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Early growth and form of coastal provenances and progenies of Douglas-fir at three sites in New Zealand

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Abstract

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) is a native of the Pacific Northwest of the United States of America. In New Zealand, Douglas-fir is the prominent alternative species to radiata pine (*Pinus radiata* D.Don) and is planted widely. Original provenances were obtained from Washington USA, but after the introduction of Swiss needle cast (*Phaeocryptopus guaemannii* [T.Rohde] Petr.), provenances needed to be re-evaluated. Trials planted in 1957 and 1959 demonstrated that the best provenances for New Zealand sites were from coastal locations in California, USA and Oregon, USA. While selections were made from these provenance trials, the need for more genotypes was also identified. Seed, comprising of 222 open-pollinated families from 19 coastal and one inland provenance from north-western USA, was collected in 1993.

This seed was planted in 1996 along with eight New Zealand land-race seedlots as controls. The latitude of the provenances ranged from 35° 07′N in California to latitude 44° 10′N in Oregon. The trial layout was a sets-in-replicates design of seven sets of progenies with 30 replicates of single-tree plots, planted on three sites: one in the central North Island; one at the top of the South Island; and one and the bottom of the South Island. Average tree height, assessed at age four years from planting, was 2.5 metres in the central North Island, and 2.2 metres at both South Island sites, with the tallest trees reaching 4.9 metres in the central North Island.

The tallest provenances came from between latitudes 38°and 39°N, especially the Fort Ross and Navarro River provenances in California. The height of provenances from locations going north and south of this latitude range was generally reduced, although individual provenances varied unpredictably. The New Zealand control seedlots all grew well. The seedlots originally from Fort Bragg, California were the most vigorous, followed by seedlots of Washington origin. Seedlots that grew fastest were three controlled-pollinated seedlots involving inter-provenance crossing, planted in Southland only.

Height, stem straightness and needle retention at age four years had moderate estimated narrow-sense heritabilities (0.2 – 0.35). Tree form in these trials was highly variable, while most of the variation in growth was at the provenance level with somewhat less variation at the level of families within provenances. Some interaction variance for height growth was found between families and sites and also between provenances and sites, but there were stable families that ranked well across all sites. Family means showed moderate correlation (r = 0.6) between height growth in the nursery and height at each site at age four. The trees in these trials form a very valuable resource for future breeding work.

Keywords: correlation; genotype-site interaction; heritability; New Zealand; *Phaeocryptopus guaemannii*; progeny/provenance tests; *Pseudotsuga menziesii*; straightness.

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Introduction

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) has been grown in plantations in New Zealand since about 1870 (Miller & Knowles, 1994). In the past, Douglas-fir has represented up to ten percent of the area of the New Zealand forest estate, but currently represents about six percent (New Zealand Forest Owners Association, 2011). However, present production of Douglas-fir tree stocks over the last three years has varied from 16 – 19% of total tree stocks produced (R. Dorey, unpublished data).

Research into Douglas-fir genetics started in New Zealand in 1955 and the first provenance trial of Douglas-fir in New Zealand was planted in 1957 at 10 sites throughout the country. The seed for this trial, supplied by commercial seed companies (Sweet, 1965; Shelbourne et al., 2007), came from Washington (WA) and Oregon (OR), USA and British Columbia, Canada. The second New Zealand trial was planted in 1959 at 19 lowland sites and one high-elevation site. It compared trees grown from seedlots collected from other US sources, particularly tree stands in the coastal fog belt of California and Oregon (Sweet, 1965; Shelbourne et al., 2007). Further New Zealand trials were planted in 1971 (nine sites) and 1974 (three sites) (Shelbourne et al., 2007) using local seed sources[1] and selected US provenances.

Douglas-fir stands in North America are classified into seed zones (USDA Forest Service, 1966) and any re-planting must use seed from within the same seed zone. However, the growth of trees in New Zealand from coastal seed sources (within the fog belt) exceeded the growth of trees from inland seed sources within the same American seed zone.

The arrival in New Zealand of Swiss needle cast (*Phaeocryptopus guaemannii* [T.Rohde] Petr.) in 1959 had reduced the growth rate of many stands (of Washington origin) by 1970 (Beekhuis, 1978). Plus-tree selection was initiated in 1969 in Kaingaroa Forest (Central North Island) stands of Washington origin, and open-pollinated progeny tests of these were planted in 1972. However, results from the 1959 provenance trials, obtained in 1974 (Shelbourne et al., 2007), showed clearly that the volume of Washington provenances was up to 30 percent less than provenances from the fog-belt on the coast of California. This information, as well as a general decline of industry interest in the species, effectively halted the breeding programme for the next 13 years.

By 1987, the timber industry had started to show greater appreciation of Douglas-fir, as exported Douglas-fir logs commanded high prices. A decision was taken to select a new breeding population from trees of the best-performing provenances that were growing in the 1957 and 1959 trials (Shelbourne et al., 2007). Under the sponsorship of PROSEED NZ Ltd, 185 trees were selected and scions from these were grafted to plant a clonal archive at Waikuku in Canterbury, New Zealand.

Materials and methods

Seed collection

Native North American provenances

Twenty provenances (populations) were located for seed collection and seed from 3 – 23 parent trees per stand was collected (Figure 1, Dungey et al., 2012). All locations except for Willamette are within 20 km of the coast and local climates are predominantly affected by latitude. Parent trees were selected a minimum of 50 m apart. Selection criteria were: good growth; stem straightness; crown form; and health. The elevation of all populations was below 500 metres, and elevation for individual trees within a population often varied from 200 to 500 metres due to the hilly terrain. For various reasons, e.g. inadequate numbers of seed or poor germination, only 95% of these seedlots were eventually raised in the nursery and planted in field trials.

New Zealand seed

There was a good seed crop in New Zealand in 1994 so seed was collected from various New Zealand stands as control seedlots (#900-906; Table 1). Seed from a seed stand at Rotoehu Forest (Code #900; Fort Bragg, California provenance) was used for surround and filler trees.

North American seed orchards

Seed of Arcata, CA provenance from the Louisiana-Pacific Seed Orchard, Humboldt County, CA (#907) was used as a control seedlot, Table 2.

Up to four families from each of three seed orchards, owned by Weyerhaeuser (Weyco) in Oregon and Washington, were included in the Kaingaroa and Golden Downs tests. Lots #601-604 were from Coos Bay, OR; lots #605-608 were from Long View, WA; and lots #609-612 were from Twin Harbours, WA, Table 2.

[1] The New Zealand Forest Service had planted a number of 10 – 20 hectare stands for seed production using seedlots that were considered to be the best available at the time. For example, the Rotoehu Forest and Golden Downs Forest stands mentioned here were of Fort Bragg origin. These stands were well-formed and well-grown (Vincent & Dunstan, 1989). All poor and malformed phenotypes were removed around age 15 and stand density was reduced from 1700 stems ha^{-1} to between 80 and150 stems ha^{-1} to encourage deep crowns and maximum seed production. Local seed for the 1971 and 1974 trials came from such provenance stands.

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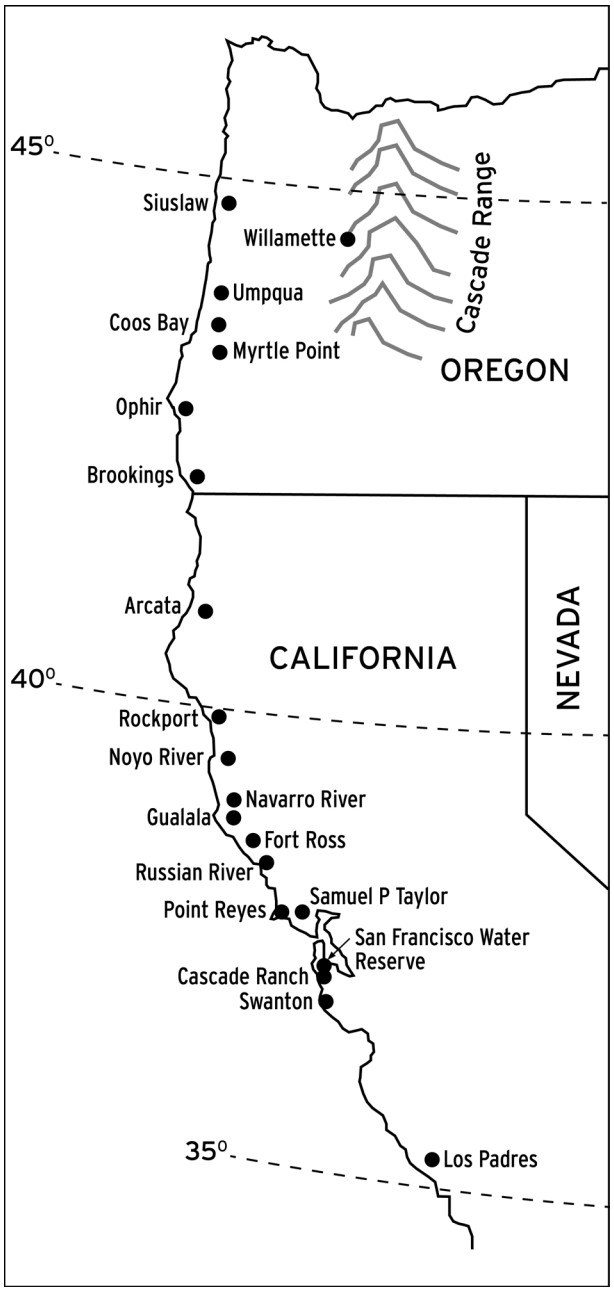

FIGURE 1: Pacific Coast, USA showing native provenances of Douglas-fir seed collected in 1993.

Controlled crosses

Four control-pollinated crosses between the 1987 provenance-trial selections were planted at only one of the trial sites, Gowan Hill. The crosses were from six to ten parents from each of four groups: California; Oregon; Washington; and the Ashley, New Zealand seed stand) pollinated by polycrosses of 2 – 3 unrelated parents of Californian origin (#721 – 724; Table 2).

Nursery sowing and raising of plants

Seed from Oregon provenances and from Oregon and Washington seed orchards was stratified for four weeks but open-pollinated seed from Californian provenances was stratified for two weeks. Stratification times were those advised by both the California Department of Forestry and Rotorua nurserymen. The seed was sown in early December 1994, to provide one-and-a-half year-old bare-rooted plants for planting in winter (August) 1996. The nursery layout of the families was in randomised complete blocks with three replicates, which helped minimise effects of growth differences along nursery beds.

Field sites, layout and planting

Progeny trials were planted at three sites in August 1996. The sites were located at Kaingaroa Forest in the North Island, and Golden Downs and Gowan Hill Forests in the South Island of New Zealand (Figure 2, Dungey et al., 2012). These sites were considered to be better-than-average since they had adequate rainfall (900 mm to 1700 mm) occurring throughout the year, a mild climate and good growth potential. Further details of each site are given in Dungey et al., 2012. At each site, the trial layout was sets in replicates, with seven sets of 36 seedlots, planted as 30 replicates of single-tree plots.

Each set comprised 34 families, composed of from one to three families from each provenance, and two control seedlots. Seed germination varied considerably amongst families, especially some families whose seed had been treated with methyl bromide. Some families failed completely, while some furnished sufficient plants for one or two sites only. Each set was designated to be a sub-line for future breeding at the time of sowing the seed, so the sets with the most surviving families dictated the size of each replicate/set block. Consequently, there were shortfalls of families in some sets, so some families that had surplus plants were used as a second entry, instead of using fillers. This resulted in between 13 and 27 families being represented by two, separately identified entries of 30 plants on the same site. The first entry of a family would be the best plants of that family in the nursery, while the second or repeated entry would be slightly smaller plants.

Fillers were used to replace missing plants of those families with less than 30 plants per site. Spacing was 3.0 m by 3.0 m, or a stocking of 1111 stems ha^{-1}. This stocking was chosen to delay the onset of competition and is rather less than the 1600 stems ha^{-1} normally used for commercial plantings. Filler trees were not used in the analyses.

Traits and their assessment

The weight of 100 seeds was estimated for each family when the seed was counted out for stratification prior to sowing at the nursery in December 1994.

Families were scored for the timing of the spring flush in the nursery on 1 November 1995, nearly one year

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TABLE 1: New Zealand Source (where relevant) and original provenance of control seedlots

Code	New Zealand source	Original provenance	
		State	Location
900	Seed Stand, Compartment 55, Rotoehu forest	CA	Fort Bragg 39° 15'
901	Compartment 1132, Kaingaroa forest (second generation ex Rotoehu, NZ)	CA	Fort Bragg 39° 15'
902	Compartment 1061, Kaingaroa (third generation in New Zealand)	WA	ca. 48°N
903	Seed Stand, Compartment 115, Golden Downs forest	CA	Fort Bragg 39° 15'
904	Seed Stand, Eyrewell forest (second generation ex Ashley, NZ)	OR	ca. 43°N
905	Seed Stand, Mount Thomas forest (second generation ex Ashley, NZ)	OR	ca. 43°N
906	Seed stand, Beaumont forest	WA	ca. 48°N

from sowing on a scale of 1 – 7, where 1 describes a tightly sealed bud and 7 describes flushed foliage of five cm or more. Heights of the 30 tallest trees per family (10 tallest trees per nursery replicate) were measured, using a ruler, to the nearest centimetre in the nursery in June 1996, one and half years from sowing. These nursery data were used for correlations with family and provenance means obtained from the trial sites at age four.

Trees at Gowan Hill were assessed in late October, Golden Downs in early November and Kaingaroa in late November to early December 2000. Numbers of trees assessed are shown in Table 3, along with numbers of trees that were dead, too small or of uncertain identity.

The following characteristics were measured:

Height: measured in metres, using height pole, to the base of the terminal bud or any new growth. Note that trees <1.4 metres tall, were not assessed at Kaingaroa and Gowan Hill, but were assessed at Golden Downs. Trees that were deemed too small were not measured or assessed at Kaingaroa and Gowan Hill because straightness and branching scores would be meaningless. Since straightness and branching were not assessed at Golden Downs, all trees were measured. The reason for this was that the Golden Downs site was sheltered, so all trees grew straight.

Forking: Ramicorn branches and forks for any year of growth (counted, but with a maximum of three occurrences).

Stem straightness: scored using a numerical system of 1 – 4 and 6 – 9, where: 1 = extremely crooked; 4 = marginally unacceptable; 6 = acceptable; 9 = perfectly straight. Scores of 5 were not assigned. Stem straightness was not assessed at Golden Downs. It was assessed for each whole tree at Kaingaroa at age four years but only for the first three years' growth at Gowan Hill.

Leader straightness (Gowan Hill site only): scored as for stem straightness, except 1 = leading shoot with some, or all, of the shoot at 90° from vertical (trees with broken or missing tops, not scored). Exposure to strong winds here often resulted in completely different tree form so the stem and the leading shoot were scored separately.

Branching: scored on a scale of 1 – 3 at Gowan Hill (1= one whorl per year, and few intermediate branches, 2 = two whorls per year, but few other branches, 3 = many intermediate branches) but 1 – 4 at Kaingaroa (same criteria as for Gowan Hill for scores 1 and 2, but 3 = many intermediate branches on half of the annual shoot and 4 = intermediate branches over the whole annual shoot extension). Branching was not assessed at Golden Downs.

TABLE 2: Details of seed-orchard families and control-pollinated crosses

Code	Type	Location	Latitude
601-604	seed-orchard family	Coos Bay, OR	43° 25'
605-608	seed-orchard family	Long View, WA	46° 30'
609-612	seed-orchard family	Twin Harbours, WA	48° 05'
721	control-pollinated cross	Ashley, NZ x CA, USA	mixed
722	control-pollinated cross	CA, USA x CA, USA	mixed
723	control-pollinated cross	OR, USA x CA, USA	mixed
724	control-pollinated cross	WA, USA x CA, USA	mixed
907	bulked seed-orchard families	Arcata, CA, USA	39° 59'

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Needle retention (Kaingaroa site only): scored in late November and early December using a scale of 1 – 6, where two points were assigned for each full year of foliage present on branches. The extremes were marked by trees with six-months' foliage or less, which scored 1 on the scale, while trees with three years foliage scored 6.

Analysis

The field layout was a sets-in-replicates design (Schutz & Cockerham, 1966). A preliminary analysis was done incorporating sets into the model, but sets were not significant ($p > 0.05$). As the provenances were shared evenly across sets, the trial was analysed as a randomised complete block design. The equation for the model of analysis of variance for such a design on a single site was as follows:

$$Y_{ijk} = \mu + R_i + P_j + F_k : P_j + E_{ijk} \quad [1]$$

Where :

Y_{ijk} = the observation on the tree of the k^{th} family in the j^{th} provenance in the i^{th} replicate;

μ = the overall mean;

R_i = the random effect of the i^{th} replicate;

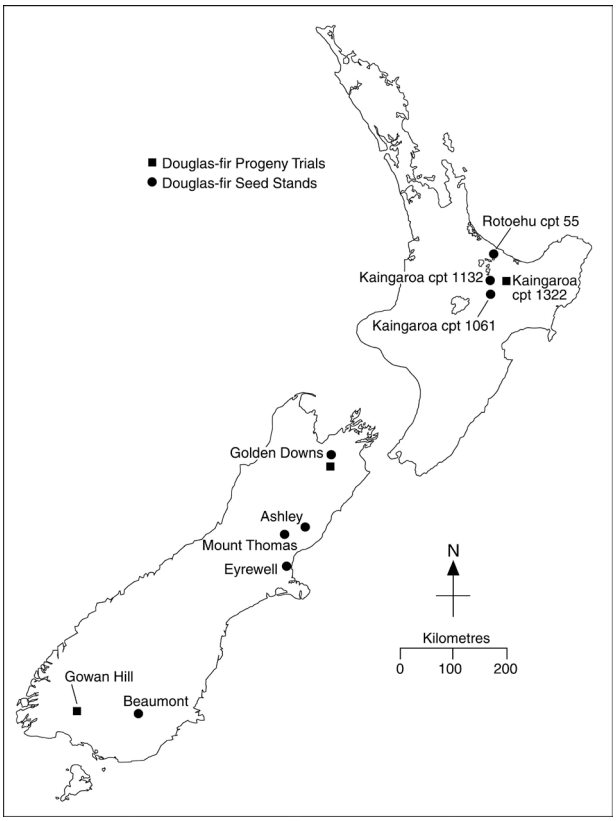

FIGURE 2: Location of provenance/progeny trials and New Zealand seed stands.

P_j = the random effect of the j^{th} provenance;

$F_k : P_j$ = the fixed effect of the k^{th} family within the j^{th} provenance; and

E_{ijk} = the random error associated with each tree of the k^{th} family in the j^{th} provenance in the i^{th} replicate

The equation for the analysis of variance model on several sites also contains a term for sites and terms for the interaction of provenance and family-within-provenance with site:

$$Y_{ijkl} = \mu + S_i + R_j : S_i + P_k + P_k * S_i + F_l : P_k + F_l : P_k * S_i + E_{ijkl} \quad [2]$$

Where :

Y_{ijkl} = the observation on the tree of the l^{th} family in the k^{th} provenance in the j^{th} replicate of the i^{th} site;

μ = the overall mean;

S_i = the random effect of the i^{th} site;

$R_j : S_i$ = the random effect of the j^{th} replicate within the i^{th} site;

P_k = the random effect of the k^{th} provenance;

$P_k * S_i$ = the random interaction effect of the k^{th} provenance with the i^{th} site;

$F_l : P_k$ = the fixed effect of the l^{th} family within the k^{th} provenance;

$F_l : P_k * S_i$ = the random interaction effect of the l^{th} family within the k^{th} provenance with the i^{th} site; and

E_{ijkl} = the random error associated with each tree of the l^{th} family in the k^{th} provenance in the j^{th} replicate of the i^{th} site

The first analysis of this set of trials examined the data from the three sites separately. Analysis of variance was carried out by PROC GLM of the SAS® statistical package (SAS Institute Inc., 1989) and provenance means were compared by Tukey's multiple range test. The terms of the analysis model were replicates, provenances, families nested within provenances and error. Control New Zealand seedlots, Weyco seedlots, control-pollinated seedlots and repeated families were omitted from the analysis. Data from Golden Downs were analysed with trees of less than 1.4 m included and also without them. There was little difference in the analysis results so the analysis with all trees is shown here.

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TABLE 3: Number of trees measured at each site.

Site	Dead or missing	Too small*	Identity problem	Assessed	Mean number of trees assessed per seedlot
Kaingaroa	1071	348	15	6126	24.92
Gowan Hill	921	691		5948	21.65
Golden Downs	1327	949*		5284	21.64

* Trees less than 1.4 metres in height were included in the analysis of Golden Downs, and these are shown separately in this table.

An overall analysis of variance for all three sites was also carried out for height and forks only, as other traits were either not assessed (Golden Downs) or were scored differently (Gowan Hill and Kaingaroa). This analysis contained the same terms as the single-site models, but also included site and its interactions with provenances and families. Analyses were also carried out for each pair of sites to check the source of any interactions.

Variance components were estimated using the SAS® procedure PROC VARCOMP and the same model as the analysis of variance. The coefficient of relationship between families was assumed to be 0.25, as most families were open-pollinated from natural populations. Variance component analysis followed the same model as the analyses of variance, where provenance variation was taken out of family variance. A model without provenance effects was tried in order to give an indication of the size of family variances and heritabilities when provenance variation and family variance were lumped together. Heritabilities were estimated from the variance component estimates using the following formulae:

Narrow-sense heritability h_i^2 per site: $$\frac{4 * \sigma^2_f}{\sigma^2_f + \sigma^2_e}$$

h_i^2 over all sites: $$\frac{4 * \sigma^2_f}{\sigma^2_f + \sigma^2_{f*s} + \sigma^2_e}$$

Family-mean heritability h_f^2 per site: $$\frac{\sigma^2_f}{\sigma^2_f + \frac{\sigma^2_e}{x}}$$

h_f^2 over all sites: $$\frac{\sigma^2_f}{\sigma^2_f + \frac{\sigma^2_{f*s}}{3} + \frac{\sigma^2_e}{x}}$$

where:

σ^2_f is the pooled family-within provenance variance;

σ^2_{f*s} is the family by site interaction variance;

σ^2_e is the error variance; and

x is the harmonic mean number of trees per family.

Standard errors of narrow-sense heritability estimates were calculated according to the method of Becker (1992, pp. 47-48).

Family means were calculated using the SAS® procedure PROC MEANS (SAS Institute Inc., 1990) and these means were used to estimate family-mean correlations using the Pearson coefficients from SAS® procedure PROC CORR. Both within-site and between-site family mean correlation coefficients were calculated. The family means were also correlated with family means from the 1996 nursery assessments and other data such as seed weight and latitude of provenance origin.

Means of control seedlots were calculated using PROC MEANS and are shown along with provenance means, although data on control seedlots were excluded from analysis of variance.

Results and Discussion

Establishment was excellent at all sites and good weed control resulted in good early growth. Some trees in lower-lying replicate/set blocks suffered damage from late spring frosts at Kaingaroa and Gowan Hill, and *Armillaria* root rot accounted for many deaths at Kaingaroa by the age of four years. The Golden Downs site suffered two landslides affecting about 240 trees, but only one or two trees per family were lost. However, a number of trees at Golden Downs were smothered by bracken or grass.

Provenance means

Provenance means for the various traits tested are given in Table 4 for the Kaingaroa site, Table 5 for the Gowan Hill site and Table 6 for the Golden Downs site. For consistency, provenances within a group are listed in order of increasing latitude.

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TABLE 4: US Provenance means for traits measured at Kaingaroa. Means for NZ control seedlots and US seed-orchard families are included for comparison.

Provenance	Original latitude (°N)	No. trees	Height (m)	Stem straightness (1 – 4 and 6 – 9) at age four years	Forks (0 – 3)	Branching (1 – 4)	Needle retention (1 – 6)
Native US population							
Los Padres	35° 49′	108	2.07 h	7.50 a	0.57	3.23 abcdef	2.49 i
Swanton	37° 06′	69	2.81 ab	6.38 fg	0.39	3.12 cdef	2.91 bcdefg
Cascade Ranch	37° 08′	311	2.57 cde	6.82 cdef	0.42	3.39 abc	2.64 fghi
SF Water Reserve	37° 27′	375	2.23 gh	7.13 abcde	0.38	3.48 ab	2.60 hi
SP Taylor FP	38° 02′	248	2.41 efg	6.95 bcde	0.52	3.31 abcde	2.62 ghi
Point Reyes	38° 04′	232	2.39 efg	6.91 bcde	0.55	3.42 ab	2.80 cdefgh
Russian River	38° 21′	198	2.56 cde	6.75 def	0.51	3.36 abcd	2.76 defghi
Fort Ross	38° 25′	225	2.96 a	6.22 g	0.53	2.96 f	2.92 bcdef
Gualala	38° 47′	173	2.64 bcd	6.70 efg	0.42	3.33 abcd	2.72 efghi
Navarro River	39° 11′	315	2.82 ab	6.84 cdef	0.51	3.11 cdef	2.97 bcde
Noyo River	39° 25′	470	2.56 cde	7.19 abcde	0.50	3.23 bcdef	3.12 ab
Rockport	39° 47′	118	2.46 de	7.12 abcde	0.55	3.31 abcde	2.93 bcdef
Arcata	39° 59′	376	2.68 bc	7.36 ab	0.40	3.08 def	3.13 ab
Brookings	42° 06′	144	2.69 bc	7.25 abc	0.48	3.01 ef	3.03 abcd
Ophir	42° 36′	46	2.44 ef	7.26 abc	0.54	3.52 a	2.76 defghi
Myrtle Point	43° 06′	108	2.51 cde	7.05 abcde	0.53	3.42 ab	3.06 abc
Coos Bay	43° 20′	192	2.43 ef	7.15 abcde	0.51	3.11 cdef	3.18 ab
Umpqua River	43° 36′	412	2.26 fgh	7.22 abcd	0.46	3.37 abcd	3.08 abc
Siuslaw Forest	44° 10′	495	2.38 efg	7.26 abc	0.45	3.31 abcd	3.30 a
Willamette Forest	43° 50′	242	2.16 h	7.35 ab	0.46	3.32 abcd	3.19 ab
US Seed orchard							
907 Arcata, CA	39° 59′	24	2.68	7.21	0.63	2.71	3.04
602 Coos Bay, OR	43° 25′	27	2.65	7.30	0.44	3.37	3.30
605 LongView, WA	46° 30′	17	2.42	7.82	0.47	3.06	2.76
606 LongView, WA	46° 30′	16	2.11	7.13	0.56	3.38	3.13
608 LongView, WA	46° 30′	24	2.02	6.79	0.54	3.46	3.21
610 Twin Harbours, WA	48° 05′	21	2.14	7.38	0.38	3.00	3.19
612 Twin Harbours, WA	48° 05′	7	2.06	7.86	0.86	3.86	3.14
NZ Seed stands							
900 Ft Bragg, CA	39° 15′	177	2.98	6.94	0.41	3.02	3.25
901 Ft Bragg, CA	39° 15′	25	2.92	7.08	0.44	3.08	3.63
903 Ft Bragg, CA	39° 15′	23	2.84	6.91	0.57	3.17	2.91
904, OR	ca. 43°N	24	2.29	7.29	0.67	3.21	3.42
905, OR	ca. 43°N	27	2.40	7.22	0.30	3.26	3.19
906, WA	ca. 48°N	26	2.46	7.54	0.38	3.00	3.35
902, WA	ca. 48°N	26	2.48	7.54	0.31	3.00	3.35
Minimum Significant Difference			0.20	0.49	0.24	0.29	0.30

Provenance means sharing the same letter code were not significantly different by Tukey's multiple range test ($p \leq 0.05$).

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TABLE 5: US Provenance means for traits measured at Gowan Hill. Means for NZ control sseedlots, US seed orchards and control-pollinated families are included for comparison.

Provenance	Original latitude (°N)	No. trees	Height (m)	Stem straightness (1 – 4 and 6 – 9) at age three years	Forks (0 – 3)	Branching (1 – 3)	Leader straightness (1 – 4 and 6 – 9)
Native US population							
Los Padres	35° 49′	63	1.72 f	6.84 a	0.62 d	2.48 ab	6.67 a
Swanton	37° 06′	74	2.26 abc	6.50 abcd	0.49 cd	2.74 a	4.49 h
Cascade Ranch	37° 08′	290	2.21 abc	6.66 abc	0.42 abcd	2.42 abc	5.54 cdefg
SF Water Reserve	37° 27′	397	2.03 de	6.84 a	0.43 abcd	2.14 cdefgh	6.51 ab
SP Taylor FP	38° 02′	239	2.13 cde	6.73 ab	0.46 bcd	2.43 abc	6.08 abcd
Point Reyes	38° 04′	205	2.18 bcd	6.69 ab	0.45 abcd	2.37 bcd	5.80 bcdef
Russian River	38° 21′	228	2.22 abc	6.56 abcd	0.51 cd	2.35 bcde	5.71 cdefg
Fort Ross	38° 25′	229	2.25 abc	6.31 cd	0.43 abcd	2.44 abc	4.53 h
Gualala	38° 47′	199	2.20 abc	6.29 d	0.39 abc	2.33 bcde	4.96 gh
Navarro River	39° 11′	332	2.36 a	6.55 abcd	0.39 abc	2.30 bcde	5.01 gh
Noyo River	39° 25′	510	2.10 cde	6.64 abc	0.39 abc	2.18 bcdefg	5.36 defg
Rockport	39° 47′	136	2.15 cde	6.49 abcd	0.47 bcd	2.37 bcd	5.37 defg
Arcata	39° 59′	398	2.20 abc	6.76 ab	0.27 ab	2.02 efgh	5.45 defg
Brookings	42° 06′	178	2.20 abc	6.57 abcd	0.43 abcd	2.22 bcdef	5.83 bcde
Ophir	42° 36′	77	2.33 ab	6.69 ab	0.32 abc	2.24 bcde	5.03 fgh
Myrtle Point	43° 06′	119	2.20 bc	6.44 bcd	0.39 abc	2.02 efgh	5.18 efgh
Coos Bay	43° 20′	262	2.16 cde	6.69 ab	0.31 abc	1.84 h	5.45 defg
Umpqua River	43° 36′	471	2.02 e	6.66 ab	0.31 abc	2.05 defgh	5.86 bcde
Siuslaw Forest	44° 10′	503	2.19 bc	6.56 abcd	0.31 abc	1.86 gh	5.63 cdefg
Willamette Forest	43° 50′	236	2.01 e	6.58 abcd	0.25 a	1.89 fgh	6.23 abc
Control-pollinated crosses							
721 Ashley, NZ x CA	mixed	25	2.55	6.64	0.56	2.42	5.71
722 CA x CA	mixed	28	2.65	6.32	0.43	2.63	2.96
723 OR x CA	mixed	26	2.58	6.88	0.42	2.36	5.52
724 WA x CA	mixed	10	2.15	6.60	0.40	2.00	5.33
US Seed orchard							
907 Arcata, CA	39° 59′	27	2.22	6.74	0.41	1.90	5.42
NZ Seed stands							
900 Ft Bragg, CA	39° 15′	196	2.43	6.48	0.48	2.13	4.77
901 Ft Bragg, CA	39° 15′	26	2.25	6.77	0.35	2.36	5.73
903 Ft Bragg, CA	39° 15′	27	2.19	6.48	0.56	2.26	4.58
904, OR	ca. 43°N	28	2.37	6.57	0.32	1.96	5.71
905, OR	ca. 43°N	26	2.16	6.50	0.46	2.17	5.35
906, WA	ca. 48°N	26	2.10	6.38	0.50	2.36	5.67
902, WA	ca. 48°N	28	2.18	6.71	0.43	1.73	5.88
Minimum Significant Difference			0.16	0.35	0.21	0.34	0.78

Provenance means sharing the same letter code were not significantly different by Tukey's multiple range test ($p \leq 0.05$).

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TABLE 6: US Provenance means for the various traits measured at Golden Downs. Means for NZ control seedlots and US seed-orchard families are included for comparison.

Provenance	Original latitude (°N)	No. trees	Height (m)	Forks (0 – 3)
Native US population				
Los Padres	35° 49′	122	1.42 j	1.07 e
Swanton	37° 06′	77	2.14 abcdef	0.82 abcde
Cascade Ranch	37° 08′	305	1.96 efgh	0.80 abcde
SF Water Reserve	37° 27′	436	1.74 i	0.91 bcde
SP Taylor FP	38° 02′	255	1.99 defg	0.94 cde
Point Reyes	38° 04′	240	1.84 ghi	0.97 de
Russian River	38° 21′	242	2.11 bcdef	0.90 bcde
Fort Ross	38° 25′	265	2.27 ab	0.69 abcd
Gualala	38° 47′	211	2.24 abc	0.73 abcd
Navarro River	39° 11′	336	2.32 a	0.69 abcd
Noyo River	39° 25′	501	2.15 abcde	0.67 abc
Rockport	39° 47′	139	2.17 abcd	0.79 abcde
Arcata	39° 59′	384	2.16 abcd	0.54 a
Brookings	42° 06′	175	2.11 bcdef	0.65 ab
Ophir	42° 36′	51	1.94 fghi	0.78 abcde
Myrtle Point	43° 06′	128	2.01 defg	0.76 abcd
Coos Bay	43° 20′	210	2.04 cdefg	0.57 a
Umpqua River	43° 36′	440	1.77 hi	0.73 abcd
Siuslaw Forest	44° 10′	471	1.94 fghi	0.64 ab
Willamette Forest	43° 50′	254	1.74 i	0.73 abcd
US Seed orchards				
907 Arcata, CA	39° 59′	23	1.94	0.48
601 Coos Bay, OR	43° 25′	28	2.29	0.54
602 Coos Bay, OR	43° 25′	16	2.08	0.44
603 Coos Bay, OR	43° 25′	20	2.18	1.05
604 Coos Bay, OR	43° 25′	20	2.00	1.00
605 Longview, WA	46° 30′	21	1.64	0.67
606 Longview, WA	46° 30′	24	1.48	0.54
607 Longview, WA	46° 30′	17	1.51	0.65
608 Longview, WA	46° 30′	22	1.77	1.05
609 Twin Harbours, WA	48° 05′	22	1.69	0.45
610 Twin Harbours, WA	48° 05′	28	1.73	0.71
611 Twin Harbours, WA	48° 05′	23	1.43	1.09
612 Twin Harbours, WA	48° 05′	21	1.66	0.81
NZ Seed stands				
900 Ft Bragg, CA	39° 15′	170	2.38	0.68
901 Ft Bragg, CA	39° 15′	24	2.36	0.67
903 Ft Bragg, CA	39° 15′	28	2.23	0.57
904, OR	ca. 43°N	26	1.85	1.08
905, OR	ca. 43°N	24	1.90	0.75
906, WA	ca. 48°N	28	2.07	0.46
902, WA	ca. 48°N	23	1.74	0.52
Minimum Significant Difference			0.20	0.28

Provenance means sharing the same letter code were not significantly different by Tukey's multiple range test (p ≤ 0.05).

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TABLE 7: Provenance means for traits measured in the nursery and at all three trial sites combined.

Provenance	Original latitude (°N)	No. trees	Nursery means		Height (m)	Forks (0 – 3)
			Height (cm)	Flushing (1 – 7)		
Native US population						
Los Padres	35° 49′	293	36.5 i	6.53 abc	1.73 f	0.75 b
Swanton	37° 06′	220	46.4 abcd	6.33 bc	2.40 abc	0.57 ab
Cascade Ranch	37° 08′	906	45.0 bcdef	6.46 abc	2.25 abcde	0.55 ab
SF Water Reserve	37° 27′	1208	42.9 cdef	6.77 a	2.00 ef	0.57 ab
SP Taylor FP	38° 02′	742	45.2 bcdef	6.68 ab	2.17 bcde	0.64 ab
Point Reyes	38° 04′	677	44.0 bcde	6.80 a	2.13 cde	0.65 ab
Russian River	38° 21′	668	46.1 bcd	6.15 c	2.30 abcde	0.64 ab
Fort Ross	38° 25′	719	50.5 a	6.17 c	2.49 ab	0.55 ab
Gualala	38° 47′	583	47.3 ab	5.37 d	2.36 abc	0.51 a
Navarro River	39° 11′	983	46.8 abc	5.40 d	2.50 a	0.53 ab
Noyo River	39° 25′	1481	46.9 abc	4.88 efgh	2.27 abcde	0.52 a
Rockport	39° 47′	393	43.9 bcde	5.42 d	2.26 abcde	0.60 ab
Arcata	39° 59′	1158	46.5 abcd	4.50 h	2.35 abc	0.40 a
Brookings	42° 06′	497	42.5 defg	5.17 def	2.33 abcd	0.52 a
Ophir	42° 36′	174	42.6 cdefg	5.28 de	2.24 abcde	0.55 ab
Myrtle Point	43° 06′	355	39.5 fghi	5.05 defgh	2.24 abcde	0.56 ab
Coos Bay	43° 20′	664	38.6 fghi	4.80 fgh	2.21 abcde	0.46 a
Umpqua River	43° 36′	1323	38.1 hi	5.22 de	2.01 def	0.50 a
Siuslaw Forest	44° 10′	1469	41.7 efgh	4.68 gh	2.17 bcde	0.47 a
Willamette Forest	43° 50′	732	38.6 ghi	4.70 gh	1.97 ef	0.48 a
US Seed orchard						
907 Arcata, CA	39° 59′	74	50.9	4.50	2.28	0.50
NZ Seed stands						
900 Ft Bragg, CA	39° 15′	543	53.3	4.82	2.60	0.52
901 Ft Bragg, CA	39° 15′	75	50.0	4.67	2.51	0.48
903 Ft Bragg, CA	39° 15′	78	48.0	5.17	2.42	0.56
904, OR	ca. 43°N	78	48.2	5.50	2.17	0.69
905, OR	ca. 43°N	77	49.0	5.33	2.15	0.50
906, WA	ca. 48°N	80	46.7	4.50	2.21	0.45
902, WA	ca. 48°N	77	44.5	3.67	2.13	0.42
Minimum Significant Difference			4.3	0.42	0.32	0.27

Provenance means sharing the same letter code were not significantly different by Tukey's multiple range test ($p \leq 0.05$).

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Height

The provenances that grew the tallest varied with site tested (Tables 4 – 6). Provenance means in the nursery and across all three sites were given in Table 7. A latitude gradient might have been expected and indeed height growth was less for the three most northerly provenances tested than for most of those from further south. However, four of the six most southerly provenances also grew slower at this stage, possibly influenced by frost damage.

Overall, the best provenances were from the central Californian coast at around latitudes 38 – 39°N. Control New Zealand seedlots from seed stands of Fort Bragg origin, which is also in the 38 – 39°N zone, were consistently near the top of the rankings, their growth exceeded by only 10 – 12 of the fastest-growing families at any site. However, there was a large proportion of provenance variation in height growth where there was no obvious trend between height and latitudinal change. For example, the Swanton provenance performed better than other provenances from similar latitudes. The slowest-growing provenance was the southernmost one (Los Padres). For the control New Zealand seedlots, those of Oregon or Washington provenance also grew more slowly than those from California (Fort Bragg). The control seedlot directly from a seed orchard in Arcata, California, also grew well. The control New Zealand seed-stand seedlots of Fort Bragg origin grew particularly well at all three sites, where they equalled or exceeded the height growth of the tallest native provenances.

The control-pollinated seedlots of California × California, California × Oregon and California × Ashley seed stand origin, whose parents were selected in the 1959 provenance trials, were 10% taller than the best native populations at Gowan Hill, the only site where they were planted. The good prospects of inter-provenance hybrids between Californian and southern Oregon provenances were suggested by the results of the crosses at Gowan Hill. The California × California crosses were perhaps too vigorous and leaders were badly damaged in exposed parts of the site, but the California × Oregon selection and the California × Ashley, New Zealand selection (which was also originally from Oregon) seedlots had exceptional vigour with no worse than average leader damage.

Stem straightness

This trait tended to be a little better in the provenances from Rockport (39° 47′N) northwards. The tallest provenances (Fort Ross, Gualala and Swanton at Kaingaroa) and (Fort Ross, Gualala and Navarro River at Gowan Hill) were slightly more crooked (Tables 4 & 5).

Leader straightness

This trait was measured only at Gowan Hill but showed the same trend as stem straightness, although more clearly. The lowest scores were from Swanton, Fort Ross and Gualala provenances and higher scores were from more northerly provenances. There were, however, plenty of exceptions to these trends and some of the tallest trees were quite straight. In most cases, really crooked trees were rare even in the fast-grown provenances. Many of worst examples had been caused by wind damage with the timing of early flushing leaving new, soft leaders at the mercy of equinoctial gales. The fastest-growing progenies tended to be those that flushed first and these scored worst for leader straightness. Most notable for crooked leaders was the extremely vigorous Californian control-pollinated seedlot #722.

Estimated heritability for progenies within provenances was also comparable with that for stem straightness (see later). The amount of leader damage sustained at Gowan Hill would serve as an ideal screening test to identify families that maintain good form in exposed locations. A separate “breed” for exposed sites could be selected in the future, as recommended by Talbert (1990).

Forking

The Los Padres provenance at Gowan Hill showed the most forking at all three sites yet there was no clear trend for other provenances at Kaingaroa. However, the most southern provenances tended to have more forks than the more northern ones at both Golden Downs and Gowan Hill. Forking at age four in the present study showed less genetic variation than that found by Stonecypher et al. (1996) at age eight. The most likely reason is that these trees are too young for this trait to be expressed properly.

Branching

Branching scores showed little in the way of provenance trends at Kaingaroa (Table 4), but at Gowan Hill (Table 5) trees with less scattered branches generally came from the northernmost provenances in Oregon. There was a strong site influence on branching, hence the need for an extended scoring system at Kaingaroa. Trees at this site showed a very clear ‘bi-nodal’ pattern that was much less marked at Gowan Hill.

Needle retention

This trait was assessed only at Kaingaroa. Mean needle retention of the northernmost provenances tended to be better (score > 3) than those from further south (score < 3). The worst affected provenances were those from south of latitude 38° N (score < 2.70).

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Three seed stand seedlots of Fort Bragg origin, #900, #901 and #903 were used in this trial but their source in New Zealand varied. The seed obtained from seedlot #900 (from a second-generation seed stand at Rotoehu) produced trees with much better needle retention than seed obtained from seedlot #903 (from a second-generation seed stand at Golden Downs Cpt 115) even though conditions were more conducive for *Phaeocryptopus gaeumannii* infection at Rotoehu than at Golden Downs. This is because *P. gaeumannii* established in Kaingaroa and Rotoehu around 1960 but did not arrive in Golden Downs Cpt 115 until the 1970s (Hood & Kershaw, 1975). Thus, the Rotoehu seed stand developed with Swiss needle cast infection but the early growth of the Golden Downs Cpt 115 seed stand was not affected by Swiss needle cast up to the time of thinning and had no selection for resistance to this disease.

In hindsight, scoring the effects of Swiss needle cast disease later in the season would have been a better approach as there is some confounding needle loss with the new flush, and many trees had not begun to flush at the time of assessment. A later assessment in February 2003 (Dungey et al., 2012) provided better heritabilities.

Overall, the Los Padres population appeared to behave as an outlier for most traits. It comes from one of the most isolated stands of Douglas-fir on the Californian coast and is located well to the south of any other population; at latitude 35° 49´N. Los Padres had the smallest height growth, the most forking, and the worst needle retention. This finding was rather disappointing, as a seedlot from the next most southerly location (Swanton at 37° 06´N) had performed better than other provenances on some sites in the 1959 provenance trial (M. D. Wilcox, unpublished report). It had been expected that the trees from the Los Padres provenance could perform even better on a mild site in New Zealand such as Kaingaroa. In fact, the Swanton provenance grew much better than Los Padres in the present trial.

Analysis of variance and variance components

Variation among populations or provenances, which were mainly from coastal locations, represented a substantial proportion of the total (genetic) variation among all open-pollinated families for all traits.

Differences among provenances were highly significant at each of the three sites for all traits (Table 8). Actual variance estimates thereof are shown in this Table, but it is the percentage of the total variance that quantifies the value of each component. The following paragraphs discuss the variance components in terms of the percentage of one component compared to another component or total variance, but percentages are not shown.

For height growth at all three sites, estimated provenance variance was larger than family-within-provenance value (Table 8). The family-within-provenance variance was 55% of total provenance variance at Gowan Hill, 66% at Kaingaroa, and 73% at Golden Downs. The provenance variance for stem straightness (measured only at Kaingaroa and Gowan Hill) was relatively small, only 21 – 33% of the size of total family variance derived from an analysis model without provenance (Table 9). The genetic signal for forking was generally weak with provenance effects being minor at Kaingaroa (Table 8) but constituting 60% of total family variance at Golden Downs. There was substantial provenance variance for branching at Kaingaroa (51%) and Gowan Hill (72%) and for needle retention at Kaingaroa (58%). In these open-pollinated family seedlots from almost entirely coastal provenances, early height growth was strongly controlled by provenance, and provenance selection would provide a substantial part of gain from early selection.

Estimated site × provenance interaction variance for height in the across-sites analysis (Table 10) represented only 23% of the provenance component, though it was highly significant. There were some provenance rank changes across the three sites, but the range of provenance mean heights was smaller at Gowan Hill and Golden Downs than it was at Kaingaroa, and is probably the main cause of the significant provenance × site interaction. The provenance that grew best at Kaingaroa was Fort Ross, (2.96 m) while the worst was Los Padres (2.07 m), Table 4. At Gowan Hill, the tallest provenance was Navarro River (2.36 m) while the shortest was again Los Padres (1.72 m), Table 5. The ratio of estimated site × provenance interaction variance to provenance variance for forking was as high as for height, though there were no significant provenance differences at Kaingaroa.

Narrow-sense and family-mean heritabilities

Estimated narrow-sense heritabilities ($\hat{h}^2$) at Kaingaroa (Table 8) were moderate for height, stem straightness and needle retention (0.24 – 0.35) but low for forking and branch-type (0.07 and 0.11). At Gowan Hill, $\hat{h}^2$ values were somewhat lower, 0.20 for height and 0.19 for stem straightness, 0 for forks and 0.10 for branch-type. At Golden Downs, $\hat{h}^2$ was 0.19 for height and 0.07 for forking. Family-within-provenance variances, and their associated narrow-sense heritabilities, expressed the proportion of additive genetic variance to phenotypic variance within provenances and were highly significant for all traits at all sites, except for forking at Gowan Hill.

Estimated family-mean (within-provenance) heritabilities (repeatabilities) followed the same trends by sites for the different traits. For height growth, they

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TABLE 8: Estimated variance components (assuming a fully random model) and of heritabilities (± standard errors) at individual sites.

Source	Df	Height (m)	Stem straightness (1 – 4 and 6 – 9)	Forks (0 – 3)	Branching (1 – 4)	Branching (1 – 3)	Needle retention (1 – 6)	Leader straightness (1 – 4 and 6 – 9)
Kaingaroa								
Rep	29	0.1481***	0.0914***	0.00352***	0.0146***		0.0312***	
Prov	19	0.4708***	0.0692***	0.00074*	0.0174***		0.0522***	
Family (Prov)	185	0.2407***	0.1434***	0.00707***	0.0166***		0.0380***	
Error	4623	2.5035	1.6010	0.39043	0.5658		0.5854	
Total	4856							
Narrow-sense $\hat{h}^2$		0.35 ± 0.05	0.33 ± 0.04	0.07 ± 0.02	0.11 ± 0.03		0.24 ± 0.04	
Family-mean $\hat{h}^2_{\bar{f}}$		0.69	0.68	0.30	0.41		0.60	
Golden Downs								
Rep	29	0.1913***		0.0360***				
Prov	19	0.4199***		0.0142***				
Family (Prov)	192	0.1521***		0.0099***				
Error	5001	3.0401		0.5891				
Total	5241							
Narrow-sense $\hat{h}^2$		0.19 ± 0.03		0.07 ± 0.02				
Family-mean $\hat{h}^2_{\bar{f}}$		0.55		0.29				
Gowan Hill								
Rep	29	0.2519***	0.0152***	0.00310***		0.0209***		0.2999***
Prov	19	0.1174***	0.0117***	0.00519***		0.0451***		0.2290***
Family (Prov)	202	0.0945***	0.0444***	-0.00039		0.0175***		0.3057***
Error	4895	1.7999	0.8746	0.31245		0.6509		4.0548
Total	5145							
Narrow-sense $\hat{h}^2$		0.20 ± 0.03	0.19 ± 0.03	-		0.10 ± 0.03		0.28 ± 0.04
Family-mean $\hat{h}^2_{\bar{f}}$		0.55	0.54	-		0.34		0.63

* *indicates that a variance component is significant at the level of* $p \leq 0.05$
** *indicates that a variance component is significant at the level of* $p \leq 0.01$
*** *indicates that a variance component is significant at the level of* $p \leq 0.001$

were acceptably high (0.55 – 0.69) at each of the three sites (Table 8) and across all three sites (0.69); (Table 10). For stem straightness, family-mean (within-provenance) heritabilities were (0.54 & 0.68) at Gowan Hill and Kaingaroa, respectively (Table 8). These high heritabilities for height growth and straightness should allow families at all sites to be ranked and provide a basis for forwards selection in future. Indications at this age are that, for forwards selection, Kaingaroa would be the site at which to get highest gain, as both family-mean and individual-tree heritabilities are highest there. These family-mean heritabilities are "within-provenance". If calculated across provenances, they would be much higher and the phenotypic variance of family means, greater, resulting in more gain from family selection across provenances. Repeatability of family means across all three sites (Table 10), lumping provenance variance into family variance, for height was 0.84 (versus 0.69 within provenance) and for forking was 0.49 (versus 0.38). Heritabilities for common traits on pairs of sites were estimated (Tables 9 & 11), to reveal impacts of possible interactions. The greatest interactions between site and family for height and forking (the only traits common to all sites) were where Kaingaroa and Gowan Hill were paired (Table 9), which might be explained by the difference of 7 degrees of latitude. Interactions between Kaingaroa and Golden Downs or between Golden Downs and Gowan Hill were substantially less (Table 11).

Selecting families across provenances would be acceptable for selecting seed-orchard parents, but not for selecting the breeding-population parents, as it would reduce effective population size too much. However, there was no intention to use these data for selection, as the best time for a further assessment and selecting best trees is when the average height is six metres and the potential butt log can be evaluated, along with selection for wood properties. A further

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TABLE 9: Estimated variance components (assuming a fully random model) and of heritabilities (± standard errors) over Kaingaroa and Gowan Hill.

Source	Df	Height (m)	Stem straightness (1 – 4 and 6 – 9)	Forks (0 – 3)	Branching (1 – 4)
Site	1	0.5436***	0.0929***	0.0040***	0.6019***
Rep(Site)	58	0.2016***	0.0523***	0.0033***	0.0176***
Prov	19	0.1980***	0.0196*	0.0016**	-0.0025
Prov*Site	19	0.0912***	0.0203*	0.0015***	0.0329***
Family(Prov)	202	0.0955***	0.0601***	0.0015***	-0.0019
Site*Family(Prov)	185	0.0694***	0.0319***	0.0017***	0.0192***
Error	9518	2.1417	1.2274	0.3503	0.6055
Total	10002				
Narrow-sense $\hat{h}^2$		0.17 ± 0.03	0.18 ± 0.03	0.02 ± 0.02	-
Family mean $h^2_{\bar{f}}$		0.54	0.59	0.15	-

Variance component is significant at the level of * p ≤ *0.05;* ** p ≤ *0.01;* *** p ≤ *0.001.*

assessment was undertaken at age eleven (Dungey et al., 2012).

The ranges and standard deviations of family means are shown for each site in Table 12. The range was found to be somewhat wider for family means than for provenance means. For instance, at Kaingaroa, family means (Table 12) varied from a minimum of 1.83 m to a maximum of 3.26 m whereas provenance mean heights (Table 4) varied only from 2.07 m for Los Padres to 2.96 m for Fort Ross. For stem straightness at Kaingaroa, where provenance effects were not so large, provenance means varied from 6.22 at Fort Ross to 7.50 at Los Padres and family means from a minimum of 5.29 to a maximum of 8.13. The consistently slower growth of "repeated" families (data not shown) points to a need for large plants from the nursery. Many of the repeated family entries were from well-grown families that had a large surplus of plants, yet the growth rate of the second group of plants was invariably inferior to the growth of the first group chosen for the family.

Correlations between traits and between sites

Correlations between all traits at all sites were calculated for provenance means and family means. Many of the correlations were not significant so subsets of these correlations for both provenance and family means are presented in Tables 13 – 15.

Correlation between provenance means for the same trait at pairs of sites provides an indication of the consistency of provenance performance between those sites and thus the strength of provenance x site interaction. Practically all of the correlations examined were stronger at the provenance-mean level than the family-mean level.

Height growth showed high provenance-mean correlations between Kaingaroa and Gowan Hill, (0.73), between Kaingaroa and Golden Downs (0.85), and between Gowan Hill and Golden Downs, (0.81) (Table 13). This reflected the fairly low level of provenance x site or family-within-provenance x site

TABLE 10: Estimated variance components (assuming a fully random model) and of heritabilities (± standard errors) heritabilities: all sites.

Source	Df	Height (m)	Forks (0 – 3)
Site	2	0.5963***	0.0368***
Rep(Site)	87	0.1980***	0.0146***
Prov	19	0.2720***	0.0036***
Site*Prov	38	0.0623***	0.0034***
Family(Prov)	202	0.1118***	0.0042***
Site*Family(Prov)	377	0.0483***	0.0012
Error	14519	2.4511	0.4326
Total	15244		
Narrow-sense $\hat{h}^2$		0.17 ± 0.03	0.04 ± 0.02
Family mean $h^2_{\bar{f}}$		0.69	0.39

Variance component is significant at the level of * p ≤ *0.05;* ** p ≤ *0.01;* *** p ≤ *0.001.*

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TABLE 11: Estimated variance components (assuming a fully random model) estimated and of heritabilities (± standard errors) for paired sites of Golden Downs with Kaingaroa and with Gowan Hill.

Source	Site pairs					
	Golden Downs & Kaingaroa			Golden Downs & Gowan Hill		
	Df	Height (m)	Forks (0 – 3)	Df	Height (m)	Forks (0 – 3)
Site	1	1.1711***	0.0368***	1	1.025*	0.0670***
Rep(Site)	58	0.1705***	0.0204***	58	2.213***	0.0197***
Prov	19	0.4209***	0.0011	19	1.980***	0.0079***
Prov*Site	19	0.0235***	0.0066***	19	0.724***	0.0019*
Family(Prov)	192	0.1526***	0.0075***	202	0.889***	0.0032*
Site*Family(Prov)	185	0.0418**	0.0009	192	0.336**	0.0013
Error	9624	2.7823	0.4938	9896	24.267	0.4523
Total	10098			10387		
Narrow-sense $\hat{h}^2$		0.21 ± 0.03	0.06 ± 0.02		0.14 ± 0.03	0.03 ± 0.02
Family mean $h^2_{\bar{f}}$		0.66	0.41		0.57	0.24

Variance component is significant at the level of * p ≤ *0.05;* ** p ≤ *0.01;* *** p ≤ *0.001.*

interaction and stable performance of the different provenances. Nursery height was moderately correlated with four-year provenance mean height at Kaingaroa (0.79), Golden Downs (0.76) and Gowan Hill (0.60) (Table 15). The provenance mean correlation between height growth and needle retention at Kaingaroa (Table 14) was extremely low (0.09), which was expected as no needle cast was observed at all until only six months before the assessment.

There were moderate negative progeny-mean correlations for height with stem straightness and for height with branching at Kaingaroa of -0.51 and -0.54 respectively (Table 14). In contrast, there was

TABLE 12: Basic statistics for family means at each site.

Site	Trait	Description	N	Mean	Standard Deviation	Minimum	Maximum
Kaingaroa	survival	survival (%)	205	81.43	8.39	60.00	100.00
	height	height (m)	205	2.48	0.28	1.83	3.26
	forks	fork score	205	0.47	0.16	0.13	1.05
	stem straightness	stem-straightness score	205	7.06	0.53	5.29	8.13
	branching	branching score	205	3.27	0.24	2.43	3.83
	needle retention	needle-retention score	205	2.94	0.34	1.95	3.68
Golden Downs	survival	survival (%)	213	83.39	8.09	50.00	100.00
	height	height (m)	213	1.99	0.27	1.20	2.71
	forks	forks	213	0.75	0.22	0.17	1.32
Gowan Hill	survival	survival (%)	222	78.53	13.00	20.00	100.00
	height	height (m)	222	2.14	0.18	1.30	2.54
	forks	fork score	222	0.39	0.14	0.04	1.00
	stem straightness	stem-straightness score	222	6.62	0.31	5.27	7.26
	branching	branch-type score	222	2.17	0.31	1.33	3.00
	leader straightness	leader-straightness score	222	5.62	0.86	3.50	7.65
Nursery	latitude	latitude of origin (°N)	222	40.29	2.60	35.82	44.17
	seed weight	weight of 100 seeds (g)	222	1.13	0.18	0.70	1.72
	height	height (cm)	222	43.48	5.75	25.50	61.95
	flushing	flushing score	222	5.54	0.92	3.67	7.00

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TABLE 13: Provenance- and family-mean correlations between the same trait at pairs of sites.

Site 1	Site 2	Trait	Provenance correlation	Provenance by site interaction	Family correlation	Family by site interaction
Kaingaroa	Golden Downs	survival	0.51*	NA	0.16*	NA
		height	0.85***	***	0.76***	***
		forking	0.19	***	0.25***	NS
Kaingaroa	Gowan Hill	survival	0.60**	NA	0.38***	NA
		height	0.73***	***	0.61***	***
		forking	0.34	***	0.16*	***
		stem straightness	0.70***	*	0.50***	NS
		branching	-0.19	***	-0.08	***
Golden Downs	Gowan Hill	survival	0.77***	NA	0.35***	NA
		height	0.81***	***	0.63***	***
		forking	0.81***	*	0.36***	NS

NA means not available
NS means not significant (p >0.05)
* *indicates that a correlation is significant at the level of* p ≤ *0.05*
** *indicates that a correlation is significant at the level of* p ≤ *0.01*
*** *indicates that a correlation is significant at the level of* p ≤ *0.001*

little correlation for height with stem straightness at Gowan Hill (-0.26). However, there was a moderate negative correlation for height with leader straightness of -0.59 at this site. This means that taller families at Gowan Hill tend to be more crooked and have more intermediate branches between annual 'nodes'. There was a moderate positive correlation of stem straightness at Kaingaroa with stem straightness and leader straightness at Gowan Hill (0.54 & 0.46) (Table 14).

There was a significant negative correlation of forking (both provenance and family) with latitude of origin at both Golden Downs and Gowan Hill, yet no correlation at Kaingaroa (Table 14). This implied that the families from lower latitudes in USA forked more at the two South Island sites than at the milder North Island site. Greater wind speeds and/or harder frosts are possible site factors (Low et al. 2012), along with the extended growing season of families from lower latitudes. Forking was poorly inter-correlated at the different sites. The correlation between forking and latitude was 0.38 at Golden Downs and 0.48 at Gowan Hill (Table 15).

There were moderate to weak, but significant, correlations of both provenance and family means for various other traits with latitude of origin, but not for height. Needle retention at Kaingaroa (0.59 for provenances, 0.75 for families) and both forking and branching at Gowan Hill (-0.48 for provenance, -0.70 for families and -0.60 for provenances and -0.77 for

TABLE 14: Provenance and family means within sites correlated between selected pairs of traits.

Site	Trait 1	Trait 2	Provenance correlation	Family correlation
Kaingaroa	height	stem straightness	-0.75***	-0.51***
	height	branching	-0.63**	-0.54***
	height	needle retention	0.09	0.14*
Golden Downs	survival	height	0.14	0.34***
	height	forking	-0.17	-0.30***
Gowan Hill	survival	height	0.76***	0.41***
	height	stem straightness	-0.39	-0.26***
	height	leader straightness	-0.70***	-0.59***
	forking	branching	0.77***	0.40***
	stem straightness	leader straightness	0.73***	0.48***

Variance component is significant at the level of * p ≤ *0.05;* ** p ≤ *0.01;* *** p ≤ *0.001.*

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TABLE 15: Selected provenance and family means from trial sites correlated with nursery traits and latitude of origin.

Trait 1	Trait 2	Provenance correlation	Family correlation
Nursery height	Height at Kaingaroa	0.79***	0.60***
	Height at Golden Downs	0.76***	0.68***
	Height at Gowan Hill	0.60**	0.54***
Nursery flushing	Needle retention at Kaingaroa	-0.84***	-0.63***
	Forking at Kaingaroa	-0.03	0.05
	Forking at Golden Downs	0.84***	0.51***
	Forking at Gowan Hill	0.75***	0.47***
	Latitude	-0.82***	-0.72***
Latitude	Needle retention at Kaingaroa	0.59***	0.75***
	Forking at Kaingaroa	-0.02	0.12
	Forking at Golden Downs	-0.38***	-0.62***
	Forking at Gowan Hill	-0.48***	-0.70***
	Branching at Gowan Hill	-0.60***	-0.77***

Variance component is significant at the level of * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

families respectively) showed moderate correlation with latitude of origin (Table 14). No traits showed significant correlation with seed weight (data not shown). Flushing time in the nursery showed a high correlation (-0.82 for provenances -0.72 for families) with latitude (Table 15) but very low correlation with height at each site (not shown). There was a high negative correlation (-0.84) between needle retention and flushing time at Kaingaroa (Table 15). Some of this calculated correlation will be due to a real effect, as the southernmost Los Padres families were hardest hit by Swiss needle cast, but some would be caused by the assessment being too early for the late-flushing families.

Conclusions

Although there were some trends with latitude of origin for all traits, the best-grown provenances (and control seedlots) needed to be identified empirically (based on performance). These were located in California from Fort Ross (38° 25´N) to Arcata (39° 59´N). In general, the faster-growing provenances had poorer stem straightness and leader straightness scores but differences between best and worst provenances in this respect were only about one score point out of nine. The Weyerhaeuser seed orchard progenies from Washington provenances grew particularly slowly. These results are consistent with data from the 1959 trial. Unexpectedly, the Los Padres provenance from southern California appeared to be an outlier, as it performed poorly for growth, forking and needle retention.

The New Zealand control seed-stand seedlots of Fort Bragg, California origin grew as well as the best two native provenances (also from California) and much better than the other New Zealand control seed-stand seedlots, especially at Kaingaroa and at Golden Downs. Again, these results provide some preliminary confirmation of the results found in the 1959 provenance trials. In summary, these Californian populations were still performing as well or better than any other population, even in Southland, well beyond their native latitudes.

Provenance rankings for height were quite stable across the three sites but there was diminished provenance variation at Gowan Hill. This contributed to significant provenance × site interaction variance, which amounted to 23% of the provenance variance in the across-sites analysis (Table 10). Estimated family × site variance for height amounted to 42% of the family-within-provenances variance, indicating that this would be sufficient to cause some reduction in gain from family selection across sites but which could be accommodated by selecting families that performed well at all sites. Considering the wide range in latitude (38 – 45°), and in climatic and site conditions at the three test sites, this was not unexpected.

These broadly-based and well-established trials of over 200 families from 22 coastal Californian and Oregon provenances form an extremely valuable genetic resource for future breeding. They also form one of the two “superlines” of the Douglas fir breeding population, the other being based on clones selected in 1988 from the 1957 and 1959 provenance trials and from land-race populations already established in New Zealand. This breeding population is, therefore, very well endowed with well-adapted genetic material to effect large gains in growth rate and other economically important traits in future.

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