathrm{fam}}}{\mathrm{V}_{\mathrm{Pfam}}} = \frac{\hat{\sigma}^2_{\mathrm{TREE}}/4}{\hat{\sigma}^2_{\mathrm{TREE}}/4 + \frac{(\hat{\sigma}^2_{\mathrm{TREE}} \times 0.75 + \hat{\sigma}^2_{\mathrm{ERR}})}{n}}$$

where $\mathrm{V}_{\mathrm{Pfam}}$ is the phenotypic family variance, $(\hat{\sigma}^2_{\mathrm{TREE}} \times 0.75 + \hat{\sigma}^2_{\mathrm{ERR}})$ is the residual variance from family model, and *n* = harmonic mean number of observations per family.

Variances are not independent of the scale and the mean of the respective traits (Sokal and Rohlf 1995). Therefore, the coefficient of additive genetic variation ($\mathrm{CV}_{\hat{\mathrm{A}}}$) was estimated in order to

compare the genetic variance across traits. The $\mathrm{CV}_{\hat{\mathrm{A}}}$ expresses the additive genetic variance relative to the mean of the trait of interest and gives a standardized measure of the genetic variance relative to the mean. The higher the $\mathrm{CV}_{\hat{\mathrm{A}}}$, the higher is its relative variation.

$$\mathrm{CV}_{\hat{\mathrm{A}}} = \frac{\sqrt{\hat{\mathrm{V}}_{\mathrm{A}}}}{\bar{\mathrm{x}}} \times 100\%$$

where $\bar{\mathrm{x}}$ is the population mean. An alternative approach was used to estimate $\mathrm{CV}_{\hat{\mathrm{A}}}$ for stem straightness and malformation which are subjectively measured traits and bounded by a scale (Burdon 2008).

$$\mathrm{CV}_{\hat{\mathrm{A}}} = \frac{\sqrt{\hat{\mathrm{V}}_{\mathrm{A}}}}{\sqrt{(X_{mean} - X_{min})(X_{max} - X_{mean})}} \times 100\%$$

where X_{mean} is the mean, and X_{min} and X_{max} are the lower and upper bounds of the scale, respectively.

Breeding values were predicted for all individuals in the trial as well as for parents. The accuracy (ACC) of breeding values was also calculated for each trait:

$$\mathrm{ACC} = \sqrt{1 - \frac{\mathrm{PEV}}{\hat{\mathrm{V}}_{\mathrm{A}}}}.$$

Accuracy is the correlation between the true and predicted breeding values, where PEV is the predicted error variance (equivalent to the squared standard error of prediction in ASReml *.sln file). The higher the accuracy the more confident one can be about the predicted breeding values.

Genetic and phenotypic correlations between pairs of traits were estimated by using a bivariate individual-tree mixed-effects model:

[3] $\mathbf{y_i} = \mathbf{X_i b_i} + \mathbf{Z_{r_i} r_i} + \mathbf{Z_{a_i} a_i} + \mathbf{e_i}$,

where $\mathbf{y_i}$ is the vector of observations indexed (i) by trait;

$\mathbf{b_i}$ is the vector of fixed effects (mean, region, seed orchard source) and $\mathbf{X_i}$ is the known incidence matrix relating observations in $\mathbf{y_i}$ to the fixed effects in $\mathbf{b_i}$, where

$$\mathbf{X_i b_i} = \begin{bmatrix} \mathbf{X_1} & \mathbf{0} \\ \mathbf{0} & \mathbf{X_2} \end{bmatrix} \begin{bmatrix} \mathbf{b_1} \\ \mathbf{b_2} \end{bmatrix};$$

$\mathbf{r_i}$ is the vector of random effect of replicates ~ $\mathrm{MVN}(\mathbf{0}, \mathbf{P} \otimes \mathbf{I_r})$ where,

$\mathbf{P} = \begin{bmatrix} \hat{\sigma}^2_{\mathrm{REP}_1} & \hat{\sigma}_{\mathrm{REP}_1\mathrm{REP}_2} \\ \hat{\sigma}_{\mathrm{REP}_1\mathrm{REP}_2} & \hat{\sigma}^2_{\mathrm{REP}_2} \end{bmatrix}$ and $\mathbf{I_p}$ is an identity matrix equal to the number of replicates;

$\mathbf{a_i}$ is the vector of random additive effects of individual trees ~$\mathrm{MVN}(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$, where

$\mathbf{G} = \begin{bmatrix} \hat{\sigma}^2_{\mathrm{A}_1} & \hat{\sigma}_{\mathrm{A}_1\mathrm{A}_2} \\ \hat{\sigma}_{\mathrm{A}_1\mathrm{A}_2} & \hat{\sigma}^2_{\mathrm{A}_2} \end{bmatrix}$ and $\mathbf{A}$ = numerator relationship matrix generated from the pedigree in ASReml,

$\hat{\sigma}_{\mathrm{A}_1\mathrm{A}_2}$ is the additive genetic covariance between traits 1 and 2, $\hat{\sigma}^2_{\mathrm{A}_1}$ and $\hat{\sigma}^2_{\mathrm{A}_2}$ are the additive genetic variances of traits 1 and 2, respectively;

$\mathbf{e_i}$ is the random vector of residual terms ~ $\mathrm{MVN}(\mathbf{0}, \mathbf{R} \otimes \mathbf{I})$, where $\mathbf{R} = \begin{bmatrix} \hat{\sigma}^2_{\mathrm{E}_1} & \hat{\sigma}_{\mathrm{E}_1\mathrm{E}_2} \\ \hat{\sigma}_{\mathrm{E}_1\mathrm{E}_2} & \hat{\sigma}^2_{\mathrm{E}_1} \end{bmatrix}$;

$\mathbf{0}$ is the null matrix; $\mathbf{I}$ is the identity matrix equal to the number of observations; $\mathbf{I_p}$ is an identity matrix equal to the number of replicates; $\mathbf{Z_{r_i}}$ and $\mathbf{Z_{a_i}}$ are the known incidence matrices relating observations in $\mathbf{y_i}$ to random effects in $\mathbf{p_i}$, and $\mathbf{a_i}$, respectively.

The additive genetic correlation ($\hat{r}_A$) between pairs of traits was estimated as:

$$r_A = \frac{\hat{\sigma}_{A_1A_2}}{\sqrt{\hat{\sigma}^2_{A_1}\hat{\sigma}^2_{A_2}}}.$$

The phenotypic correlation ($\hat{r}_P$) between pairs of traits was estimated as:

$$r_P = \frac{\hat{\sigma}_{A_1A_2}+\hat{\sigma}_{E_1E_2}}{\sqrt{(\hat{\sigma}^2_{A_1}+\hat{\sigma}^2_{E_1})(\hat{\sigma}^2_{A_2}+\hat{\sigma}^2_{E_1})}}.$$

Statistical significance of genetic correlations was tested using two-tail LRT.

For all variance components, correlations, and heritability estimates, approximate standard errors were calculated using Taylor Series expansion method in ASReml (Gilmour *et al*. 2009).

Appendix 3. Regression of heights on diameter in adjacent demonstration plots

	Slope	Intercept	R^2	Average ht (m)	n
Forestry Tas	0.1839	98.7	0.41	126	10
Drumfern	0.4598	62.1	0.11	135	11
Tinkers	0.1637	107.6	0.08	133	9
Alexandra	0.1517	109.1	0.06	132	9
Waikuku	0.1525	107.3	0.35	131	9
ATSC control (Provenance unidentified)	0.4487	56.79	0.57	122	9

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