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Genetic variation between and within *ex-situ* native-provenance collections of *Pinus radiata* D. Don planted in Australia and New Zealand

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Abstract

A total of 1226 increment cores were sampled from two provenance trials of *Pinus radiata* D. Don planted in New Zealand (Kaingaroa) and Australia (Kangaroovale), to study variation and inheritance of wood density in selections from three mainland California natural populations: Año Nuevo, Monterey and Cambria. The study represents a back-to-back comparison of the same provenance and family material on contrasting sites between New Zealand and Australia. Monterey was significantly different to Año Nuevo and Cambria at Kaingaroa ($p < 0.05$), and had slightly higher density, whereas all provenances were almost identical and not significantly

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different at Kangaroovale. However, there were significant differences for wood density at family level for Año Nuevo and Cambria at Kangaroovale. No significant provenance or family differences were detected for core length at either site. The estimates of heritability for wood density were all above 0.50 and generally higher at Kaingaroa than at Kangaroovale. Estimates of additive genetic correlations between wood density and core length were imprecise. Genotype × site interactions for density appeared minor (estimated type-B genetic correlation = 0.70) despite substantial differences in rainfall and soils. The similarity of Cambria to Año Nuevo for density is an interesting result because the genetic base of the present Australian and New Zealand plantations has been shown to be from Año Nuevo and Monterey. Infusion of Cambria material would increase the overall genetic base of the radiata pine breeding programs, with potential long-term benefits, despite the often disappointing growth performance of material collected from Cambria.

Key words: provenance, genotype x environment interaction, breeding population, infusion, radiata pine,

Introduction

Active breeding of radiata pine (*Pinus radiata* D. Don) has been under way in Australia and New Zealand for over 60 years. Early tree improvement work on *P. radiata* in Australia and New Zealand concentrated mostly on improving growth and form traits (Wu et al., 2007; Burdon et al., 2008). Breeding for growth rate and tree form in the first two generations has reduced wood density slightly in radiata pine because of a negative genetic correlation between growth rate and wood density (Cotterill and Dean, 1990; Dean et al., 1990; Wu et al., 2004). Density features importantly in both the New Zealand breeding program and that of the Southern Tree Breeding Association, based in Mount Gambier, South Australia (White et al., 1999; Jayawickrama and Carson, 2000).

Wood density is generally a highly heritable trait, but assessing density can be time-consuming and expensive. However, it can be measured relatively easily and inexpensively compared to other wood quality traits such as microfibril angle (MfA), modulus of elasticity (MoE), and spiral grain. Tree-to-tree variation in most wood properties is not only significant but is typically strongly heritable (Shelbourne, 1997; Burdon et al., 2001; Zamudio et al., 2005; Wu et al., 2008), which makes it easy to improve specific properties by selective breeding. For example, considerable genetic variation and high heritabilities in density in corewood (historically called juvenile wood) (Burdon et al., 2004) have been reported in Australia and New Zealand (Jayawickrama, 2001; Kumar, 2004; Kumar et al., 2002; Li and Wu, 2005). However, a negative relationship between radial growth and wood density has been widely reported (e.g., Zamudio et al., 2002). The strength of the relationship is variable among softwood species; it is very strong for spruces (*Picea* spp.) and especially Norway spruce (*Picea abies*) (Zobel and Jett, 1995; Rozenberg and Cahalan, 1997), and apparently very weak for some pine species (Zobel and Jett, 1995). For example, several studies have reported adverse genetic correlations between wood density and growth in radiata pine (Dean et al., 1983; Burdon and Low, 1992; Jayawickrama, 2001; Kumar, 2004; Li and Wu, 2005; Baltunis et al., 2007; Wu et al., 2008). Little evidence of genotype-by-environment interaction (GxE) has been reported for density in radiata pine (Baltunis et al., 2010; Gapare et al., 2010).

Burdon and Low (1992) studied several wood properties in native-population material of radiata pine grown in New Zealand. For example, wood density averaged about 10% higher in slower-growing island populations (Guadalupe and Cedros) than in the Californian mainland ones (Burdon and Low, 1992). Recent work showed that Guadalupe provenance to have the highest density, both for the innermost five rings and across the stem at age 30 years (Burdon et al., 2001; Raymond et al., 2009).

Our previous study on selections from three mainland California populations planted at two sites in New Zealand and one site in Australia showed significant provenance differences for growth and form traits at age nine years (Gapare et al., 2011). The availability of such provenance/progeny trials which sampled the whole range of the mainland populations provides an excellent opportunity to study the genetic control of wood density in native-population material. The present study represents a back-to-back comparison of the same provenance and family material on contrasting sites between New Zealand and Australia at age 14 years. This will also provide an opportunity to include information on both growth and wood density when making decisions about possible infusion of new germplasm.

This paper presents results from two provenance/progeny trials of radiata pine, one planted in Kaingaroa Forest, New Zealand and the other one near Tumut, New South Wales, Australia. The objectives of this paper were to (1) determine the relative magnitudes of variation in wood density and core length that is due to provenances and families, (2) estimate genetic correlations between the traits, (3) investigate the effect of G×E for wood density.

Materials and Methods

Genetic material

The 1978 "Eldridge" collection included open-pollinated (OP) seed from individuals from the Monterey, Cambria and Año Nuevo provenances (Eldridge, 1997). These provenances were initially subdivided into subpopulations with Año Nuevo, Monterey and Cambria and having four, six, and three sub-populations, respectively. The study of Burdon et al. (1992) showed no evidence of substantial local differentiation for growth and form traits for the 1964 collection grown in New Zealand. Raymond and Henson (2009) reported significant differences between sub-populations for DBH at age 26 years within Año Nuevo and Cambria, for straightness at age 26 years within Año Nuevo and for 'nodality' (intervals between branch clusters) score at age 26 years (from 1 = uninodal to 4 = highly multinodal) within Cambria for the 1978 'Eldridge' collection. However, the magnitude of the sub-population differences in both studies was relatively small, and the sub-popula-

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tions classification was disregarded in this study. The seed was used to establish provenance trials and large block plantings of gene-resource plantings between 1979 and 1982 at many locations in Australia, New Zealand and a few in Chile and South Africa. The gene-resource stands planted in New Zealand in 1982 had approximately 833 stems per ha. In 1994, plus trees were selected in the gene-resource plantings at a selection rate of one tree per hectare, and a separation of at least 50 metres between selected trees was ensured. Selection criteria were based on growth, health, straightness and lack of malformation, and the selected trees also had to be carrying cones. Seed from the plus trees was used to establish tests at two sites in New Zealand and one site in Australia, in 1995.

Site details and trial design

Table 1 provides general information about the field trials that were involved in this study. Each trial contained 128 families from three provenances: Año Nuevo had 37, Monterey had 57, and Cambria 34 families. Each trial had a sets-within-replicates layout containing 30 replicates, with four sets per replicate, and 36 families per set (including four controls). Given the large number of families, a sets-in-replicate, single-tree plot design was used (e.g., KING et al., 1993). The allocation of families to each set from each of the three provenances was systematic. This was designed to have more or less equal representation of each provenance in each set. The families in each set were sampled at random from within each provenance. The controls consisted of two seedlots of unimproved selections (GF6), one seedlot of open-pollinated seed-orchard stock (GF14) and one seedlot of current (i.e., control-pollinated) breeding stock (GF28). However, control seedlots were not included in the estimation of genetic parameter estimates as they were considered not to be part of the population.

Sampling of wood increment cores

At age 14 years from planting, a total of 640 trees were sampled from Kaingaroa in New Zealand, while 586 were sampled at Kangaroovale in Australia (*Table 1*). On average, four to five replicates chosen at random (individual trees) of each of 128 families were sampled at each site. Twelve millimetre bark-to-bark increment cores were collected at breast height (1.3 m); almost all had 10 to 12 growth rings, rings in excess of the twelfth being trimmed off. Borings were repeated as needed to obtain at least one core per tree without severe compression wood. Cores were labelled and dipped in 95% ethanol for 24 hours. Core length was measured on green increment cores by measuring the length of the whole cores excluding the bark.

Wood density measurements

Wood density of each sample was estimated using the maximum moisture method (SMITH, 1954). Saturated volume was measured on fully saturated samples, using the water displacement method; oven dry-mass was measured after drying in an oven at 105 degrees for 24 to 48 hours. The wood density of each sample was calculated using the following formula:

$$DEN = \frac{m_{od}}{V_{Green}} \times 1000 \quad [1]$$

where *DEN* is the basic wood density of whole increment cores based on green and oven-dry volumes, respectively; m_{od} is the oven-dry weight in grams; V_{Green} is green volume in cubic centimetres.

Statistical analyses

Single-site variance components and across-sites correlations were estimated within the framework of the general linear mixed model:

$$y = Xb + Za + e \quad [2]$$

where y is a vector of phenotypic values for a trait; b is a vector of fixed effects with the population mean as the first element; a is a vector of random effects including additive genetic values; e is a vector of residual deviations; and X and Z are incidence matrices relating a given phenotypic observation to its corresponding fixed or random effects.

Normality of the distribution of the residuals were checked within the ASReml program (GILMOUR et al., 2009) which was used for subsequent data analysis.

Table 1. – Site characteristics and particulars of field trials in New Zealand and Australia.

Particulars	Kaingaroa, New Zealand	Kangaroovale, Australia
Test number	FR259/1	FR259/3
Date planted	June 1995	June 1995
Latitude	38°16' S	35°05' S
Longitude	176 ° 43' E	148 ° 15' E
Elevation (m)	330	480
Annual rainfall (mm)	1600	840
Annual temp (°C) (mean min)	5.9	6.6
Annual temp (°C) (mean max)	12.0	21.0
Soil type and parent material	Shallow covering of basaltic scoria over layers of rhyolitic pumice	Solodic, derived from rangle-volcaniclastic andstone, polysistic conglomerate
Site type	Undulating terrain; on a 2nd pine rotation	Gently sloping terrain, ex-pasture
Spacing (m)	4×4	4×4
Number of cores	640	586

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One-tailed likelihood ratio tests (LRT) (STRAM and LEE, 1994) were applied to assess the statistical significance of provenance and family-within-provenance variances.

Observed variance components were used to estimate the causal variance components and individual-tree narrow-sense heritability for each trait:

Additive genetic variance pooled across provenances = $\hat{\sigma}_A^2 = 4\hat{\sigma}_{fam}^2$; [3]

Phenotypic variance = $\hat{\sigma}_P^2 = \hat{\sigma}_{fam}^2 + \hat{\sigma}_e^2$; and [4]

Individual-tree narrow-sense heritability =

$$\hat{h}^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2} = \frac{4\hat{\sigma}_{fam}^2}{\hat{\sigma}_{fam}^2 + \hat{\sigma}_e^2}. \quad [5]$$

where σ^2_P is the phenotypic variance, σ^2_{fam} is family genetic variance.

We used a ¼ as the covariance among sibs of open-pollinated families. However, in some cases, the covariance among sibs of open-pollinated families will often be higher than ¼ of additive genetic variance; this could results from inbreeding and or from a smaller number of effective male pollinators leading to the presence of some percentage of full-sibs with the open-pollinated family (SQUILLACE, 1974). In this study, we assumed that the material represented a collection of half-sib families; specifically that the seed parents were a random sample of their respective provenances, and that each one was pollinated from a large random sample of trees from its own provenance. In plantation conditions, the estimates should be minimally inflated by the departures from this assumption.

Variances were not independent of the scale and mean of the respective traits (SOKAL and ROHLF, 1995). Therefore, to compare the relative genetic variances of the different traits across tests, the genetic coefficient of variation (CV_A) was estimated as:

$$\overline{CV}_A = \frac{\hat{\sigma}_A}{\bar{x}} \times 100\%, \quad [6]$$

where CV_A is the coefficient of additive genetic variation, σ^2_A is the square-root of the additive genetic variance for a trait, and $\bar{x}$ is the trial mean for the trait. The CV_A expresses the genetic variance relative to the mean of the trait of interest and gives a standardized measure of the genetic variance relative to the mean of the trait. The higher the CV_A for a trait, the higher is its relative variation.

A multivariate, multi-site (all traits and all trials) analysis was also conducted in order to estimate heritability and additive genetic correlations between traits across trials using a model similar to equation 2, except that here, trial is a fixed effect. Results from single-site analyses were used to obtain starting values for the joint analyses. Both heterogeneous additive and error variances were included in the model.

In turn, an unbiased estimate of narrow-sense heritability was estimated as:

$$\hat{h}^2 = \frac{4\hat{\sigma}_{fam}^2}{\hat{\sigma}_{fam}^2 + \hat{\sigma}_{Tfam}^2 + \hat{\sigma}_e^2} \quad [7]$$

where σ^2_{Tfam} is interaction between site and family and all other terms as in Equation 5.

Additive genetic correlations between traits x and y were obtained from the estimated additive covariance and variance components as

$$r_A = \frac{\hat{\sigma}_{a_x a_y}}{\sqrt{\hat{\sigma}_{a_x}^2 \hat{\sigma}_{a_y}^2}} \quad [8]$$

where:

$\sigma_{a_x a_y}$ = additive genetic covariance component between trait x and trait y,

$\sigma^2_{a_x}$ = additive genetic variance for trait x at each site,

$\sigma^2_{a_y}$ = additive genetic variance for trait y at each site.

For the additive genetic correlations between traits, two-tailed LR tests were used to test the departure of an estimated trait correlation from zero. This was done by using a parameterisation of (co)variance matrix based on a correlation form and constraining the correlation parameter to be +1 under the null hypothesis to be tested. If $\log L_1$ and $\log L_2$ are the REML log-likelihoods from the nonrestricted and the restricted ($r_A = 1$) models, respectively, the test statistic (D) is given by

$$D = 2(\log L_1 - \log L_2) \quad [9]$$

which is distributed approximately as X^2 under H_0, with degrees of freedom given by the difference between the number of parameters estimated under the non-restricted and the restricted models (COSTA E SILVA et al., 2005; GILMOUR et al., 2009).

In order to determine the extent of GxE for each of the traits, univariate, paired-site analyses were conducted and Type-B genetic correlations estimated using a model similar to equation [2], except trial is a fixed effect, and $\mathbf{y}i$ is now defined as the vector of observations for a single trait indexed (i) by trial. Type-B additive genetic correlations were then estimated as in BURDON (1977):

$$r_B = \frac{\hat{\sigma}_{A_1 A_2}}{\sqrt{\hat{\sigma}_{A_1}^2 \hat{\sigma}_{A_2}^2}} \quad [10]$$

where values closer to unity indicate little genotype by environment interaction, and lower values indicate that genotype by environment interactions exist. Approximate standard errors of statistics were obtained by Taylor expansion (KENDALL and STUART, 1963) in ASReml (GILMOUR et al., 2009). One-tailed LT tests were used to test the departure of an estimated correlation from +1. These were done as in Eq 9.

Results

Comparison of provenance means for wood density and core length

The overall mean values at provenance level for density and core length are presented in *Table 2*. Mean provenance density across trials ranged from 356 kg/m^3 to 369 kg/m^3. Monterey performed best at Kaingaroa with an overall mean of 368.9 kg/m^3. All provenances per-

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Table 2. – Provenance averages for wood density and core length and associated standard errors for radiata pine. The same letter across a row indicates no significant difference between means at $p \leq 0.05$ (experiment-wise error).

Trial/Trait	Año Nuevo	Monterey	Cambria
FR259/1 (Kaingaroa)			
Wood density (kg/m^3)	364.9 ± 1.6^b	368.9 ± 1.4^a	362.4 ± 2.1^b
Core length (cm)	27.9 ± 0.6^a	28.0 ± 0.4^a	27.6 ± 0.6^a
FR259/3 (Kangaroovale)			
Wood density (kg/m^3)	357.2 ± 1.2^a	355.6 ± 1.4^a	357.0 ± 1.6^a
Core length (cm)	24.7 ± 0.2^a	24.4 ± 0.2^a	24.1 ± 0.3^a
Across sites			
Wood density (kg/m^3)	360.9 ± 1.6^a	362.1 ± 1.0^a	359.4 ± 1.3^a
Core length (cm)	26.2 ± 0.3^a	25.7 ± 0.3^a	26.2 ± 0.2^a

Table 3. – Estimates of genetic parameters for wood density from sib-analysis by provenances, assuming half-sib families.

Trial/Provenance	No. of families	Among family variance ($\hat{\sigma}^2_{fam}$)	Narrow-sense heritability ($\hat{h}^2$)	Phenotypic variance ($\hat{\sigma}^2_p$)	$\overline{CV_A}$ (%)
FR259/1 (Kaingaroa)					
Año Nuevo	37	112.17**	0.89 ± 0.17	392.10	5.8
Monterey	57	56.92*	0.51 ± 0.25	447.48	10.7
Cambria	34	112.12*	0.86 ± 0.19	518.25	5.7
Pooled	128	95.68***	0.83 ± 0.18	460.68	5.4
FR259/3 (Kangaroovale)					
Año Nuevo	37	65.42*	0.56 ± 0.25	465.43	4.5
Monterey	57	43.48^{ns}	0.51 ± 0.36	369.20	3.4
Cambria	34	46.18*	0.56 ± 0.22	331.55	3.8
Pooled	128	57.38***	0.57 ± 0.16	402.68	4.2
Across-sites	128	44.80*	0.43 ± 0.13	422.19	3.7

$^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$; ^{ns}not significant; significance levels based on one-tailed LR tests that were used to test the departure of σ^2_{fam} from zero; Statistical significance for estimated heritability is same as for additive genetic variance.

formed similarly at Kangaroovale (mean = 357 kg/m^3). Monterey was slightly but significantly different from Año Nuevo and Cambria at Kaingaroa ($p = 0.05$). Differences among provenances were negligible at Kangaroovale. However, there were significant differences at family level for all provenances across sites (*Table 3*). No significant provenance or family differences were detected for core length at either site.

Genetic parameters

Estimates of genetic parameters for wood density for each provenance at each trial are presented in *Table 3*. The estimates of heritability were all above 0.50 and generally higher at Kaingaroa than at Kangaroovale, pooled estimates across provenances within sites high (0.83 and 0.43 respectively). There were significant family differences within provenance at both sites, with the exception of Monterey at Kangaroovale (*Table 3*). Genetic coefficient of variation (CV_A) were highest in Monterey at Kaingaroa.

Estimates of heritability for core length for each provenance were very imprecise at both sites (*Table 4*). The pooled estimates across provenances were low at both sites (0.28 and 0.12). for core length averaged 8.7 across provenances. The family variance for Cambria was less than zero and insignificant, probably on account of smaller sample size (n = 34).

Estimates of additive genetic correlations between density and core length for each of the provenances at each site are provided in *Table 5*. The estimates were generally insignificant and imprecise, probably due to the smaller number of families within each provenance (see *Table 3* for number of families within a provenance). The pooled additive genetic correlation estimate across provenances between density and core length at Kaingaroa was also not significant (0.35 ± 0.26) whereas at Kangaroovale it was barely significant (–0.77 ± 0.29). Likewise, type B- genetic correlation (measure of G x E) estimates for density and core length for each provenance were imprecise. The overall estimates of type B-

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Table 4. – Estimates of genetic parameters for core length from sib-analysis by provenances assuming half-sib families.

Trial/Provenance	No. families	Among family variance ($\hat{\sigma}^2_{fam}$)	Narrow-sense heritability ($\hat{h}^2$)	Phenotypic variance ($\hat{\sigma}^2_P$)	$\overline{CV_A}$ (%)
FR259/1 (Kaingaroa)					
Año Nuevo	37	1.40^{ns}	0.16 ± 0.26	34.87	8.5
Monterey	57	5.45*	0.51 ± 0.25	42.03	8.3
Cambria	34	NE	--	--	--
Pooled	128	2.77*	0.28 ± 0.15	39.31	8.7
FR259/3 (Kangaroovale)					
Año Nuevo	37	0.73*	0.40 ± 0.23	7.15	7.0
Monterey	57	0.61^{ns}	0.31 ± 0.32	7.66	6.4
Cambria	34	0.57^{ns}	0.34 ± 0.27	6.58	6.3
Pooled	128	0.55*	0.31 ± 0.14	7.11	6.1
Across-sites	128	0.66*	0.12 ± 0.07	23.13	3.7

NE – not estimable and assumed to be zero; $^{*}P<0.05$; ^{ns} not significant; significance levels based on one-tailed LR tests that were used to test the departure of σ^2_{fam} from zero; Statistical significance for estimated heritability is same as for additive genetic variance.

Table 5. – Estimates of additive genetic correlations (r_A) ± approximate standard errors between wood density and core length by provenance.

FR259/1 (Kaingaroa)					
		Año Nuevo	Monterey	Cambria	Overall $\hat{r}_A$
Wood density	Core length	0.34 ± 0.56^{ns}	0.37 ± 0.34^{ns}	0.54 ± 0.68^{ns}	0.35 ± 0.26^{ns}
FR259/3 (Kangaroovale)					
		Año Nuevo	Monterey	Cambria	Overall $\hat{r}_A$
Wood density	Core length	0.17 ± 0.64^{ns}	NE	-0.83 ± 0.37^{ns}	-0.77 ± 0.29**

$^{**}P<0.01$; $^{***}P<0.001$; ^{ns} not significant. Significance levels were based on two-tailed LR tests to test the departure of r_A from zero.

Table 6. – Estimates of type B genetic correlations (r_B) ± approximate standard errors between wood density and core length across sites by provenance.

Wood density					
		Año Nuevo	Monterey	Cambria	Overall $\hat{r}_B$
FR259/1	FR259/3	0.62 ± 0.28*	0.93 ± 0.31^{ns}	0.33 ± 0.47***	0.70± 017*
Core length					
		Año Nuevo	Monterey	Cambria	Overall $\hat{r}_B$
FR259/1	FR259/3	0.22 ± 0.71***	0.60 ± 0.38***	NE	0.72 ± 0.37*

$^{*}P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$; ^{ns} not significant. Significance levels based on one-tailed LR tests that were used to test the test the departure of r_B from +1.

genetic correlation for density and core length were 0.70 ± 0.17 ($p<0.05$) and 0.72 ± 0.37 ($p<0.05$), respectively (*Table 6*).

Discussion

The three mainland provenances were generally very similar for density at age 14 years from planting. Mean basic density of radiata pine wood at age 14 years from planting was 361 kg/m^3 (measured at 1.3 m above ground). It appears density values reported in the literature are somewhat variable. For example, RAYMOND et al (2009) reported density values for first 10 rings from the pith in the same magnitude as in this study, ranging from 354–369 kg/m^3 for mainland provenances. However, other studies have reported higher values for density at similar age. For example, LI and WU (2005) reported average density of 436 kg/m^3 at cambial age 14 years in radiata pine planted in Australia. BURDON and LOW (1992) reported mean basic density values of

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320 kg/m^3 for five rings for mainland provenances and 359 kg/m^3 for the slower-growing island provenances. Possible discrepancies among studies may be due to cores containing both corewood and outerwood (BURDON et al., 2004). Corewood in radiata pine has lower density than outerwood (COWN, 1992; BURDON et al., 1992; KUMAR and LEE, 2002), and the transition from corewood to outerwood is typically in the range from seven to twelve rings from the pith, depending on site (GAPARE et al., 2006).

Compared to Monterey, Año Nuevo and Cambria averaged 1.1% and 2% lower, respectively at Kaingaroa. An earlier study by BURDON and LOW (1992) that compared density at age 8 years for these provenances reported that Año Nuevo and Cambria averaged 1.5% and 4% lower respectively, than Monterey.

Monterey had the best growth at age nine years from planting while Año Nuevo and Cambria performed similarly at Kaingaroa (GAPARE et al., 2011). As observed for core length and DBH at Kangaroovale, all three provenances performed similarly for density. On both sites the mainland provenances showed minimal differences in wood density and growth potential, in accordance with some earlier studies. For example, BURDON and LOW (1992) reported mainland provenances to be very similar for density at one site in Kaingaroa forest (mean annual rainfall = 1600 mm; elevation = 320 m asl) in New Zealand (see *Table 1*). Similarly, RAYMOND et al. (2009) reported mainland provenances to be very similar for density and acoustic velocity at Batlow (mean annual rainfall = 1250 mm; elevation = 700 m asl) in New South Wales. However, significant differences for wood density were reported between mainland and island provenances in two independent studies (BURDON and LOW, 1992; RAYMOND et al., 2009). In both studies, Guadalupe had higher wood density than mainland provenances. As often observed for wood traits, there was significant variation in basic density due to families within provenances.

The variation in wood density may be due to genetic, environmental, physiological or silvicultural treatments (PANSHIN and DE ZEEUW, 1980; SPLECHTNA et al., 2001). Physiological variation of wood density is related to cambial activity and varies with age, season, climate and environmental conditions (PANSHIN and DE ZEEUW, 1980). Physiological variation is the main cause of within-a-tree variations which include axial, radial, and within-a-ring (intra-ring) variations (PANSHIN and DE ZEEUW, 1980; ZOBEL and VAN BUIJTNEN, 1989). Intra-ring variation is mainly due to differences between cell structure, and formations between earlywood and latewood. Wood density is closely related to the percentage of small-diameter latewood cells in the annual ring and radial diameters of tracheids cells are controlled by auxins translocated from terminal shoots (PANSHIN and DE ZEEUW, 1980). The rate of auxin synthesis is dependent upon activity in the terminal shoots which in turn is dictated by the moisture status of the site. With increasing moisture stress there is less shoot activity, a lower level of auxin production and a transition occurs from large (earlywood) to small (latewood) diameter tracheid cells. For example, radiata pine grown in Victoria produced low density wood when grown on a site with bountiful spring and summer rainfall and good soil-water holding capacity (NICHOLLS and WRIGHT, 1976). Variation in the availability of soil moisture is largely a factor that determines the proportions of earlywood and latewood in pines (e.g., BARNES et al., 1977). Generally, low temperatures, drought and short photoperiods adversely affect shoot extension and leaf development, lower levels of diffuse auxin, and bring about the formation of smaller or radially flattened tracheids of latewood type (e.g., ZIMMERMANN and BROWN, 1971). Kangaroovale receives less rainfall and is warmer than Kaingaroa (*Table 2*). It appears low temperature may be the driving factor for density at Kaingaroa. However, one might have expected more latewood formation and higher density at Kangaroovale on account of lower growth rate and therefore lower level of auxin production.

The similarity of Cambria to Año Nuevo for growth and density is an interesting result because the genetic base of the present Australian and New Zealand plantations has been shown to be from Año Nuevo and Monterey (MORAN and BELL, 1987; BURDON, 1992). Infusion of Cambria material would broaden the overall genetic base of the radiata pine breeding programs with potential long-term benefits, despite the often disappointing performance of material collected from Cambria (e.g., ADES and SIMPSON, 1991; BURDON et al., 1992).

There is a significant 'knowledge' gap on the performance of the native provenances, especially for wood quality. Although somewhat imprecise the estimates of genetic parameters for native populations are useful for 1) evaluation and monitoring of genetic progress (benchmarking of Best Linear Unbiased Predictions (BLUPs)) over generations of tree improvement and 2), for choosing the provenances and individuals for genetic infusion.

Although the individual provenance heritability estimates were imprecise (large standard errors), our results indicated that the high heritability often reported for wood density holds for all provenances. Heritability estimates (narrow- and broad-sense) for radiata pine wood density from a total of 63 estimates in 17 publications ranged between 0.33 and 1.00 with a mean of 0.69 using clonal and family trials (WU et al., 2008). New Zealand estimates (average 0.82) were higher than estimates from Australian studies (average 0.57). The more precise heritability estimate from pooled provenances was relatively high (>0.57) and similar to other studies. For example, BURDON and LOW (1992) reported heritability estimates of 0.74 to 0.96 for the mainland provenances. The high heritability estimate of 0.83 for wood density at Kaingaroa was similar to that reported by KUMAR et al. (2008) for density at age eight years at Hawke's Bay on the North Island of New Zealand.

As expected, core length was less heritable than wood density. The heritability estimate for core length was higher at Kaingaroa (0.28) than at Kangaroovale (0.12). It appears heritability for growth at Kaingaroa did not change from age nine (0.23 for DBH) (GAPARE et al., 2011) to age 14 years (0.28 for core length).

The low number of families in each provenance was certainly insufficient to allow for reliable estimates of

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genetic correlations. The number of OP families in each of the provenances was not a big population to estimate genetic correlations, a highly derivative parameter. Neither provenance × site nor family × site interaction were significant among Kaingaroa and Kangaroovale sites, even though heritabilities at Kaingaroa (0.83) were higher than at Kangaroovale (0.43) for density. This was supported by our estimate of type-B genetic correlation for density (0.70), which suggested only minor G × E. BURDON (1977) used an indirect measure of genotype × site interaction (type B genetic correlation) for density and got correlations close to unity. BURDON and LOW (1992) reported minimal family × site interaction for wood density in New Zealand. LI and WU (2005) also reported that family × site interaction was not significant among Tantanoola and Flynn sites in Australia, even though heritabilities were different between sites. This concurs with observations in New Zealand where minimal family × site interaction has been observed for wood density (BURDON and LOW, 1992). Minimal genotype × site interaction in wood density indicates that a single breeding population for improvement of wood density should be an efficient approach. Our estimate of type-B genetic correlation for core length was imprecise. Generally, there is G × E for growth traits. We reported significant G × E for DBH at age 9 years from planting between Kaingaroa and Kangaroovale (GAPARE et al., 2011).

Generally, statistically significant negative genetic correlations are observed between growth and wood density. Our estimates of additive genetic correlations were not significant and very imprecise (large standard errors). BURDON and LOW (1992) reported an average partial genetic correlation between density and ring width/diameter for constant height of around –0.4. For the mainland provenances, a negative genetic correlation was reported between tree diameter and density (–0.46 for 6 to 10 rings from pith) and –0.69 for rings 11 to 15 from pith) by RAYMOND et al. (2009). KUMAR et al. (2008) reported adverse genetic correlations between density and DBH for radiata pine grown at Hawke's Bay and Kaingaroa sites in the North Island, New Zealand (–0.30). Similar estimates were reported for second generation selections of radiata pine in Australia (–0.23 to –0.57) (BALTUNIS et al., 2010).

Conclusion

Our previous work on performance differences among *ex situ* native-provenance collections of radiata pine (GAPARE et al., 2011) suggested that there was appreciable genetic variation in native populations for growth and form traits. In particular, we recommended infusion of Cambria material into the breeding population because the base of the present Australian and New Zealand plantations is principally derived from Año Nuevo and Monterey. Our results confirmed that Cambria is just as good as Año Nuevo and Monterey for density. This makes a strong case for infusion of Cambria into breeding populations.

On both sites the mainland provenances showed minimal differences in wood density and growth potential, in accordance with some earlier studies. While other studies may have shown some differences in density between the mainland provenances, there were very little differences in relation to heritable within-provenance variation. While growth potential does not vary materially between these provenances, the main issue appears to be site tolerances.

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Primer Note: Microsatellite-AFLP development for *Araucaria araucana* (Mol.) K. Koch, an endangered conifer of Chilean and Argentinean native forests

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Abstract

Araucaria araucana (Mol.) K. Koch is one of the most important native species of Chile and Argentina, and also one of the most endangered. In this study, we report the development and characterization of a set of microsatellite markers in the species by means of the microsatellite-AFLP (M-AFLP) technique. A total of 25 M-AFLP derived bands, showing a typical microsatellite pattern, were selected and sequenced. Of these, 12 that contained microsatellite sequences, were used for primer extension. Six of the resulting SSR markers provided easily interpretable patterns and were used to investigate the level of genetic diversity in two populations of *A. araucana*. A total of 43 alleles were amplified. The mean overall loci of observed and expected heterozygosities for the Conguillio and Villa Araucaria populations were 0.322 and 0.443, respectively. The primers presented in this study may provide useful information for the establishment of a conservation strategy in the species.

Key words: Microsatellite, endangered species, *Araucaria araucana*, conservation.

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Araucaria araucana (Mol.) K. Koch is one of the oldest conifers in South America and a representative symbol of Chilean and Argentinean forest biodiversity due to its endemicity and longevity. Likewise, it is the major tree species in the traditional lands of the indigenous Mapuche Pehuenche community, showing that both the ecological and cultural significance of araucaria forests are key elements for its conservation. The species occurs mainly in the Andean region at the border of Chile and Argentina and also in the Coastal Cordillera of Chile. *A. Araucana* is considered an endangered species due to its restricted current distribution, slow growth and low regeneration (Veblen, 1982), and it is included in Appendix I of CITES and listed as 'vulnerable' species on the IUCN Red List (1996).

Microsatellite markers have been developed in other species of Araucaria genera such as *A. cunninghamii*, *A. rulei*, *A. subulata* and *A. angustifolia* (Scott et al.,

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