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EARLY SELECTION FOR *PINUS RADIATA* IN NEW ZEALAND USING A FARM-FIELD EXPERIMENTAL DESIGN

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ABSTRACT

The effectiveness of early selection for growth and form traits to maximise gain per annum in *Pinus radiata* D.Don was examined in a "farm-field" experiment based at two farm sites and one field site in the North Island of New Zealand. "farm-field" experiments are tests that are established on highly fertile "farm" sites, with intensive site preparation, intensive weed control, and close spacing, paired with tests of the same material on "field" sites.

Family mean correlations among growth traits at early ages (1–3 years) on the farm sites were relatively high (0.54–1.0) but correlations between early ages at the farm sites and measurements at age 8 years at the field site were low to moderate (0.29–0.65). Correlations between form traits measured at age 3 and then age 8 years showed similar trends. Early assessments of growth and form did not provide good prediction of later-age performance, although the best prediction was obtained from the age-3 measurement. Selecting the highest-ranked 20 families for diameter at age 3 years gave higher relative efficiency of selection than selection at earlier ages.

The use of bare-root seedlings rather than container stock, and persistent nursery effects may have contributed to the low selection efficiencies. Maternal effects were also likely to have affected early-age measurements. However, although including 100-seed weight in the model did lower heritability estimates and some genetic correlations for height growth, genetic correlations were not greatly changed by including this factor and early-age selection efficiency did not improve.

The potential for early selection for growth and for form in farm-field experiments with *P. radiata* in New Zealand appears to be very limited.

Keywords: early selection; growth; form; genetic parameters; heritability; genetic correlation; New Zealand; *Pinus radiata*.

INTRODUCTION

The economic justification for tree breeding depends on realisation of genetic gains. After the first generation of breeding, genetic gain may be more difficult to obtain and needs to be optimised through efficient selection techniques and through optimising the age of selection (Burdon 1989). Greater gain can be realised from progeny trial data obtained at later ages where trees are closer to rotation age, but genetic gain per year is dependent on

the length of the whole breeding and testing cycle and thus the generation interval. An efficient compromise must be made between reliability of selection (measurements close to rotation age are more reliable) and the length of the generation interval. A breeder's mandate is to find a balance between these two factors while at the same time balancing selection costs (Burdon 1989). Early selection may offer increased realised gains per year for material deployed in commercial plantations and continues to attract interest (e.g., in *Pinus radiata* Matheson *et al*. 1994; King & Burdon 1991; Apiolaza *et al*. 2000).

For *P. radiata* in New Zealand, the optimal age for selection based on growth and form is accepted as being around 8 years (King & Burdon 1991), although 10-year-old measurements gave almost the same gain as direct selection at age 17 (King & Burdon 1991). In terms of early selection, Burdon *et al*. (1992) found that for *P. radiata* correlations between family mean height growth measurements from years 1–3 and height at age 9 were generally only moderate (approximately 0.53–0.74). However, by age 6 the correlations had improved considerably (approximately 0.80–0.98), suggesting that selection age for height could be dropped from 9 to 6 years.

"Farm-field" experiments are tests that are established on highly fertile "farm" sites, with intensive site preparation, intensive weed control, and close spacing, paired with tests of the same material on "field" sites. The correlation between progeny performance at the "farm" and "field" sites determines whether early growth at the "farm" site is a good predictor of later-age performance at the "field" site (the higher the correlation, the more effective early selection would be). In New Zealand, the desire to find a method for early selection was pursued further after a review by S.J.Lee & P.Jefferson (unpubl. data) revealed that highly fertile fast-growing "farm" sites may be more effective in showing early genetic differences than normal progeny testing "field" sites in the forest. This conclusion was based largely on early growth and wood density "farm-field" studies in *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) open-pollinated progeny in British Columbia (Ritters *et al*. 1987; Fins *et al*. 1990; Woods *et al*. 1995). Comparisons of early growth and wood density at year 1 from a farm site with volume and density from 11 field sites at age 13 gave moderate correlations, but the same comparison at age 3 at the "farm-field" was high, at about 0.7 (Woods *et al*. 1990). Selection efficiencies for a target trait of age 13 volume were 162% from age 3 "farm-field" assessments of height and diameter. This result was enough to motivate tree breeders in New Zealand to test the trials here.

A "farm-field" study was subsequently established to determine whether early selection using a farm site would indeed be effective compared with later-age selection at a field site. This experiment was planted in 1992, based on "880" series material (Jayawickrama & Carson 2000). Early growth data were analysed, comparing the two farm sites planted (Long Mile near Rotorua, and Onepu in the Bay of Plenty) with five previous trials with the same genetic material; correlations between family means for growth and form traits (not malformation) between the two farm sites were good; correlations of family means of the farm sites with field sites were higher with the better-grown field sites at ages 6–8 years (G.T.Stovold, M.J.Carson, M.Hong & P.Jefferson unpubl. data). Overall correlations among farm and field sites were not high enough, however, to endorse early selection (approximately 0.02–0.12).

Recently, measurement of the "field" progeny trial established in conjunction with the two trials at the "farm" sites was completed at age 8. The growth data collected allowed the

estimation of family-mean correlations between the farm sites at early ages (from planting through to 3 years) and the field site (8 years). We therefore examined the effectiveness of early selection using "farm-field" experiments for *P. radiata* in New Zealand, and the most effective timing for early measurement at the homogeneous and highly productive "farm" sites.

MATERIALS AND METHODS
Experimental Material

Open-pollinated seed-orchard seed was collected from 128 ortets from the 1981 "880" series of the New Zealand *P. radiata* breeding population in the Kaingaroa seed orchard (Jayawickrama & Carson 2000). The weight of 100 seeds of each family (100 swt) was also taken before planting. Progeny were tested on three sites — two highly fertile, uniform farm sites and one field site. One farm site was located at Onepu Orchard near Te Teko in the Bay of Plenty, and the other at a nursery site at the Long Mile, Rotorua (Table 1). The single field site was at Tarawera Forest (Table 1). Site preparation at Long Mile was ripping and rotary hoeing, and at Onepu boring of planting spots. The site at Tarawera received a line rake, then ripping at 70 cm followed by mounding. Intensive silviculture including maintaining a totally weed-free environment was implemented at all sites until age 3 years, after which the field site received standard silvicultural treatment, with access pruning at age 5. The same experimental design was used at all sites: single-tree-plots with 20 replicates with four sets-in-reps. Spacing between trees was 1.5×1.5 m at Onepu, and 1.3×1.3 m at Long Mile. Spacing at Tarawera was 3×6 m. All trials were established in September 1992. Individual site details are given in Table 1. Growth and form measurements were taken regularly at all sites (Table 2).

TABLE 1–Trial site information for the farm sites at Long Mile (1) and Onepu (2) and the single field site Tarawera (3).

Site No.	Forest name	Farm or field site	Latitude (S)	Longitude (E)	Altitude (m)	Soil
1	Long Mile	Farm	38º10′3″	176º15′	270	Pumice overlaying old lake bed
2	Onepu Orchard	Farm	38º	176º43′	16–19	Water-sorted scoria and pumice
3	Tarawera	Field	38º5′	176º37′	90–100	Basalt/scoria on pumice

Analysis
Exploratory analysis

Exploratory analyses to test for normality utilised the Univariate Procedure in SAS (SAS Institute 1990) and showed that the majority of traits were within reasonable bounds (generally $p > 0.05$) for normality. However, data from the height and root collar diameter measurements at planting were close to these normality limits and therefore less reliability can be placed on these estimates. Branching, scored at the age of 3 years at the two farm sites, was markedly non-normal. Malformation scores were highly non-normal and could

TABLE 2–Measurements taken at the two farm sites and at the single field site planted at Tarawera, and the corresponding abbreviations used in this report.

Trait*	Date at measurement	Age at measurement	Abbr.*	Long Mile	Onepu Orchard	Tarawera
HT	Sept. 1992	planting	HT00	×	×	×
DRC	Sept. 1992	planting	DRC00	×	×	×
HT	April 1993	7 months	HT_7	×	×	
DRC	April 1993	7 months	DRC_7	×	×	
HT	Sept. 1993	12 months	HT01	×	×	
DRC	Sept. 1993	12 months	DRC01	×	×	
HT	Sept. 1994	24 months	HT02	×	×	
DRC	Sept. 1994	24 months	DRC02	×	×	
HT	May 1995	32 months	HT03	×	×	
DRC	May 1995	32 months	DRC03	×	×	
STR	May 1995	32 months	STR03	×	×	
BR	May 1995	32 months	BR903	×	×	
MAL	May 1995	32 months	MAL03	×	×	
MAL	Nov. 2000	8 years	MAL08			×
BR	Nov. 2000	8 years	BR908			×
STR	Nov. 2000	8 years	STR08			×
DBH	Nov. 2000	8 years	DBH08			×

* HT = total height
DRC = diameter of the root collar
STR = straightness (1–9) where 1 = very crooked and 9 = straight
BR = branching (1–9) where 1 = uninodal and 9 = multinodal
MAL = malformation (1–9) where 1 = highly malformed and 9 = no malformation
DBH = diameter at breast height.

not be normalised by any standard transformation and were thus excluded from the correlation analysis.

Initial analyses were undertaken including sets in replicates in the model, but this term was not found to be significant and was subsequently dropped.

Correlations between family means across sites and ages

Least-squares family means within sites and overall site means were estimated for individual sites using the GLM procedure in SAS (SAS Institute 1990) according to Model [1].

$$y_{ij} = \mu + r_i + f_j + e_{ij} \qquad [1]$$

where: μ is the overall mean,

r_i is the fixed effect of the ith replicate,

f_j is the random effect of the jth family, and

e_{ij} is the random residual error term.

Family mean correlations and their significance of departure from zero were then estimated using the CORR procedure in SAS (SAS Institute 1990).

Genetic parameters

Genetic variances were estimated for individual sites using Model [1] and across the two farm sites using Model [2] in ASREML (Gilmour *et al.* 1998):

$$y_{ijk} = \mu + s_i + r_{ij} + f_k + fs_{ik} + e_{ijk} \qquad [2]$$

where: μ is the overall mean,

s_i is the fixed effect of the ith site,

r_{ij} is the fixed effect of the jth replicate nested within the ith site,

f_k is the random effect of the kth family,

fs_{ik} is the random interaction between the kth family and the ith site, and

e_{ijk} is the random residual error term.

Individual narrow-sense heritabilities were estimated as the additive genetic variance divided by the phenotypic variance ($h^2 = \sigma^2_a / \sigma^2_p$), assuming that the family variance σ^2_f was $^1/_4$ the additive genetic variance σ^2_a, and for individual sites the phenotypic variance σ^2_p was estimated as $\sigma^2_f + \sigma^2_e$. For both farm sites the phenotypic variance σ^2_p was estimated as $\sigma^2_f + \sigma^2_{fs} + \sigma^2_e$, where σ^2_f was the variance due to families, σ^2_{fs} was the family × site interaction variance, and σ^2_e was the residual variance.

Genetic correlations (r_g) were estimated in a multivariate analysis using Model [1] in ASREML (Burdon 1977; Gilmour *et al*. 1998). Standard error estimates were obtained by using the variance component estimation function in ASREML (Gilmour *et al.* 1998).

Importance of maternal effects in early measurements was investigated by including 100-seed weight in either Model [1] or Model [2] as an additional fixed effect. If the seed weight effect is significant, it will inflate the family variance in the standard genetic parameter estimation procedure. Separating seed weight from the family variance will therefore reduce the size of the heritability estimate, since the variance in the denominator remains the same but the family variance is reduced. If the seed weight effect is large, then there will be a large reduction in the subsequent heritability estimate.

It is important to note that individual site estimates of genetic parameters are biased because the genotype × environment effects are confounded with the family variance. This means that heritabilities estimated from a single site and genetic correlations among traits from a single site are likely to be inflated.

Relative efficiency of selection

Relative efficiency of selection was estimated as the ratio between gain estimated from indirect selection of a target trait at an earlier age (Δg_i, Equation [1]) and the gain estimated from direct selection at age 8 (Δg_d Equation [2]; Falconer & Mackay 1996, p. 189).

$$\Delta g_i = i.h_x.h_y.r_g.\sigma_p \qquad [1]$$

$$\Delta g_d = i.h^2.\sigma_p \qquad [2]$$

where i is the intensity of selection and was equal to 0.1 in this instance. The heritabilities h_x^2 and h_y^2 were heritabilities previously estimated for trait x and trait y.

RESULTS

Means

Least squares site means of growth traits (height and diameter) at planting showed that very similar-sized stock was planted across all sites (Table 3). Growth rates (height, and

TABLE 3–Least-squares site means, standard error of the means (S.E.), minimum and maximum values for all traits measured in the trials: Onepu, Long Mile (farm sites), and Tarawera (field site). The numbers of families at each site used for these estimations were 132 at Onepu, 133 at Long Mile, and 132 at Tarawera.

Site	Trait	Age	Trait	Mean	S.E.	Min.	Max.
Onepu	Height (cm)	Planting	HT00	24.94	2.12	18.90	30.65
		7 months	HT_7	68.06	4.04	57.50	77.85
		1 year	HT01	100.25	6.16	85.20	117.95
		2 years	HT02	262.94	13.69	223.80	299.00
		3 years	HT03	423.65	18.31	380.00	476.50
	Diameter (mm)	Planting	DRC00	4.77	0.30	3.70	5.40
		7 months	DRC_7	11.61	0.76	9.55	13.20
		1 year	DRC01	23.90	1.43	20.46	27.70
		2 years	DRC02	66.96	2.94	60.29	75.50
		3 years	DRC03	96.17	4.89	86.65	111.90
	Branching (1–9)	3 years	BR903	2.48	0.09	2.22	2.67
	Malformation (1–9)	3 years	MAL03	5.31	0.74	3.51	7.47
	Straightness (1–9)	3 years	STR03	4.94	0.45	3.79	6.10
Long Mile	Height (cm)	Planting	HT00	28.18	2.42	19.25	33.85
		7 months	HT_7	66.30	3.78	55.21	75.10
		1 year	HT01	90.34	5.05	76.77	102.85
		2 years	HT02	246.59	10.89	215.60	276.25
		3 years	HT03	428.20	16.54	385.48	466.53
	Diameter (mm)	Planting	DRC00	5.23	0.32	4.12	6.05
		7 months	DRC_7	11.27	0.60	9.55	12.65
		1 year	DRC01	20.99	0.97	18.90	23.45
		2 years	DRC02	53.18	2.05	48.16	57.60
		3 years	DRC03	81.26	3.34	73.05	89.40
	Branching (1–9)	3 years	BR903	1.95	0.08	1.77	2.12
	Malformation (1–9)	3 years	MAL03	6.01	0.84	3.87	7.95
	Straightness (1–9)	3 years	STR03	5.19	0.51	3.80	6.45
Tarawera	Height	Planting	HT00	25.36	2.31	18.81	30.63
	Diameter	Planting	DRC00	4.81	0.29	4.00	5.41
		8 years	DBH08	221.34	7.82	204.92	243.33
	Branching (1–9)	8 years	BR908	5.98	0.48	4.93	6.95
	Malformation (1–9)	8 years	MAL08	6.35	0.62	4.89	7.73
	Straightness (1–9)	8 years	STR08	4.73	0.47	3.73	5.84

root collar diameter) across the two farm sites were very similar 7 months, 1 year, and 2 years post-planting (Table 3). Straightness and branching means were comparable, even between the age 3 measurements at the farm sites and measurements of malformation at age 8 from Tarawera. The mean branching score was slightly higher (more multinodal) at Onepu than at Long Mile (2.48 and 1.95 respectively), but both age 3 measurements were very different from the age 8 mean branching score at Tarawera, which was much more multinodal (5.98, Table 3).

Correlations Between Family Means Across Sites and Ages

Growth traits

Comparison of height-growth between the farm and field sites was limited as measurements were taken only up to age 3 years. Family means between the field and two farm sites were highly correlated at planting (0.84–0.88 phenotypic, 0.99–1.10 estimated genetic*, Table 4). At 7 months of age, this correlation was still strong (0.73 phenotypic, 0.91 estimated genetic), but it gradually decreased with age up to 3 years (0.53 and 0.41 phenotypic, 0.68 and 0.43 estimated genetic, Table 3). This trend was also noted when height at planting of either of the two farm sites was similarly compared. While still reasonable, it is likely that by rotation age these correlations would be weak, and it would not be worth selecting for height using early-age measurements. Unfortunately, height was not measured at 8 years and so no comparisons with later-age height were possible. When 100-seed weight was included in the model, very similar results were obtained (data not shown), although the correlation between height at planting from Tarawera and height at ages 2 and 3 from both farm sites did increase slightly. Maternal effects between measurements at this early age were therefore not large, or were consistent between the ages sampled.

Correlations for diameter included measurements taken from the field site at Tarawera at age 8, allowing a much more effective comparison between growth at early and later ages. Family-mean and genetic correlations estimated were again high between all sites at planting (Table 6). Just as with height, these correlations decreased by age 3 to between 0.39 and 0.34 (phenotypic) and 0.60 and 0.41 (genetic). By the time the trees were 8 years of age, family means from the farm sites were poorly correlated with those at the field site (0.12–0.13 phenotypic) and genetic correlations were also considerably lower than earlier ages (0.29–0.38). Later-age (year 8) diameter growth from the field site was predicted the best using data from the farm sites at age 3 (0.30 and 0.32 phenotypic and 0.65 and 0.62 genetic, Table 6). This also happened when 100-seed weight was included in the model, although some estimates were higher and some lower than those from estimates obtained from the above analysis. There was no general improvement in correlations by the inclusion of this term as a fixed effect.

Correlations between the later-age measurement of diameter at the field site (Tarawera) and the farm site at Onepu were consistently higher than correlations between Tarawera and Long Mile. Onepu therefore appeared to be a better predictor of later-age performance than Long Mile, which was consistent with the geographical proximity and site similarities of these two sites. In fact, at 1 year from planting, Onepu had a strong genetic correlation for diameter with the later-age measurement at Tarawera (0.60±0.18; Table 6). This trend was apparent even when 100-seed weight was included in the model used for analysis (data not shown). It appeared from the genetic correlations that, at this site, selection this early may be risky but the better of the two options available. Certainly, given the data available in this

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* Note: genetic correlations above one occasionally occur, and in reality are correlations that are not greater than 1.0. These large correlations reflect inadequacies in the estimation process, including other genetic effects that could not be accounted for in the model, and experimental design and random estimation error. At this early age, maternal and nursery effects are also likely to have affected this estimate.

TABLE 4—Family-mean correlations (below diagonal) and estimated genetic correlations (above diagonal) for height growth between the two farm sites (Long Mile and Onepu) and the field site (Tarawera). Standard errors of the genetic correlations are given in parentheses. The most important correlations are given in bold type. All phenotypic correlations given were highly significant (p<0.001).

		Tarawera HT00	Onepu HT00	Long Mile HT00	Onepu HT_7	Long Mile HT_7	Onepu HT01	Long Mile HT01	Onepu HT02	Long Mile HT02	Onepu HT03	Long Mile HT03
Tarawera	HT00		**0.99 (0.04)**	**1.10 (0.04)**	**0.91 (0.07)**	**0.94 (0.06)**	**0.85 (0.08)**	**0.89 (0.08)**	**0.72 (0.11)**	**0.64 (0.12)**	**0.68 (0.11)**	**0.43 (0.14)**
Onepu	HT00	**0.84**		1.04 (0.03)	ψ	ψ	ψ	ψ	ψ	ψ	ψ	ψ
Long Mile	HT00	**0.88**	0.81		ψ	ψ	ψ	ψ	ψ	ψ	ψ	ψ
Onepu	HT_7	**0.73**	0.78	0.72		1.03 (0.05)	ψ	ψ	ψ	ψ	ψ	ψ
Long Mile	HT_7	**0.73**	0.71	0.76	0.72		ψ	ψ	ψ	ψ	ψ	ψ
Onepu	HT01	**0.69**	0.74	0.67	0.92	0.70		1.04 (0.06)	ψ	ψ	ψ	ψ
Long Mile	HT01	**0.68**	0.66	0.67	0.70	0.95	0.71		ψ	ψ	ψ	ψ
Onepu	HT02	**0.58**	0.63	0.59	0.76	0.54	0.83	0.54		0.93 (0.08)	ψ	ψ
Long Mile	HT02	**0.53**	0.51	0.59	0.58	0.70	0.59	0.74	0.59		ψ	ψ
Onepu	HT03	**0.53**	0.55	0.52	0.69	0.49	0.73	0.48	0.85	0.58		0.99 (0.08)
Long Mile	HT03	**0.41**	0.41	0.47	0.45	0.51	0.50	0.52	0.55	0.83	0.62	

ψ Because of the high correlations between sites (Table 9), genetic correlations between the two farm sites were estimated from a pooled data set. Equivalent correlations are presented in Table 5.

TABLE 5–Estimated genetic correlations (r_g) and standard errors of the correlations (given in parentheses) among height, root collar diameter, and form traits, for pooled data across farm sites (Onepu and Long Mile).

	HT00	DRC00	HT_7	DRC_7	HT01	DRC01	HT02	DRC02	HT03	DRC03	STR03
DRC00	0.99 (0.04)										
HT_7	1.00 (0.02)	0.82 (0.06)									
DRC_7	0.93 (0.05)	0.94 (0.06)	1.09 (0.04)								
HT01	0.93 (0.03)	0.80 (0.07)	1.17 (0.03)	1.07 (0.04)							
DRC01	0.80 (0.06)	0.77 (0.09)	1.04 (0.04)	1.30 (0.06)	1.08 (0.04)						
HT02	0.84 (0.05)	0.72 (0.08)	0.98 (0.03)	0.94 (0.05)	1.05 (0.03)	0.94 (0.06)					
DRC02	0.76 (0.07)	0.76 (0.09)	0.98 (0.05)	1.17 (0.05)	1.04 (0.04)	1.25 (0.06)	1.00 (0.05)				
HT03	0.69 (0.07)	0.54 (0.10)	0.81 (0.06)	0.72 (0.08)	0.86 (0.05)	0.69 (0.08)	1.13 (0.03)	0.81 (0.07)			
DRC03	0.72 (0.07)	0.60 (0.09)	0.94 (0.04)	1.03 (0.05)	1.01 (0.04)	1.15 (0.04)	1.04 (0.04)	1.24 (0.05)	0.90 (0.05)		
STR03	-0.06 (0.12)	0.14 (0.13)	-0.04 (0.12)	0.13 (0.13)	0.02 (0.12)	0.11 (0.13)	0.18 (0.12)	0.15 (0.13)	0.32 (0.12)	0.13 (0.13)	
BR903	0.23 (0.11)	0.04 (0.13)	0.30 (0.11)	0.22 (0.13)	0.24 (0.12)	0.31 (0.13)	0.36 (0.11)	0.40 (0.12)	0.40 (0.11)	0.36 (0.12)	0.25 (0.13)

TABLE 6—Family mean correlations (below diagonal) and genetic correlations (above diagonal) for diameter growth between the two farm sites (Long Mile and Onepu) and the field site (Tarawera). Probability level is indicated below phenotypic correlations. Standard errors of the genetic correlations are given in parentheses. The most important correlations are presented in bold type.

	Tarawera DRC00	Onepu DRC00	Long Mile DRC00	Onepu DRC_7	Long Mile DRC_7	Onepu DRC01	Long Mile DRC01	Onepu DRC02	Long Mile DRC02	Onepu DRC03	Long Mile DRC03	Tarawera DBH08
Tarawera DRC00		**0.89** (0.12)	**1.03** (0.16)	**0.86** (0.13)	**0.87** (0.13)	**0.68** (0.14)	**0.84** (0.18)	**0.68** (0.13)	**0.58** (0.17)	**0.60** (0.14)	**0.41** (0.16)	**0.25** (0.14)
Onepu DRC00	**0.60** ***		**1.22** (0.12)	ψ	ψ	ψ	ψ	ψ	ψ	ψ	ψ	**0.38** (0.20)
Long Mile DRC00	**0.59** ***	0.61 ***		ψ	ψ	ψ	ψ	ψ	ψ	ψ	ψ	**0.29** (0.23)
Onepu DRC_7	**0.55** ***	0.62 ***	0.51 ***		1.11 (0.11)	ψ	ψ	ψ	ψ	ψ	ψ	**0.51** (0.20)
Long Mile DRC_7	**0.52** ***	0.47 ***	0.40 ***	0.58 ***		ψ	ψ	ψ	ψ	ψ	ψ	**0.46** (0.20)
Onepu DRC01	**0.45** ***	0.46 ***	0.43 ***	0.86 ***	0.55 ***		1.16 (0.14)	ψ	ψ	ψ	ψ	**0.60** (0.18)
Long Mile DRC01	**0.42** ***	0.38 ***	0.35 ***	0.54 ***	0.78 ***	0.56 ***		ψ	ψ	ψ	ψ	**0.55** (0.22)
Onepu DRC02	**0.46** ***	0.53 ***	0.40 ***	0.77 ***	0.56 ***	0.84 ***	0.51 ***		1.09 (0.14)	ψ	ψ	**0.54** (0.18)
Long Mile DRC02	**0.36** ***	0.38 ***	0.31 ***	0.49 ***	0.64 ***	0.51 ***	0.71 ***	0.53 ***		ψ	ψ	**0.36** (0.21)
Onepu DRC03	**0.39** ***	0.42 ***	0.32 ***	0.73 ***	0.50 ***	0.83 ***	0.46 ***	0.90 ***	0.46 ***		1.03 (0.09)	**0.65** (0.16)
Long Mile DRC03	**0.34** ***	0.35 ***	0.31 ***	0.45 ***	0.67 ***	0.54 ***	0.74 ***	0.59 ***	0.79 ***	0.61 ***		**0.62** (0.17)
Tarawera **DBH08**	**0.16** n.s.	**0.13** n.s.	**0.12** n.s.	**0.20** *	**0.14** n.s.	**0.25** **	**0.15** n.s.	**0.25** **	**0.13** n.s.	**0.32** ***	**0.30** ***	

Significance levels are given by *** p≤0.001, ** 0.01 ≥ p ≥ 0.001, * 0.05 ≥ p ≥ 0.01, n.s. = not significant.

ψ Because of the high correlations between sites (Table 9), genetic correlations between the two farm sites were estimated from a pooled data set. Equivalent correlations are presented in Table 5.

experiment, the greatest confidence was gained from the genetic correlations between the sites 3 years after planting (Onepu and Tarawera 0.65; Long Mile and Tarawera 0.62, Table 6). However, choosing the right site was evidently also important in optimising early selection.

It must be noted that while the genetic correlations were moderate, indicating that early selection may be feasible although risky, the phenotypic correlations were poor to very poor for diameter between Onepu and Long Mile at age 1, and Tarawera at year 8 (0.25 and 0.15 respectively, Table 6). Some breeders place more credence on the size of the phenotypic correlations than the genetic correlations for any early selection exercise (C.J.A.Shelbourne pers. comm.). The poor phenotypic correlations can therefore indicate that there is likely to be more risk involved in early selection than the genetic correlations imply.

The genetic correlations estimated were generally higher than the phenotypic correlations (Tables 4–7). However, the standard errors on the genetic correlations were quite high, and it was only for the estimated genetic correlation between diameter at age 8 (DBH08) at Tarawera, and root collar diameter at age 3 (DRC03) at the two farm sites, that the standard error was a reasonable size when compared with the estimate.

At the farm sites it was interesting to note that diameter at planting was generally less strongly correlated with the other diameter measurements (7 months and 1, 2, and 3 years) than these subsequent measurements were between each other (Table 6), although the consequences of this are not known.

Accounting for seed weight by adding it as a fixed effect in the model did reduce some correlation estimates (data not shown). Correlations between 100-seed weight and early growth indicated that seed weight effects decreased considerably after only 1 year, and were even lower by age 3 (Fig. 1). Using individual seed weights rather than the weight of 100 seeds at the family level used here, would allow a more efficient removal of individual-specific maternal effects and help optimise correlation estimates. It would be worth investigating the benefits of using individual seed data in the future, although this may not be a practical alternative.

Form traits

For stem straightness and branching, assessments were made only at age 3 at the farm sites (Onepu and Long Mile) and at age 8 at the field site (Tarawera). Family-mean
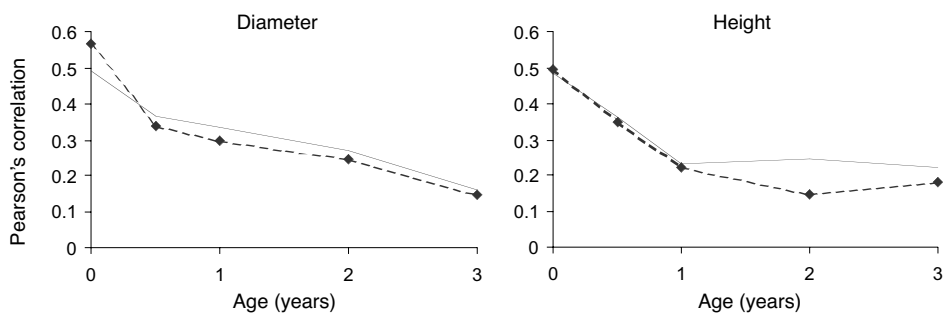

FIG. 1–Pearson's correlations between seed weight and height or diameter growth at early ages. Both farm sites Onepu (solid line) and Long Mile (dashed line) are given.

correlations were moderate between the two farm sites for straightness measured at age 3 (0.44), but considerably lower between straightness measurements at age 3 from Onepu and Long Mile and measurements at age 8 from Tarawera (0.21–0.22, Table 7). Similarly, the genetic correlation between age-3 straightness at Onepu and Long Mile was high (0.92), whereas the genetic correlations between age-3 straightness from the same sites, and age-8 straightness at Tarawera were only moderate (0.35–0.38, Table 7). Some differences were likely to occur between these two ages as, although faster-growing trees seem to be straighter, their greater diameter may mask some of their early form characteristics.

TABLE 7–Family-mean correlations (below diagonal) and genetic correlations (above diagonal) for form traits between the two farm sites (Long Mile and Onepu) and the field site (Tarawera). Standard errors of the estimates of the genetic correlations are given in parentheses. Probability level is indicated below phenotypic correlations. Equivalent genetic correlation estimates for pooled farm sites for those values not presented here can be found in Table 5.

		Onepu STR03	Long Mile STR03	Tarawera STR08	Onepu BR903	Long Mile BR903	Tarawera BR908
Onepu	STR03		0.92 (0.14)	0.38 (0.15)			
Long Mile	STR03	0.44 ***		0.35 (0.14)			
Tarawera	STR08	0.22 *	0.21 *				
Onepu	BR903					1.09 (0.12)	0.43 (0.15)
Long Mile	BR903				0.55 ***		0.38 (0.14)
Tarawera	BR908				0.24 **	0.23 **	

Significance levels are given by *** $p \leq 0.001$, ** $0.01 \geq p \geq 0.001$, * $0.05 \geq p \geq 0.01$, n.s. = not significant.

Correlations for branching followed the same trends as those estimated for straightness. The family-mean correlation between age-3 measurements for branching at Onepu and Long Mile was moderate at 0.55 (Table 7). When correlated with age-8 measurements from Tarawera, the values dropped significantly (0.24 Onepu and 0.23 Long Mile). Genetic correlations were again high between the age-3 branching measurements from Onepu and Long Mile (1.09), but were only moderate between the same age-3 measurements and age-8 branching scored at Tarawera (0.38–0.43).

Correlations obtained for form traits when 100-seed weight was included in the model were very similar to those obtained above (data not shown). It appeared that seed weights were not important for these traits at age 3.

Heritabilities

Growth traits

Narrow-sense heritability estimates obtained for growth traits were generally low to moderate (0.12–0.57), although some moderate to high estimates were obtained (e.g., 0.72

for height at planting at Tarawera; Fig. 2A, 2B, and Table 8). Trends for growth-trait heritabilities appeared similar for both farm sites (Fig. 2A, 2B). Heritability estimates for height at all sites were initially high but decreased with age (Fig. 2A, 2B, Table 8). Heritability estimates at the two farm sites for diameter growth up to 3 years of age indicated a slight increase in additive genetic control with time (Fig. 2A, 2B,Table 8). By age 8 at Tarawera, the heritability of diameter was low (0.16, Table 8).

Heritability estimates obtained from pooled data across both the farm sites (Onepu and Long Mile), as estimated genetic correlations between the sites indicated, were very similar (Table 9). As expected, these pooled estimates (Table 8) were generally intermediate between the individual site estimates and therefore exhibited essentially the same characteristics as single-site estimates, as described above.

Including 100-seed weight in the model reduced early heritability estimates considerably (Table 8, Fig. 2C, 2D), particularly for height at planting which decreased from 0.56–0.57 to 0.36–0.39 across both farm sites (Table 8, Fig. 2). Heritabilities of root collar diameter decreased from 0.16 (Long Mile) and 0.20 (Onepu) to 0.08 (Long Mile) and 0.16 (Onepu). The same trends in heritability of diameter were evident at the field site (Tarawera, Table 8, Fig. 2).
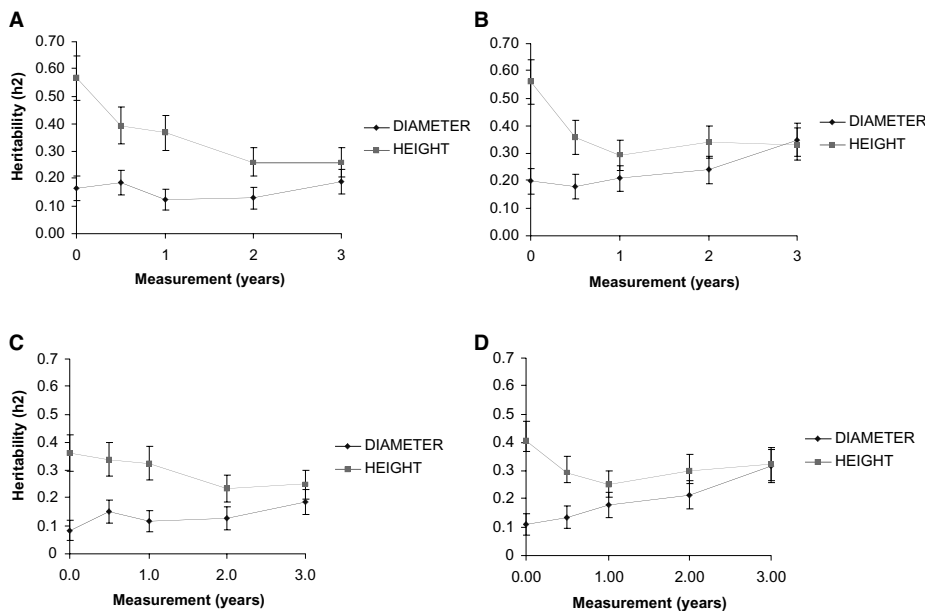
FIG. 2A and B–Trends in narrow-sense heritability estimates from planting through to 7 months and 1, 2, and 3 years of age. Heritability estimates are given **without** seed weight included in the model. The vertical bars indicate the standard errors of the heritability estimates. A = Long Mile farm site; B = Onepu farm site.

FIG. 2C and D–Trends in narrow-sense heritability estimates from planting through to 7 months and 1, 2, and 3 years of age. Heritability estimates are given **with** seed weight included in the model. The vertical bars indicate the standard errors of the heritability estimates. C = Long Mile farm site; D = Onepu farm site.

TABLE 8–Heritability estimates for growth and form traits.

	Long Mile		Onepu		Combined farm sites (Onepu and Long Mile)		Tarawera	
	h^2	S.E.	h^2	S.E.	h^2	S.E.	h^2	S.E.
Seed weight unaccounted for in model								
HT00	0.57	0.08	0.56	0.08	0.54	0.07	0.72	0.09
DRC00	0.16	0.04	0.20	0.05	0.20	0.04	0.28	0.05
HT_7	0.39	0.07	0.36	0.06	0.41	0.06	–	–
DRC_7	0.19	0.04	0.18	0.04	0.24	0.04	–	–
HT01	0.37	0.06	0.29	0.06	0.38	0.06	–	–
DRC01	0.12	0.04	0.21	0.05	0.18	0.03	–	–
HT02	0.26	0.05	0.34	0.06	0.28	0.05	–	–
DRC02	0.13	0.04	0.24	0.05	0.19	0.04	–	–
HT03	0.26	0.05	0.33	0.06	0.29	0.05	–	–
DRC03	0.19	0.04	0.35	0.06	0.26	0.04	–	–
STR03	0.21	0.05	0.16	0.04	0.17	0.04	–	–
BR903	0.20	0.04	0.15	0.04	0.22	0.04	–	–
MAL03	0.09	0.04	0.07	0.03	0.09	0.02	–	–
DBH08	–	–	–	–	–	–	0.16	0.04
STR08	–	–	–	–	–	–	0.32	0.05
BR908	–	–	–	–	–	–	0.22	0.04
MAL08	–	–	–	–	–	–	0.05	0.02
Seed weight accounted for in model								
HT00	0.36	0.06	0.41	0.07	0.44	0.06	0.47	0.07
DRC00	0.08	0.03	0.11	0.04	0.12	0.03	0.18	0.04
HT_7	0.34	0.06	0.30	0.06	0.37	0.06	–	–
DRC_7	0.15	0.04	0.13	0.04	0.20	0.04	–	–
HT01	0.32	0.06	0.25	0.05	0.35	0.06	–	–
DRC01	0.12	0.04	0.18	0.04	0.20	0.04	–	–
HT02	0.23	0.05	0.30	0.06	0.26	0.04	–	–
DRC02	0.13	0.04	0.21	0.05	0.23	0.04	–	–
HT03	0.25	0.05	0.32	0.06	0.30	0.05	–	–
DRC03	0.18	0.04	0.32	0.06	0.25	0.04	–	–
STR03	0.21	0.05	0.17	0.05	0.17	0.04	–	–
BR903	0.20	0.05	0.16	0.04	0.23	0.04	–	–
MAL03	0.10	0.04	0.07	0.04	0.09	0.02	–	–
DBH08	–	–	–	–	–	–	0.16	0.04
STR08	–	–	–	–	–	–	0.33	0.05
BR908	–	–	–	–	–	–	0.23	0.04
MAL08	–	–	–	–	–	–	0.05	0.02

Form traits

Heritability estimates obtained for branching and straightness were low to moderate (0.15–0.21 at age 3 at Onepu and Long Mile) and were highest after 8 years of growth at the forest site (Tarawera, 0.32 and 0.22 respectively). At age 3 the trial at Long Mile had higher heritabilities and appeared to give greater genetic discrimination than the trial at Onepu (Table 8).

TABLE 9–Genetic correlations (r_g) and standard errors of the correlations (S.E.) between the farm sites Onepu and Long Mile for the same traits.

Trait	Age	Variable	r_g	S.E.
Height	Planting	HT00	1.04	0.03
	7 months	HT_7	1.03	0.05
	1 year	HT01	1.04	0.06
	2 years	HT02	0.93	0.08
	3 years	HT03	0.99	0.08
Diameter	Planting	DRC00	1.22	0.12
	7 months	DRC_7	1.11	0.11
	1 year	DRC01	1.16	0.14
	2 years	DRC02	1.09	0.14
	3 years	DRC03	1.03	0.09
Branching	3 years	BR903	1.08	0.12
Straightness	3 years	STR03	0.92	0.14

Malformation was not normally distributed and could not be normalised by any standard transformation. While heritabilities were estimated for malformation, they should be used as a guide only and should not be used to estimate gains. Nevertheless, the heritabilities estimated indicated that, at these sites, variance available for breeding was low (0.03–0.09, Table 8).

When seed weight was included in the model, estimates obtained for form traits were very similar (Table 8). Thus, seed weight appeared to have little influence on malformation, straightness, and branching at ages 3 or 8.

Selection of the 'top 20' families

In practice, the highest-ranked families are selected from any given analysis; so, as a selection exercise, the change in ranking of the top 20 families (out of 128) was tracked over time.

The best 20 families at Tarawera were selected from their root collar diameters at planting. When compared with the ranking of diameter at breast height at age 8 at the same site, 45% of the original selections were ranked lower than 50. In addition, 30% of the original selections were in the lower 50% at age 8. When results at the farm sites (Onepu and Long Mile) were combined for the estimation of new rankings of root collar diameter obtained at age 3, and then these rankings were compared with age-8 diameter at breast height rankings from Tarawera, 30% of the top 20 were in the worst 50% at age 8. Therefore, the use of early selection at this stage involves considerable risk, particularly as age 8 is still only an approximation of rotation-age ranking (20–35 years).

These results did not justify early selection of the best performers for diameter growth, but early selection might be able to be used as a means of culling the worst performers. Of the families that ranked one hundredth or below for diameter at age 8 (from a total of 128), only three were ranked at 100 or below at any of the sites at planting. Nevertheless, 18 (62%) were ranked at or below 100 for at least one of the sites. At age 3, the situation was not much better, with only four families ranked 100 or below at age 8 being within the lowest-ranked

100 at age 3 at both sites. Seventeen families of the 29 ranked 100 or below for at least one of the two farm sites at age 3 were found in the lower rankings (100 or below) at age 8.

Therefore, if early ranking is done across multiple sites, the ability to predict the worst families improves. However, even in the best scenario, only 62% of the worst 29 families were predicted at early ages. Nevertheless, these lower-ranked families were found only once in the top 20 at later ages; so, although culling some of these families at a young age may mean that some of the better-than-average performers are lost, the best performers are not. (One family was ranked at 115 (Long Mile) and 106 (Onepu) at age 3, and at age 8 it was ranked 14.) A balance would have to be struck between the potential loss of high-value clones and the cost of testing and selection at age 8.

Adding seed weight to the model did not improve reliability of selection for the top 20 families. Selecting the top 20 at planting and comparing the selections with family rankings at age 8 showed that 45% of the original selections were later ranked in the lower 50% of the families. While selecting the top 20 at age 3 improved this percentage to 35%, rankings using seed weight appeared to be less efficient than the rankings compared above.

Relative efficiency of selection

The above results are reinforced by the low estimated relative efficiencies of selection (Fig. 3). Below 3 years of age, neither of the two farm-sites tested gave relative efficiencies greater than 20%. Only at 3 years did the relative efficiencies exceed 20%, and only at the Onepu site. The size of the relative efficiencies estimated here appears inadequate for use in a breeding programme. Relative efficiencies for selection of straightness and branching characteristics at age 3 *vs* age 8 were also poor, estimated as being between only 6 and 9%.
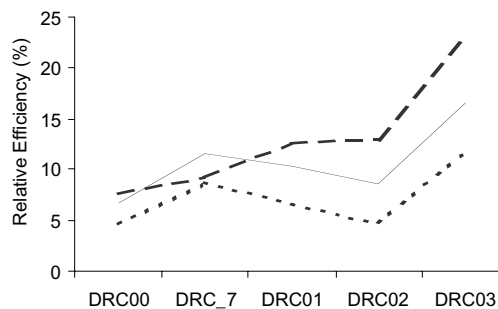

FIG. 3–Relative efficiency (%) of selection for diameter at early ages (planting, 7 months, 1, 2, and 3 years) at the farm sites Onepu (dashed line) and Long Mile (dotted line) and for an average of the two (solid line), compared with diameter at age 8 from the Tarawera field site.

DISCUSSION

Genetic and family-mean correlations between early diameter-growth at age 1 year from two farm sites and age-8 diameter at breast height measurements from one field site were low. These correlations improved with age, up to approximately 0.30 at age 3. Results from selecting the first 20 ranked families for diameter growth on early-age farm sites also

showed that selection at age 3 gave better results and the highest relative efficiency. Nevertheless, out of a total of 128 families ranked for diameter growth across the two farm sites, 30% of the top 20 were in the worst 50% at age 8. When seed weight was added to the model, the selection of the top 20 became even less efficient. Therefore, the use of early selection for diameter at these sites does not seem to be worthwhile.

Although it appeared from these results that early selection is not reliable, it is important to note that this experiment had a number of limitations that may have reduced correlations between early diameter growth and diameter at age 8. Seed weight can have a substantial influence on early growth (Wilcox 1983; Menzies *et al*. 1985). Including 100-seed weight in the model lowered heritability estimates and genetic correlations for height growth as expected, sometimes to a large extent, but inclusion of seed weight did not improve selection efficiency at early ages. Furthermore, genetic correlations for diameter and form traits did not change greatly by including this factor. In addition, all plants were initially raised in the nursery as bare-root stock. It is well known that nursery effects expressed as differences in bare-root stock can be persistent in the field (Menzies & Arnott 1992; Mescal & South 1991), and on a high-quality farm site these differences are likely to be exacerbated. In this experiment, it appeared that nursery and/or maternal effects (seed weight) were reduced by age 3, given that the heritabilities estimated also appeared to stabilise by this age. Nevertheless, it was likely that nursery effects may have contributed to the lower correlations between early growth and growth at age 8, and this relationship might be improved by using container stock rather than bare-root stock to minimise nursery and transplanting shock effects.

In this experiment, growth and form traits only were studied. With *P. radiata* breeding moving towards improving wood quality, a similar trial where wood quality traits are measured would certainly help ascertain the usefulness of these trials in the current breeding climate in New Zealand. A recent study of *P. radiata* wood density in New Zealand in 30-year-old trees (Kumar & Lee in prep.), indicated that early selection for wood properties might be possible. Family selection for density of the third ring in a 5-mm increment core showed a moderately high relative selection efficiency (79%) and a corresponding family-mean correlation between harvest-age density and density in the third ring of approximately 0.80. The relative efficiency of selection also increased with ring-age up to around 93% at ring-age 10. This result indicated that it might be possible to select at early ages for high heritability traits such as wood density. However, selection efficiency may often be reduced through an untoward event such as infection by Cyclaneusma needle-cast disease (King & Burdon 1991). Hence, even though a nursery trial can be perfect in itself, some rank changes are to be expected.

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