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Effect of seed source of Douglas-fir at high-elevation New Zealand sites: performance at age eight years

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Abstract

A seed-source trial was established in 1996 using open-pollinated seed of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco). The trial involved seed from 11 native populations in coastal California, three Californian seed orchards, one Oregon seed orchard and two Washington seed orchards. Open-pollinated progeny seedlots were bulked by native population. Seed from seven New Zealand seed stands of Washington, Oregon or Californian origin was also included. This trial was conducted at five sites with a range of climatic features.

The purpose of this trial was to test the performance of bulked Californian seedlots on four cold, high-elevation sites prone to snow and exposed to strong winds compared to a mild, low-elevation site. Overall, there were significant differences in height growth of trees from different seedlots but little difference was observed in the growth performance of trees from individual Californian provenances of varying latitude at the four trial sites with harsh climates. Also, the three New Zealand seedlots of California origin grew at about the same rate as the three seed-orchard seedlots of southern Oregon and Washington origin. At the four harsh-climate sites, the severe effect of environment on stem straightness, malformation and acceptability appear to have largely obliterated any provenance differences at the assessment age (eight – nine years).

At the sheltered site, trees from northern Californian seedlots clearly grew best and trees from the New Zealand seedlots originating from California substantially outgrew trees from the New Zealand seedlots of Oregon and Washington origin. This result paralleled that at three progeny-trial sites featuring many of the same seed sources, which all had mild climates. The southernmost provenance from Los Padres at latitude 35° 49´ behaved differently from all other provenances. It had slower growth, but better form that may have resulted from shelter from faster-growing trees.

Keywords: Douglas-fir; height; malformation; provenance; *Pseudotsuga menziesii*; site; straightness.

Introduction

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) has been grown in plantations in New Zealand since about 1870 (Miller & Knowles, 1994). This species currently represents about six percent of the New Zealand plantation area (Ministry of Agriculture and Forestry (MAF), 2011). The history of Douglas-fir growing in New Zealand has been reviewed recently by Maclaren (2009). He suggested that seed of Californian and southern Oregon origin was most suitable for New Zealand growers.

There has been a recent increase in planting of Douglas-fir, particularly on snow-prone, cold, exposed and high-elevation (harsh) sites in the South Island, especially as the snow at these sites is often “wet snow” that sticks to the foliage. There is considerable interest in whether the Californian/southern Oregon provenances that are suitable for good-quality, low-

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elevation sites are the best option for these harsh sites. Differences between the climates of the South Island of New Zealand and the Pacific Northwest of America mean that empirical studies are necessary to determine the best provenances for harsh New Zealand sites.

Malformation and stem sinuosity have been noted in a number of young Douglas-fir stands in the South Island. This could result in timber degrade due to grain deviation or large and/or spike knots. Sinuosity is usually obscured in older stands. Also, big branches will rot off after canopy closure or be wiped off during thinning operations. Even so, a proportion of the timber is likely to be degraded as a result of poor early form. Thus, assessment of early form (at eight – nine years) was an important objective in this trial.

Historical provenance trials in New Zealand

The first provenance trial of Douglas-fir in New Zealand was planted in 1957 at 10 sites throughout the country. The seed for this initial trial, supplied by commercial seed companies (Sweet, 1965; Shelbourne et al., 2007), was collected from areas of Washington (WA) and Oregon (OR), USA and British Columbia, Canada. The second trial in New Zealand was planted in 1959 at 19 lowland sites and one high-elevation site and 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 and selected US provenances.

Breeding programme in New Zealand

A Douglas-fir breeding programme was initiated in 1969 at Kaingaroa Forest in the North Island of New Zealand. This programme incorporated plus-tree selection and open-pollinated seed collected from existing stands in Kaingaroa Forest of commercial Washington USA origin. Seed was sown and progeny trials were planted in 1972. Coincidentally, an assessment of the 1959 provenance trials carried out this same year (M. D. Wilcox, unpublished report) showed clearly that growth rates of trees from seed of Washington USA provenances was inferior to that from other US provenances. Seed from provenances located in the fog belt on the coast of California USA produced trees with up to 30% more volume, for example. Such information, combined with a general decline of industry interest in the Douglas-fir, effectively halted this breeding programme. Fifteen years later, the timber industry was starting to show a greater appreciation of Douglas-fir and a new breeding programme was initiated. One hundred and eighty-five trees from plots of the best-performing provenances grown in the 1957 and 1959 provenance trials and related seed stands (Shelbourne et al., 2007) were selected for grafting of scions to be planted at Waikuku in Canterbury as a clonal archive.

The need to broaden the genetic base of the breeding programme resulted in selection and additional collection in 1993 of open-pollinated seed from 200 trees in the coastal fog-belt populations of California and Oregon (Shelbourne et al., 2007). This seed was used to set up a progeny trial in 1996 at three New Zealand sites characterised by a relatively mild climate (Low et al., 2012, Dungey et al., 2012). Surplus seed was bulked by population and used to establish a seed-source trial also in 1996 in which tree performance was to be examined at sites where harsher conditions prevailed. An assessment of the seed-source trial at age eight years is reported here.

Material and Methods

Seed sources

Parent trees from native stands in California were non-intensively selected at a minimum distance of 50 m apart. Selected trees had to exceed average standards for growth, stem straightness, crown form and health. The elevation of all parent-tree sites was below 500 m although elevation for individual trees within a population often varied between 200 and 500 m in hilly terrain. Up to four families from each of three seed orchards owned by the Weyerhaeuser Company in Oregon and Washington were chosen because they were well represented in the orchards and could furnish a substantial amount of seed.

The seedlot trial involved seed from 11 native populations in coastal California, three Californian seed orchards, one Oregon seed orchard and two Washington seed orchards. Open-pollinated progeny seedlots from the Oregon seed orchard and the two Washington seed orchards were bulked by native population (Table 1). Seed from seven New Zealand seed stands of Californian, Oregon or Washington origin collected in 1994 was also included. Seedlots #900 (planted 1960), #901 (planted 1981) and #903 (planted 1959) were all derived from seed stands of Fort Bragg origin (Latitude 39°15´N on the Californian coast). Seedlots #904 (planted 1969, Eyrewell Forest) and #905 (planted 1973, Mt. Thomas Forest) were derived from an older seed stand at Ashley Forest whose origin was unknown but was assigned to southern Oregon origin on the basis of the timing of the spring flush (Miller & Knowles, 1994). Seedlot #906 (planted 1952, Beaumont Forest Tramway Seed Stand) was also of unknown origin, but was assigned to Washington origin. However, trees in the nearby Ashley Forest Seed Stand may have contributed some pollen parentage. Seedlot #902 (Kaingaroa Forest Cpt 1061, planted 1968) represented a second-generation commercial stand of Washington origin.

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TABLE 1: Origins of seedlots used in the seedlot and progeny trials

Origin			Provenance/ Seed source	No. of parents	Latitude[1]	Seedlot No.	Seed-collection site type
Country	**State**	**Site**					
Native provenances							
USA	CA	Monterey County	US Los Padres National Forest	4	35° 49´N	808	Native forest
USA	CA	Santa Cruz County	US Cascade Ranch	12	37° 08´N	810	Native forest
USA	CA	San Mateo County	US San Francisco Water Reserve	14	37° 27´N	809	Native forest
USA	CA	Marin County	US SP Taylor State Park	10	38° 02´N	812	Native forest
USA	CA	Marin County	US Point Reyes	8	38° 04´N	811	Native forest
USA	CA	Sonoma County	US Russian River	6	38° 21´N	813	Native forest
USA	CA	Sonoma County	US Fort Ross	10	38° 25´N	814	Native forest
USA	CA	Mendocino County	US Gualala	9	38° 47´N	815	Native forest
USA	CA	Mendocino County	US Navarro River	11	39° 11´N	816	Native forest
USA	CA	Mendocino County	US Noyo River	18	39° 25´N	817	Native forest
USA	CA	Mendocino County	US Rockport	8	39° 47´N	818	Native forest
US seed orchards							
USA	CA	Mendocino County	US Georgia Pacific	2	39° 25´N	819	Seed orchard
USA	CA	Humboldt County	US Louisiana Pacific	15	39° 59´N	907	Seed orchard
USA	CA	Humboldt/Del Norte	US Simpsons Timber	>10	40 – 41°N	825	Seed orchard
USA	OR	Coos Bay	US Weyerhaeuser, family 1	1	43° 25´N	122	Seed orchard
USA	OR	Coos Bay	US Weyerhaeuser, family 2	1	43° 25´N	222	Seed orchard
USA	OR	Coos Bay	US Weyerhaeuser, family 3	1	43° 25´N	322	Seed orchard
USA	OR	Coos Bay	US Weyerhaeuser, family 4	1	43° 25´N	422	Seed orchard
USA	WA	Long View	US Weyerhaeuser, family 1	1	46° 30´N	123	Seed orchard
USA	WA	Long View	US Weyerhaeuser, family 2	1	46° 30´N	223	Seed orchard
USA	WA	Long View	US Weyerhaeuser, family 3	1	46° 30´N	323	Seed orchard
USA	WA	Long View	US Weyerhaeuser, family 4	1	46° 30´N	423	Seed orchard
USA	WA	Twin Harbours	US Weyerhaeuser, family 1	1	48° 05´N	124	Seed orchard
USA	WA	Twin Harbours	US Weyerhaeuser, family 2	1	48° 05´N	224	Seed orchard
USA	WA	Twin Harbours	US Weyerhaeuser, family 3	1	48° 05´N	324	Seed orchard
USA	WA	Twin Harbours	US Weyerhaeuser, family 4	1	48° 05´N	424	Seed orchard
New Zealand seed stands							
USA	CA	56/654 Ft Bragg	NZ Rotoehu 55	>50	(39°15´N)	900	Seed stand
USA	CA	R78/34 ex Rotoehu cpt.55	NZ Kaingaroa 1132	>50	(39°15´N)	901	Seed stand
USA	CA	56/654 Ft Bragg	NZ Golden Downs 115	>50	(39°15´N)	903	Seed stand
USA	OR	Ashley (ex Oregon)	NZ Eyrewell Main Race	>50	(ca. 43°N)	904	Seed stand
USA	OR	Ashley (ex Oregon)	NZ Mount Thomas	>50	(ca. 43°N)	905	Seed stand
USA	WA		NZ Beaumont, Tramway	>50	(ca. 48°N)	906	Seed stand
USA	WA	R63/701, R64/734 (Kaingaroa, ex Washington)	NZ Kaingaroa 1061	>50	(ca. 48°N)	902	Road edge

[1] *Latitudes in parentheses indicate the latitude of the USA origin, rather than the latitude of the stand within New Zealand.*

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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 1.5-year-old bare-rooted plants for planting in winter (August) 1996. A randomised complete block design with three replicates was used for layout in the nursery. This helped to minimise differential effects of position along the nursery beds.

Field sites, layout and planting

Seedlings were planted in August 1996 at five sites all located in the South Island (Figure 1). Particulars of each site are given in Table 2. At each site, seedlots were laid out in a randomised complete block design. Plants were spaced at 3 × 3 m. The basic unit of a 5-tree row plot was replicated 10 times at Golden Downs, Hanmer and Waipori, but only six times at Beaumont and Gowan Hill (due to a shortage of plants). One site (Golden Downs) was considered sheltered while the other four sites had much harsher climates.

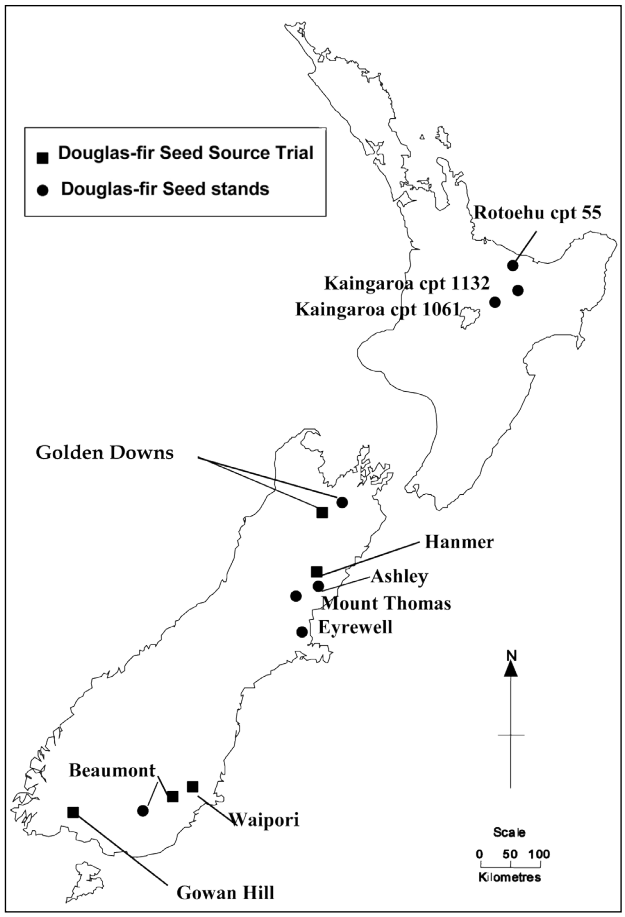

FIGURE 1: Location of the trial sites and the New Zealand Douglas-fir seed stands.

TABLE 2: Site descriptions of the 1996 seed-source trial in the South Island of New Zealand

Forest	Cpt	Latitude	Elevation (m)	Soil order/ series[1]	Mean Annual Rainfall (mm)	Mean temperature July/February, (°C)	Previous land use	Terrain	Weed control/ cultivation	Remarks
Golden Downs	247	41° 33′	370	Brown/ Glenhope	1710	3/15	*Pinus radiata* D.Don cutover	Valley bottom	Herbicide application	Browsed by possums in first year.
Hanmer	13	42° 32′	500	Brown/ Tekoa	1097	3/15	*Pinus nigra* J.F.Arnold cutover	Mid-slope		Browsed by hares and rabbits, frosted, heavy broom in places.
Waipori	8/15	45° 50′	300	Brown/ Waipori	822	4/15	*Pinus ponderosa* Laws./ *Pseudotsuga menziesii* cutover	Near ridgetop	Spot mounded	Frosted and browsed. Some Douglas-fir regeneration (heavy in patches).
Gowan Hill	746	45° 54′	630	Brown/ Taringatura	1023	2/12	Farmland	Hilltop	Ripped lines	Slow start but good survival amongst tall tussocks.
Beaumont	27	45° 56′	430	Brown/ Pukekoma	967	5/14	*Pinus radiata* cutover	Top of forest	Root-raked and spot mounded	Good survival. Some regeneration of blackberry (*Rubus* sp.) and gorse (*Ulex* sp.), mainly browntop grass (*Agrostis* sp.)

[1] *New Zealand Soil Classification*

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TABLE 3: Assessment methods

Trait	Description
Height	(m), by height pole
Diameter[1]	(cm), by tape
Stem Straightness	Scored 1 – 9 (1 – 4 = unacceptably crooked; 6 – 9 = acceptably straight)
Malformation	Scored 1 – 9 (1 = repeated forking; 9 = no forks or ramicorns).
Six months of needle retention[2]	Scored 1 (minimum) – 8 (maximum)[2]
Acceptability	Scored 0 or 1 (0 = unacceptable development; 1 = acceptable growth, form and health). Seedlot means were shown as percentage of acceptable trees

[1]*Hanmer and Waipori only*
[2]*Golden Downs only*

Assessment

Trees were measured at age eight at the Hanmer, Waipori, Beaumont and Gowan Hill sites. At the Golden Downs site, a profusion of gorse (*Ulex europeaus* L.) had been noted at age two and it was feared that access would be impractical. However, the gorse was treated with herbicide and it was possible to assess the trees at age nine.

Details of the traits measured or assessed are given in Table 3. The height of each tree in the trial was measured. Diameter at breast height (1.4 m; DBH) was measured on trees only at Hanmer Forest and Waipori Forest, where additional help was available. Stem straightness was estimated from the magnitude of the stem deviation from a central core irrespective of cause (sweep, crook or sinuosity). The level of malformation was assessed according to the presence/absence of ramicorn branches and forks. A score of 1 signified a multi-leadered bush or a tree that forked annually, while a score of 9 represented a tree with no forks or ramicorns. Acceptability is a composite trait that included good growth, stem form and health. It was scored as either 0 (unacceptable) or 1 (acceptable). Needle retention, on a scale of 1 (minimum) to 8 (maximum) was scored at Golden Downs Forest, the only site in this trial where needle cast (caused by *Phaeocryptopus gaeumanii* [T.Rohde] Petr.) was evident.

Data analysis

The trees from all progenies within a Weyerhaeuser Co. seed orchard were aggregated together for the analyses. This was done to provide a fairer comparison with the other seedlots that all had multiple parents.

The model used for analysis of variance for a randomised complete block at a single site was as follows:

$$Y_{ij} = \mu + R_i + P_j + R_i * P_j + E_{ij} \quad [1]$$

Where :

Y_{ij} = the observation on a tree of the j^{th} provenance (or seedlot) in the i^{th} replicate

μ = the overall mean

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

P_j = the fixed effect of the j^{th} provenance

$R_i * P_j$ = the random interaction effect of the i^{th} replicate with the j^{th} provenance

E_j = the residual error (a random effect) associated with each tree of the j^{th} provenance in the i^{th} replicate.

The relationship used for analysis of variance over several sites contained additional terms; one for sites and one for the interaction of provenance with site:

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

Where :

Y_{ijk} = the observation on the tree of 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 fixed effect of the k^{th} provenance

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

E_{ijk} = the residual error (random effect) associated with each tree of the k^{th} provenance in the j^{th} replicate of the i^{th} site.

The results were initially examined with Equation [1] using the data from each site separately. Analysis of variance was carried out by PROC GLM of the SAS® statistical package (SAS Institute Inc., 1989) and provenance means were compared using the Tukey multiple range test option with the minimum significant difference ($p \leq 0.05$). The heritability (or repeatability) of provenance means was estimated by $(F - 1) / F$ (Baker, 1986), where F is the value provided by Fisher's F test in the analysis of variance.

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Data from all five trial sites combined were examined using Equation [2]. Least-squares provenance means were estimated for an overall analysis using PROC GLM, dropping the provenance x replicate-within-site effect. It was decided to estimate least-squares means as some sites had data for more trees per provenance than others and the precision of the estimates of provenance means also varied by site.

Seedlot means were estimated using PROC MEANS of the SAS® software package (SAS Institute Inc., 1990) at each site. Pearson correlation coefficients between sites of provenance means (*r* values) were calculated by PROC CORR of the SAS® software package. Genetic correlations between sites were estimated using the method of Burdon (1977). Correlations of seedlot means were offered as the basis for testing significance of genetic correlations.

Results and Discussion

Seedlot means for height, stem straightness, malformation score and acceptability score at age eight years (age nine years for Golden Downs) at each of the five trial sites are given in Tables 4, 5, 6 & 7, respectively. For each within-site analysis, the minimum significant difference between means, site mean, standard deviation and F ratio for the seedlot term in the ANOVA are shown at the bottom of each table. Least-squares provenance means across sites are shown in Table 8. Native-provenance and seed-orchard seedlots, all from coastal populations, are listed in order of increasing latitude of origin within groups. Heritabilities, or repeatabilities of seedlot means were good for height, straightness and needle retention, but poor for malformation and acceptability at some sites.

Site effects

A strong influence on New Zealand South Island weather is the southern ocean, which encircles the globe to the south of New Zealand, and produces a predominantly cool, westerly wind. This strong westerly is frequently blocked on the west coast of New Zealand by a combination of warmer pressure systems from the North and a tall range of mountains (Southern Alps) aligned roughly north-east/south-west.

This situation initially creates a nor-wester (Föhn wind in Europe), which generates hot, dry winds down the eastern side of the mountains (where the four harsh sites were planted). The nor-wester persists from one to three days then the pressure is released around the southern end of the mountains. This results in a strong southerly wind up the east side of the South Island. Either event can have wind speeds of 160 km per hour or more. Temperatures will typically drop at least 15 ºC within an hour and the southerly front often carries snow. These events are most pronounced in spring and early summer, when Douglas-fir leaders are soft and floppy. This contrasts with the Pacific Northwest of the USA where the powerful storms in the natural range of Douglas-fir almost all occur in the winter.

Survival

Although there were fewer replicates at Beaumont and Gowan Hill, trees at these sites were not browsed and suffered very little mortality. Minimum seedlot survival rates were 90% at Beaumont and 77% at Gowan Hill. In comparison, browsing and rapid growth of broom (*Cytisus scoparius* L.) suppressed many trees at Hanmer. Poorest survival (43%) was noted in Seedlot #812 (Noyo River, CA). The New Zealand seed-stand and US seed-orchard seedlots survived better than the native provenances at all sites.

Tree Height

The effects of site on height growth were far greater than the effects of provenance (Table 4). In particular, trees grew much more slowly at the highest site (Gowan Hill, 630 m a.s.l), which was also very exposed to both northerly and southerly winds. At this site, tree mean height (2.16 m) was approximately half that at any of the other four sites (4.42 – 4.64 m), which are located at elevations ranging between 300 and 500 m. Various countervailing factors, including elevation, temperature, exposure, moisture, fertility and browsing by possums have resulted in quite similar height growth at these sites.

Tree form

Stems were much straighter at the sheltered Golden Downs site (mean score 8.39), than at Hanmer (mean score 6.8), Table 5. The worst scores (5.45 and 5.53) were obtained at the exposed Beaumont and Gowan Hill sites, respectively. An example of good tree form at Golden Downs is illustrated in Figure 2 and examples of poor tree form at Beaumont and Gowan Hill are illustrated in Figures 3 and 4, respectively. Malformation was most pronounced at Gowan Hill (score 5.9) and least at either Hanmer (8.4) or Golden Downs (8.7). General acceptability, based on tree growth, stem form and health, varied widely. Scores of 32% at Gowan Hill, 36% at Waipori, 48% at Beaumont, 51% at Hanmer and 77% at Golden Downs were recorded. Although trees at the sheltered Golden Downs site had the best tree form, height growth had been retarded at an early age by possum (*Trichosurus vulpecula* Kerr) browsing and was no better than at Beaumont, Waipori or Hanmer.

Seedlot variability

Height growth

Although seedlot differences in height growth were apparent at all sites (Table 4), Tukey Multiple Range

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TABLE 4: Seedlot mean heights (m) at eight years

***Seedlot*[1]/Statistics**	**Site[2]**				
	Gowan Hill	**Beaumont**	**Waipori**	**Hanmer**	**Golden Downs**
Native Forest, CA					
808	1.46	3.80	3.82	4.02	3.49
810	1.90	4.31	3.95	4.92	4.32
809	1.80	4.48	417	4.46	4.36
812	1.95	4.48	4.15	4.64	3.72
811	2.03	4.46	4.07	4.68	4.51
813	2.14	4.51	4.32	4.52	4.17
814	1.76	4.19	4.18	4.79	4.94
815[3],	1.77	4.39	4.01	-	4.51
816	1.83	4.72	4.46	5.15	5.31
817	1.95	4.16	4.47	4.95	4.44
818	1.95	4.18	4.20	4.62	5.07
Seed stand, NZ					
900	2.27	4.69	4.63	4.55	5.66
901	2.41	4.59	4.58	5.25	5.49
903	2.39	4.45	4.43	4.93	5.27
904	2.41	4.74	4.48	4.73	4.30
905	2.58	4.51	4.80	4.73	3.88
906	2.35	4.35	4.45	5.10	4.55
902	2.37	4.33	4.71	4.89	4.60
Seed Orchard, CA					
819	1.92	4.42	4.23	5.02	5.05
907	2.22	4.61	4.43	5.39	4.67
825	2.43	4.46	4.26	4.90	4.52
Seed Orchard, OR					
22[4]	2.28	4.77	4.64	5.11	4.73
Seed Orchard, WA					
23[4]	2.37	4.35	4.46	4.79	4.59
24[4]	2.21	4.58	4.68	4.80	4.75
Overall site mean	2.16	4.46	4.42	4.55	4.64
Minimum significant difference, $p \leq 0.05$	0.57	0.57	0.65	1.09	1.63
Standard deviation	0.27	0.24	0.26	0.40	0.48
F ratio[5] for seedlots (within sites)	5.32***	2.84***	2.20***	1.79*	2.71***
Heritability[6]	0.82	0.65	0.55	0.45	0.63

[1] CA = California; OR = Oregon; WA = Washington; NZ = New Zealand.

[2] Golden Downs was assessed at age nine, other four sites assessed at age eight.

[3] Seedlot 815 was not planted at Hanmer because of a shortage of plants.

[4] Four separate seedlots combined.

*[5] * p ≤ 0.05, *** p ≤ 0.001.*

[6] Heritability of observed mean estimated by (F-1)/F.

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TABLE 5: Stem straightness means at the five sites. Trees were scored on a scale of 1 – 9 where 1 = unacceptably crooked; 9 = acceptably straight.

Seedlot[1]/Statistics	Site[2]				
	Gowan Hill	**Beaumont**	**Waipori**	**Hanmer**	**Golden Downs**
Native Forest, CA					
808	6.77	6.18	6.96	7.38	8.67
810	5.45	5.07	6.39	7.56	8.81
809	5.45	6.14	6.33	7.47	8.26
812	5.62	5.53	6.21	7.11	8.48
811	5.64	5.43	6.33	6.90	8.40
813	5.68	5.79	6.93	6.79	8.37
814	5.70	5.21	5.12	6.47	8.00
815[4]	5.09	4.80	5.31	-	8.25
816	5.67	5.15	5.91	6.32	8.48
817	5.95	5.26	5.33	6.83	8.12
818	5.48	5.93	5.81	6.95	8.45
Seed stand, NZ					
900	5.44	4.48	5.58	6.28	8.29
901	4.96	5.23	5.46	6.88	8.44
903	5.54	5.37	5.63	6.78	8.42
904	6.00	5.55	6.46	6.62	8.47
905	4.93	5.56	6.42	6.68	8.58
906	5.39	5.68	6.38	7.22	8.32
902	4.62	5.72	6.13	6.63	8.26
Seed Orchard, CA					
819	5.73	5.64	6.03	6.82	8.57
907	5.89	5.33	5.91	6.59	8.42
825	5.42	5.96	5.90	7.29	8.42
Seed Orchard, OR					
22[4]	5.50	5.28	6.14	6.07	8.40
Seed Orchard, WA					
23[4]	5.35	5.61	5.88	6.61	8.49
24[4]	5.68	5.07	5.80	6.67	8.17
Mean	5.53	5.45	6.00	6.76	8.39
Minimum significant difference	1.60	1.66	1.65	1.59	0.93
Standard deviation	0.41	0.46	0.43	0.41	0.18
F ratio[5] for seedlots (within sites)	1.43	1.74*	1.19	1.12	1.10
Heritability[6]	0.30	0.43	0.16	0.11	0.09

[1] *CA = California; OR = Oregon; WA = Washington; NZ = New Zealand.*

[2] *Golden Downs was assessed at age nine, other four sites assessed at age eight.*

[3] *Seedlot 815 was not planted at Hanmer because of a shortage of plants.*

[4] *Four separate seedlots combined.*

[5] * $p \leq 0.05$

[6] *Heritability of observed means estimated by (*F*-1)/*F.

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TABLE 6: Malformation means at the five sites. Trees were scored on a scale of 1 – 9 (1 = repeated forking; 9 = no forks or ramicorns).

Seedlot[1]/Statistics	Site[2]				
	Gowan Hill	**Beaumont**	**Waipori**	**Hanmer**	**Golden Downs**
Native stand, CA					
808	5.85	6.43	6.83	8.38	8.26
810	6.10	6.40	6.82	8.28	8.88
809	6.00	7.07	6.82	8.65	8.42
812	5.86	7.03	7.00	8.06	8.85
811	5.73	6.57	6.93	8.30	8.66
813	5.91	5.97	6.52	8.20	8.33
814	5.85	5.89	7.00	8.00	8.46
815[3]	5.91	6.27	6.69	-	8.97
816	6.06	6.52	6.71	8.58	8.91
817	6.26	5.85	7.33	8.67	8.42
818	6.10	6.60	7.54	8.33	8.79
Seed stand, NZ					
900	5.80	5.90	6.64	8.00	8.81
901	5.64	5.87	6.83	8.54	8.72
903	6.12	6.20	6.44	7.83	8.65
904	6.07	7.21	7.32	8.57	8.91
905	5.90	7.41	6.42	8.32	8.85
906	5.68	6.46	7.10	8.43	8.65
902	5.81	5.72	7.40	8.00	8.65
Seed Orchard, CA					
819	5.41	5.82	6.81	8.27	8.70
907	6.00	6.67	6.69	8.59	8.72
825	6.15	6.75	6.83	8.50	8.82
Seed Orchard, OR					
22[4]	5.96	6.37	6.79	8.22	8.76
Seed Orchard, WA					
23[4]	6.06	6.64	6.67	8.52	8.82
24[4]	5.95	5.27	7.04	8.37	8.81
Mean	5.94	6.39	6.87	8.36	8.73
Minimum significant difference	1.59	1.79	1.91	1.53	0.73
Standard deviation	0.21	0.51	0.33	0.27	0.18
F ratio[5] for seedlots (within sites)	0.45	2.38***	0.84	0.94	1.86**
Heritability[6]	-	0.58	-	-	0.46

[1] CA = California; OR = Oregon; WA = Washington; NZ = New Zealand.

[2] Golden Downs was assessed at age nine, other four sites assessed at age eight.

[3] Seedlot 815 was not planted at Hanmer because of a shortage of plants.

[4] Four separate seedlots combined.

*[5] ** p ≤ 0.01, *** p ≤ 0.001*

[6] Heritability of observed means estimated by (F-1)/F.

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TABLE 7: Overall acceptability at all five sites, and needle retention at Golden Downs. Trees were scored as either 0 or 1 for acceptability and seedlot means were converted to a percentage of acceptable trees

Seedlot[1]/Statistics	Site[2]					
	Gowan Hill	Beaumont	Waipori	Hanmer	Golden Downs[2]	Golden Downs needle retention
Native Stand, CA						
808	0.22	0.46	0.48	0.53	0.48	2.15
810	0.27	0.47	0.64	0.62	0.73	2.65
809	0.30	0.76	0.58	0.65	0.74	1.97
812	0.36	0.63	0.57	0.67	0.44	2.03
811	0.26	0.61	0.59	0.86	0.83	3.23
813	0.56	0.62	0.65	0.69	0.73	2.50
814	0.31	0.50	0.48	0.53	0.74	3.31
815[3]	0.11	0.43	0.52	-	0.79	2.78
816	0.30	0.44	0.59	0.68	0.94	3.52
817	0.40	0.33	0.56	0.65	0.68	2.31
818	0.31	0.53	0.55	0.77	0.76	3.15
Seed Stand, NZ						
900	0.29	0.24	0.52	0.55	0.97	3.81
901	0.46	0.40	0.49	0.85	0.86	4.03
903	0.39	0.53	0.45	0.57	0.97	3.06
904	0.50	0.62	0.62	0.59	0.77	3.82
905	0.30	0.67	0.58	0.70	0.57	3.88
906	0.38	0.43	0.55	0.85	0.72	3.97
902	0.21	0.45	0.60	0.63	0.77	4.32
Seed Orchard, CA						
819	0.19	0.46	0.52	0.70	0.84	3.27
907	0.34	0.43	0.49	0.88	0.75	3.47
825	0.39	0.61	0.55	0.71	0.77	3.27
Seed Orchard, OR						
22[4]	0.37	0.45	0.55	0.61	0.77	3.71
Seed Orchard, WA						
23[4]	0.35	0.55	0.48	0.73	0.82	3.75
24[4]	0.38	0.37	0.55	0.69	0.82	3.68
Mean	0.32	0.48	0.36	0.51	0.77	
Minimum Significant Difference	0.48	0.48	0.44	0.54	0.44	1.33
Standard Deviation	0.09	0.11	0.06	0.11	0.12	
F ratio[5] for seedlots (within sites)	0.93	1.30	0.68	0.99	2.15***	6.57***
Heritability[6]	-	0.23	-	-	0.53	0.85

[1] *CA = California; OR = Oregon; WA = Washington; NZ = New Zealand.*

[2] *Golden Downs was assessed at age nine, other four sites assessed at age eight.*

[3] *Seedlot 815 was not planted at Hanmer because of a shortage of plants.*

[4] *Four separate seedlots combined.*

[5] *** $p \leq 0.001$.

[6] *Heritability of observed means estimated by (*F*-1)/*F.

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TABLE 8: Least-squares means across all sites for four growth traits.

Seedlot[1]/Statistics	Height	Straightness	Malformation	Acceptability
Native stand, CA				
808	3.22	7.16	7.14	0.44
810	3.77	6.59	7.35	0.55
809	3.76	6.66	7.33	0.60
811	3.90	6.50	7.21	0.62
812	3.70	6.55	7.43	0.52
813	3.94	6.68	6.96	0.64
814	3.94	6.05	7.05	0.52
815[2]	3.79	5.92	7.23	0.49
816	4.25	6.33	7.36	0.61
817	3.86	6.18	7.28	0.52
818	4.03	6.49	7.49	0.58
Seed stand, NZ				
900	4.38	5.99	7.04	0.51
901	4.47	6.18	7.15	0.61
903	4.23	6.32	7.10	0.59
904	4.07	6.60	7.64	0.62
905	4.02	6.42	7.31	0.55
906	4.02	6.42	7.31	0.55
902	4.10	6.25	7.15	0.53
Seed Orchard, CA				
819	4.13	6.55	7.04	0.55
907	4.20	6.42	7.31	0.56
825	4.02	6.58	7.40	0.60
Seed Orchard, OR				
22[3]	4.23	6.31	7.25	0.56
Seed Orchard, WA				
23[3]	4.23	6.22	6.97	0.58
24[3]	4.11	6.36	7.30	0.58
Mean	4.05	6.39	7.26	0.56
Standard error	0.083	0.13	0.14	0.04
F ratio[4] for seedlot	3.21***	2.52***	1.01	1.01
F ratio[4] for site-by-seedlot interaction	1.61***	0.96	1.12	1.12
Heritability[5]	0.69	0.60		

[1] *CA = California; OR = Oregon; WA = Washington; NZ = New Zealand.*

[2] *Seedlot 815 was not planted at Hanmer because of a shortage of plants.*

[3] *Four separate seedlots combined.*

[4] *** $p \leq 0.001$.

[5] *Heritability of observed means estimated by* (F-*1)/F.*

tests showed that only those with extremely high and low values were significantly different from each other. The letters normally assigned to significance classes by the Tukey test are not shown in Tables 4 – 6 for reasons of clarity. The F-ratios for seedlots were significant ($p \leq 0.001$) at all sites except Hanmer ($p > 0.05$). Trends in the influence of latitude of seedlot origin with tree height growth were evident (Figure 5) and the effect was significant, Table 8. Although the southernmost provenance, from Los Padres National

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Forest (lat. 35°49´N), grew the slowest at all sites, the overall pattern of provenance differences varied somewhat at different sites. Observations in older trials (J. T. Miller unpublished data, 1994) suggest that canopy closure will provide some relief from wind damage, so the height-growth performance of trees from provenances from lower latitudes may improve with time.

At the Gowan Hill site in this trial, mean heights of trees from all native provenances at age eight years were lower than those aged four years at a nearby, but lower-elevation and less-exposed site also called Gowan Hill (Low et al., 2012). In contrast, for certain seedlots from New Zealand seed stands, trees were slightly taller at age eight years than those aged four years at the Gowan Hill provenance trial site (Low et al., 2012).

At the sheltered Golden Downs site, the best growth was observed in trees from native northern California coastal provenance seedlots. The same northern California provenances all grew well in a provenance trial at a similar site nearby (Low et al., 2012, Dungey et al., 2012). A lack of seedlots from native populations north of Rockport, California means that direct comparison with latitude above 39°47´N cannot be made. Comparison of orchard-grown and native provenances does show that seedlots from US orchards greater than 40 °N produced taller trees (2.2 – 2.4. m) than seedlots from native Californian populations (1.5 – 2.1 m) at the highest and most exposed site (Gowan Hill) in this trial (Table 4). Little height differentiation was observed between seed-orchard seedlots with provenances from northern California to Washington. For example, trees from the Point Reyes, CA seedlot were, at most, 0.5 m shorter than those from the fastest-growing Fort Bragg seedlots.

Data for height growth of New Zealand seed-stand seedlots in relation to their provenance origins is consistent with the results from US seedlots (Table 4). The average height of trees from the three New Zealand seedlots of Fort Bragg, CA origin (seedlots #900, #901 & #903) was 2.36 m at Gowan Hill. This average was very slightly lower than the average (2.5 m) for trees from the two seedlots of Oregon origin (#904 from Eyrewell and #905 from Mt. Thomas). This was the only occasion when the Fort Bragg seedlots did not have the best growth. At the Beaumont, Waipori and Hanmer sites, there was little difference between New Zealand seedlots. At the Golden Downs site, however, the three seedlots from Fort Bragg material were clearly superior to the other four New Zealand seedlots.

FIGURE 2: Excellent stem straightness of eight-year-old Douglas-fir at a sheltered site in Golden Downs Forest.

FIGURE 3: Stem sinuosity in eight-year-old Douglas-fir at a moderately exposed site in Beaumont Forest.

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FIGURE 4: Stem sinuosity and leader breakage in eight-year-old Douglas-fir at a very exposed site, Gowan Hill Forest.

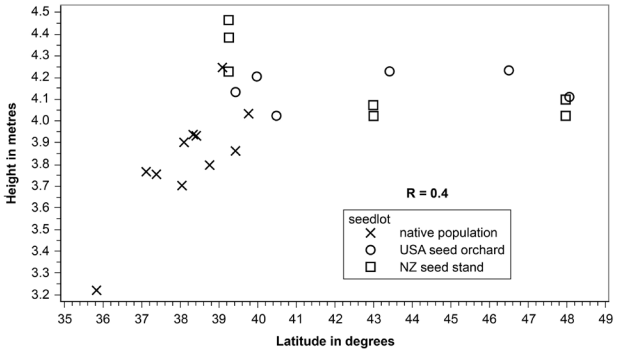

FIGURE 5: Relationship between height of Douglas-fir trees and latitude of seedlot origin. Values are Least-square means for height across all sites.

Diameter growth

Stem diameter was measured only at Waipori and Hanmer (data not shown). Provenance means for height and DBH were strongly correlated (r = 0.87) at both sites, indicating that height at age eight was a good predictor of diameter and, therefore, also volume growth.

Stem straightness

Differences (F ratio) between provenance means for stem straightness scores at individual sites other than Beaumont were not statistically significant (Table 5). At the Beaumont site, only the highest and lowest-scoring provenances differed significantly. Here the lowest mean score (4.48 for Seedlot #900) was not repeated at other sites and may have resulted from the effect of wind on long leader extensions. Trees from seedlot #808 (Los Padres, CA), which showed slowest growth at all sites (Table 4), also had the straightest stems. There was no other evidence that site or provenance latitude affected stem straightness. Excluding the Los Padres provenance, least-squares means for stem straightness (all sites, Table 8) differed by only 0.76 of a point on the 1 – 9 scoring scale. Among the New Zealand seed-stand material, seedlots of Fort Bragg, CA origin averaged 6.16; seedlots of Oregon origin averaged 6.50, and seedlots of Washington origin averaged 6.34.

Malformation

Differences (F ratio) among provenances in terms of malformation were only apparent at the Beaumont and Golden Downs sites (Table 6). At Beaumont, trees from the two New Zealand seedlots of Oregon origin (#904 and #905) had the highest score, averaging 7.3. No effect of latitude of origin on malformation was apparent in trees at Golden Downs. Tree form was much better at this low-elevation site than at the other, harsh-climate sites. Least-squares provenance means for malformation at all sites (Table 8) ranged between 6.96 (#813, Russian River, CA) and 7.64 (#904 New Zealand of Oregon origin).

Acceptability

High scores reflecting a satisfactory combination of growth rate, stem form and tree health were recorded only at Golden Downs (Table 7). Here the level of acceptability was very variable with values ranging between 0.44 for Seedlot #812 (S.P. Taylor State Park, north of San Francisco, CA), and 0.97 for the New Zealand seed stand Seedlot #900 (Fort Bragg, CA origin). Trees from the three New Zealand seedlots of Fort Bragg origin all performed well at Golden Downs. The superiority of the New Zealand ex Fort Bragg seedlots to other native or New Zealand seed-stand seedlots in this respect was probably

TABLE 9: Correlation coefficients[1] of seedlot means for pairs of seedlot traits at each site.

Traits	Gowan Hill	Beaumont	Waipori	Hanmer	Golden Downs
Height & straightness	-0.47**	-0.43*	-0.15	-0.43*	-0.28
Height & malformation	0.11	0.07	0.05	0.21	0.23
Straightness & malformation	0.18	0.27	0.05	0.12	0.22
Height & needle retention					0.41*
Malformation & needle retention					0.40*

[1] * $p \leq 0.05$, ** $p \leq 0.01$.

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TABLE 10: Correlation coefficients for seedlot means (below diagonal) and estimated genetic correlations (above diagonal) for tree height (all seedlots) at paired sites.

Site	Gowan Hill	Beaumont	Waipori	Hanmer	Golden Downs
Gowan Hill		0.90	1.03	0.77	0.18
Beaumont	0.51**		0.89	1.04	0.50
Waipori	0.70***	0.53**		0.48	0.67
Hanmer	0.47**	0.57**	0.24		0.60
Golden Downs	0.13	0.32	0.39*	0.32	

* p ≤ *0.05,* ** p ≤ *0.01,* *** p ≤ *0.001*

due to a combination of the effects of silvicultural and natural selection. There was no obvious effect of provenance latitude on acceptability score apart from the poor performance (mainly poor growth rate) of the southernmost seedlot (#808 from Los Padres, CA). Seed from this provenance also performed poorly to age four years at three sites in the concurrent progeny trial (Low et al., 2012).

Needle retention

Needle retention was assessed only at Golden Downs as this was the only site where there was apparent infection due to *Phaeocryptopus gaeumanii*. Seedlots from three of the southernmost provenances, Los Padres, CA (#808), San Francisco Water Reserve, CA (#809) and S.P. Taylor State Park, north of San Francisco, CA (#812) were found to be most severely affected by *Phaeocryptopus guaeumanii* (Table 7). There was some indication that the more northerly provenances exhibited better needle retention. The highest needle retention score overall (4.32) was recorded for Seedlot #902, collected from a second-generation stand of Washington origin in Kaingaroa Forest.

Three seed-stand seedlots of Fort Bragg, CA 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), conditions having been more conducive for *P. 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 needle cast infection but the early growth of the Golden Downs Cpt 115 seed stand was not affected by needle cast up to the time of thinning and had no selection for resistance to needle cast.

The more humid climate characteristic of both Washington and Kaingaroa Forest result in higher levels of needle cast infection in Douglas-fir stands (Hood & Kershaw, 1975). This may also have facilitated natural selection for resistance to fungal infection, when seed is collected from dominant trees in stands in these locations. A similar result was observed during comparison of needle cast in natural (US) provenances of *Pinus radiata* D.Don (radiata pine) and a seedlot of *Pinus radiata* from Kaingaroa (Burdon et al., 1992).

Effects of exposure observed in other trials

Long-term effects of elevation and exposure on Douglas-fir growth have been demonstrated in the following example. At Glendhu (elevation 650 – 720m) near Waipori, a number of forest tree species were planted in 1981 in an area of maximum exposure indicated by use of "tatter flags". Malformation in Douglas-fir was initially serious, but growth improved after canopy closure (J. T. Miller, unpublished data 1994). In the high-elevation extension of the 1959 provenance trials, the Cartwheel Hut site (elevation 600 m) near Beaumont, was planted with eight

TABLE 11: Correlation coefficients seedlot means for stem straightness (all seedlots) at paired sites.

Site	Gowan Hill	Beaumont	Waipori	Hanmer
Beaumont	0.29			
Waipori	0.28	0.39*		
Hanmer	0.20	0.50***	0.16	
Golden Downs	0.06	0.26	0.46**	0.26

* p ≤ *0.05,* ** p ≤ *0.01,* *** p ≤ *0.001*

TABLE 12: Correlation coefficients for malformation (all seedlots) at paired sites.

Site	Gowan Hill	Beaumont	Waipori	Hanmer
Beaumont	0.14			
Waipori	0.11	-0.02		
Hanmer	0.08	0.41*	0.15	
Golden Downs	0.05	0.32	-0.07	0.09

* p ≤ *0.05*

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seedlots, only one of which was of coastal origin (Darrington, WA). Although scheduled for termination at age 16 due to the negative effects of frost and wind on tree form, the trial continued to age 40. Assessment at this time showed provenance mean heights of 19 – 23 m and provenance mean DBH of 330 – 380 mm. Darrington, WA and Mendocino, CA provenances were the best performers (P. J. de la Mare, unpublished data). Douglas-fir evidently has a remarkable capacity not only for persistence but also for production of a harvestable stand on exposed sites.

The effect of tree exposure on wood properties has been noted by South Island Douglas-fir growers (P. J. de la Mare pers. comm.). Future Forests Research has commissioned a study of outerwood density and wood stiffness as estimated acoustically. Preliminary findings are that both traits are adversely affected by elevation, especially above 800 m. (S. G. Kennedy unpublished data). Kennedy also found that tree heights were shorter, trees were more tapered, branches were thicker and coarser, and stems were more sinuous.

Relationships between traits and performance at different sites

Correlation between seedlot traits at each site (Table 9) is considered to be generally a good approximation to genetic correlation. Negative correlation of tree height with stem straightness was demonstrated among seedlot means at three out of the five sites. This implies that seedlots producing smaller trees were more likely to have straighter stems. It may reflect wind damage to taller trees which sheltered those of other seedlots. At Golden Downs, tree height was positively correlated with needle retention (provenances less susceptible to needlecast tended to grow better). Malformation was positively correlated with needle retention (provenances less susceptible to needlecast tended to have a lower incidence of malformation). This result could have been affected by difficulty in assessing malformation where foliage was well retained.

Between-sites correlation of seedlot mean height was usually statistically significant and positive (r = 0.39 – 0.70; Table 10). Correlation values for relationships involving the Golden Downs site were generally lower than elsewhere. Genetic correlation estimates (Table 10) confirmed that the ranking of seedlots for height growth was very consistent across the four harsh sites. Seedlot stem straightness was sometimes significantly positively correlated between sites (Table 11). The corresponding correlation for malformation (Table 12) was only statistically significant in one case. This result was consistent with the lack of significant provenance or seedlot effects associated with this trait.

Summary

Data for early (eight-nine year) height growth, stem straightness and malformation (forking) of Douglas-fir showed strong site effects associated with exposure (strong winds and low, variable temperature). Exposure and temperature would have been related to elevation and latitude of the planting site. Trees grew almost twice as fast at Beaumont (430 m) than at Gowan Hill (630 m) even though both sites were open to harsh climatic conditions. Trees at both Gowan Hill and Beaumont had greater stem sinuosity and more malformation than those at the other three sites.

Differences in trees between seedlots in terms of height growth were detected at all four of the harsh seedlot trial sites. There was little difference in the growth performance of provenances located between mid-California (ca. 38°N) and Washington. However, these indications of the comparative performance of provenances from either Oregon or Washington are based on a small number of seedlots each represented only by 1 – 4 progenies. At the four harsh sites, trees from New Zealand seedlots of California origin (Fort Bragg, Lat. 39°15′N) grew at a similar rate to trees from the two New Zealand seedlots of southern Oregon origin (Mt. Thomas and Eyrewell) and those of Washington origin (Beaumont and Kaingaroa Cpt. 1061). At the only mild seed-source trial site (Golden Downs), trees from the three northern California provenances (Navarro River, Rockport and the Georgia Pacific Seed Orchard) grew best among the native US material, and trees from New Zealand seedlots of Fort Bragg, CA origin grew better than those from New Zealand seedlots of Oregon or Washington origin. Similar results were observed in trees aged four years at progeny trial sites which were all at relatively low elevation (Low et al., 2012).

At the four harsh sites, the effects of environment on stem straightness, malformation and acceptability were so strong as to mask any effects of provenance. No conclusive effects of provenance latitude on either stem straightness or malformation were detected among the faster-growing provenances. Only at the Beaumont site did trees from New Zealand seedlots of coastal southern Oregon origin (Mt Thomas and Eyrewell) exhibit less malformation than those of Fort Bragg CA origin, yet those of Washington origin were no better than the Fort Bragg representatives.

Conclusions

Results of this study suggest that no apparent advantage or disadvantage is attached to use of Douglas-fir planting stock of California fog-belt origin rather than stock of southern Oregon or even Washington coastal origin for higher-elevation sites

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in New Zealand. In future, clonal seed orchards will provide a variety of provenance and provenance hybrid parentages. These will offer more options for the investigation of suitability for harsh sites. For sheltered lower-elevation sites between the central North Island and Southland, improved seed from parents of coastal California and southern Oregon origin should be used in order to capitalise on proven higher growth rates.

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