

Susceptibility of Douglas-fir provenances to Swiss Needle-Cast disease in New Zealand

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NZ Douglas-fir Cooperative

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NEW ZEALAND DOUGLAS-FIR COOPERATIVE

EXECUTIVE SUMMARY

SUSCEPTIBILITY OF DOUGLAS-FIR PROVENANCES TO SWISS NEEDLE CAST DISEASE IN NEW ZEALAND

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Recent work has confirmed that Swiss needle-cast disease, caused by the needle fungus *Phaeocryptopus gaeumannii*, is responsible for substantial growth loss in many New Zealand Douglas-fir plantations. A country-wide sample of six sites of a 13-year-old New Zealand provenance trial, planted in 1959, was assessed in 1973 for infection and needle retention, at a time when the pathogen was still extending its distribution throughout the country. A wide-ranging sample of six provenances, including two best-grown coastal Californian ones and a New Zealand seedlot, were chosen for assessment. Needle retention was lower at four heavily infected North Island trial sites than at two South Island locations where infection was still only negligible or absent. Incidence of infection was high in all seedlots sampled at the North Island sites, and there was no evidence of between-provenance variation. However, foliage retention did vary significantly between provenances in these infected stands. There was much less variation in foliage retention between provenances at the two marginally or uninfected South Island sites, but rankings nevertheless appeared to follow those in the infected North Island stands. The level of variation in foliage retention in the North Island stands indicated that opportunities existed for selecting healthier seedlots from among better-grown Douglas-fir provenances, even when heavily infected.

Introduction

Swiss needle-cast disease, caused by the needle ascomycete fungus *Phaeocryptopus gaeumannii* (Rohde) Petrak, has been present in New Zealand Douglas-fir since about the mid 1950s (Hood *et al.*, 1990). Recent work has confirmed that this pathogen is responsible for a substantial loss in growth increment in a number of Douglas-fir plantations in both the North and South Islands (Knowles *et al.*, 2001). Operational control of the disease through aerial spraying and suitable silviculture has not been realised (Hood and Sandberg, 1979; Hood and van der Pas, 1979), and the best approach to managing this disease appears to be the genetic selection of populations (and individuals), that are tolerant of infection. There was some evidence in 1973 for variation in both resistance and tolerance to *P. gaeumannii* within the natural population of Douglas-fir (eg. Thulin, 1949; Merkle, 1951; Marks and Pederick, 1976; Hood, 1982; Kuus and van Dam, 1993). A sample of seedlots in a range-wide New Zealand provenance trial, including some better-grown coastal fog-belt provenances, were therefore chosen for assessment at age 13 years, in order to confirm the existence of usable provenance variation in tolerance of infection.

Material And Methods

Sampling was undertaken in a New Zealand Forest Research Institute Douglas-fir provenance trial which had been established at 19 sites throughout New Zealand in 1959 (Sweet, 1964a,b; Thulin, 1967; Wilcox, 1974). Seed for the trial came from 44 locations in Washington, Oregon, and California, and a New Zealand source was also included comprising a bulk seedlot collected from Kaingaroa Forest. The trial design was a randomised complete block, with from one to three replications of 144-tree (12 x 12 row) plots of each seedlot per site, with several seedlots missing in the site/seedlot matrix. Initial spacing was 1.8 x 1.8 m, 3100 stems per ha.

A sample of seven provenances (Table 1) was assessed in the trial at age 13 years during the 1972-73 summer in conjunction with a full assessment of all trials for growth, form, needle retention and wood properties (Wilcox 1974). A systematically-selected line of trees was felled through each plot at a total of seven sites in the North and South Islands (Table 2). On each of usually 15 trees per provenance at each site, two observers assessed a sample of foliage on a typical primary branch at the fourth whorl down from the top. Assessments were made on all four internodes along the first-order branch axis, ignoring the current season's flush, and on all three internodes along the second-order branch axis arising from the basal (third) node on the first-order branch axis. Observers varied between sites, but one (Observer 1) evaluated the trial at all but two sites. The same foliage samples were assessed independently by each observer. Precise sampling details are given in Tables 2 and 3.

Table 1: Details of provenances

Seedlot No.	Location	Latitude N	Altitude (m)
586	Pe Ell, Washington	46°45'	80
636	Deadwood, Oregon	44°06'	80
647	Mad River, California	40°55'	200-250
603	Eel River, California	40°20'	160
660	Santa Cruz, California	37°05'	330
653	Inskip, interior California	39°59'	1500
530	Kaingaroa Forest, New Zealand	-	500

Table 2: Assessors used at each site

Site		Observer number
North Island	Maramarua Forest	2
	Rapanui, near Tokoroa	1, 4
	Kaingaroa Forest	3, 8 ¹
	Patunamu Forest	1, 2
South Island	Golden Downs Forest	1, 5
	Hanmer Forest	1, 6
	Rankleburn Forest	1, 7

¹Observer 4 assessed one provenance at the Kaingaroa site

Table 3: Number of plots assessed and total number of trees assessed for each provenance at each site

Site	Provenance						
	530	586	603	636	647	653	660
Maramarua	1/15	1/15	1/15	1/15	1/15	1/14	2/15
Rapanui	3/15	1/15	1/15	1/15	3/15	1/10	3/15
Kaingaroa	3/15	0/0	2/16	1/15	2/16	0/0	2/15
Patunamu	2/15	1/15	1/15	1/15	2/15	1/8	2/15
Golden Downs	3/15	2/15	2/15	3/15	3/15	3/13	2/15
Hanmer	3/15	3/15	3/15	3/15	3/15	3/15	3/15
Rankleburn	3/15	3/15	3/15	3/15	3/15	3/15	3/15

Assessments were made of needle retention and infection by *P. gaeumannii* on each foliage age class. Percentage foliage retention was assessed on a 10% interval scale: 0.0, no foliage present; 0.1, 10% retained; 0.2, 20%;1.0, all foliage retained. To assess infection, the percentage of retained needles bearing ascocarps of *P. gaeumannii*, was estimated using a hand lens on a scale: 0, no infection; 1, 1-20% infected; 2, 21-80%; 3, 81-100% needles infected, regardless of ascocarp maturity or density.

Analyses

Analyses of variance (ANOVA) and least significant difference (LSD) tests were used to compare variation among sites and among provenances. The ANOVAs included observer, provenance and site as main effects, and the interaction between provenance and site. These terms were all fitted as fixed effects, while random effects for plot within trial and tree within plot were also included. These analyses employed the SAS procedure PROC GLM. Needle retention data were arcsin transformed before analyses. Relationships between the seven needle age class and branch order variables (first-order \times four age classes plus second order \times three age classes) were determined by performing a principal component analysis (PCA) on the arcsin transformed values.

Results

Overall mean infection scores for each site (Table 4) indicate that infection was heavy (averaging more than 80% needles infected) on all foliage at the four North Island sites, except on the youngest, one-year-old needles of both branch orders, where infection varied between sites. Infection was present at intermediate levels at Golden Downs, at trace levels at Hanmer, and was absent at Rankleburn.

Table 4: Mean needle infection score by site¹

Site	1 st order branches						2 nd order branches					
	1-year	2-year	3-year	1-year	2-year	3-year	1-year	2-year	3-year	1-year	2-year	3-year
Maramarua	3.0	a	3.0	a	3.0	a	3.0	a	3.0	a	3.0	a
Rapanui	2.5	b	3.0	a	3.0	a	2.5	b	3.0	a	3.0	a
Kaingaroa	1.8	c	3.0	a	3.0	a	1.6	c	2.8	a	3.0	a
Patunamu	2.7	ab	3.0	a	3.0	a	2.6	b	3.0	a	3.0	a
Golden Downs	1.0	d	2.4	b	2.5	b	0.6	d	2.4	b	2.5	b
Hanmer	0.0	e	0.1	c	0.1	c	0.0	e	0.1	c	0.0	c
Rankleburn	0.0	e	0.0	c	0.0	c	0.0	e	0.0	c	0.0	c

¹Values in the same column followed by the same letter do not differ significantly ($p=0.05$); values for 4-year needles are not shown because the low retention of these needles made statistical analysis impossible.

A principal component analysis of foliage retention showed that 55% of the total variation could be explained by a composite variable, with approximately even weighting across all seven measurements (Table 5). A further 29% of the variance was explained by components 2 and 3, which are principally related to foliage age. Component 2 is a contrast between year 1 and years 3 and 4, while component 3 is a contrast of years 2 and 3 against 1 and 4. Component 4, which is a contrast between branch order 1 and 2, explained only seven percent of the variation. It was thus concluded that a mean of all measurements explained a large proportion of the overall variation in foliage retention, but that a further examination of each foliage age was also warranted. However, the analysis suggested that differences between branch orders were likely to be of limited value.

Table 5: Principal component eigenvectors and percentage variance accounted for by each component

Branch order	Foliage age (years)	1	2	3	4	5	6	7
1	1	0.30	0.54	0.30	0.45	0.44	-0.34	0.08
	2	0.42	0.11	-0.29	0.56	-0.43	0.41	-0.25
	3	0.39	-0.42	-0.23	0.07	0.43	0.27	0.59
	4	0.27	-0.46	0.80	0.10	-0.25	0.01	-0.03
2	1	0.36	0.41	0.21	-0.59	0.12	0.53	-0.12
	2	0.44	0.15	-0.16	-0.31	-0.51	-0.49	0.39
	3	0.42	-0.33	-0.23	-0.17	0.30	-0.36	-0.64
% variance explained		55	20	9	7	4	3	2

This conclusion was supported by ANOVA of each of the seven needle retention measurement variables. This showed highly significant differences between provenances (Table 6). Needle retention values decreased sharply with foliage age and were higher for second- than first-order branches. However, although there appeared to be some differences in provenance performance between foliage ages, provenance relativities were very similar for first- and second-order branches within each foliage age class. Subsequent analyses were therefore carried out firstly on the overall mean retention across all seven measurement variables, and secondly on the means of each foliage age across the two branch orders.

Table 6: Mean needle retention (%) by provenance¹

Provenance	1 st order branches					2 nd order branches								
	1-year		2-year		3-year	4-year		1-year		2-year		3-year		
530 K’roa, NZ	69.0	ab	62.2	a	41.8	a	7.2	abc	93.9	a	86.9	a	64.7	a
636 Deadwood, O	75.8	a	63.9	a	42.7	a	10.7	a	94.4	a	86.6	a	64.9	a
586 Pe Ell, Wa	75.2	a	60.4	a	37.0	ab	10.0	ab	92.2	ab	84.4	a	58.5	ab
647 Mad R., Cal.	66.5	ab	48.2	b	32.6	b	5.7	abc	88.1	bc	75.1	b	54.1	b
603 Eel R., Cal.	69.3	ab	46.4	b	22.4	cd	2.8	c	88.9	bc	75.5	b	37.2	cd
660 Sta. Cruz, Cal	61.2	b	42.1	c	25.8	c	5.9	abc	84.8	cd	65.5	c	45.1	c
653 Inskip, Cal.	64.5	b	31.7	d	16.4	d	5.0	bc	78.8	d	52.1	d	29.4	d

¹Values in the same column followed by the same letter do not differ significantly ($p=0.05$)

The analysis of variance of individual-tree mean needle retention across all seven needle and branch order variables is shown in Table 7. There were highly significant differences between sites and provenances, but not for the interaction between site and provenance. There were significant differences between observers, but the interaction between observer and provenance, although statistically significant, was small compared with the other effects in the model. When analyses were conducted for separate age classes (Table 8), there were significant differences between site and provenance, for 1-year foliage, and particularly for 2- and 3-year foliage. There was a significant site \times provenance interaction for 2-year foliage (Table 8, Appendix 3).

Table 7: ANOVA for mean needle retention Across all seven measurement variables¹

	df	MS	F	p-value
Site (F)	6	0.9900	17.08	<.0001
Provenance (P)	6	0.9463	16.33	<.0001
F \times P	30	0.0754	1.30	0.19
Between Plot	54	0.0580		
Between Tree	589	0.0258		
Observer (O)	7	0.1945	78.98	<.0001
P \times O	33	0.0057	2.42	<.0001
Error	516	0.0025		

¹Site, provenance and S \times P were tested against the variance between plots, while observer and O \times P were tested against the variance within trees (the error term); an interaction between observer and site could not be included in the model because of the unbalanced assignment of observers between sites.

Table 8: ANOVA for needle retention in 1-year, 2-year and 3-year.foliage¹

	df	MS	1-year		MS	2-year		MS	3-year	
			F	p-value		F	p-value		F	p-value
Site (F)	6	0.8553	5.54	0.0002	1.1988	12.85	<.0001	4.5473	30.68	<.0001
Provenance (P)	6	0.8179	5.30	0.0002	2.1169	22.70	<.0001	2.7144	18.31	<.0001
F×P	30	0.1114	0.72	0.83	0.2584	2.77	0.0005	0.2124	1.43	0.12
Between Plot	54	0.1544			0.0933			0.1482		
Between Tree	589	0.0606			0.0612			0.0748		
Observer (O)	7	0.3065	35.42	<.0001	0.3106	42.35	<.0001	0.2989	33.28	<.0001
P×O	33	0.0123	1.42	0.064	0.0158	2.15	0.0003	0.0158	1.76	0.0063
Error	516	0.0087			0.0073			0.0090		

¹ Site, provenance and S×P were tested against the variance between plots, while observer and O×P were tested against the variance within trees (the error term). An interaction between observer and site could not be included in the model because of the unbalanced assignment of observers between sites.

Mean needle retention scores for different age classes at each site are shown in Table 9. Retention levels at the three moderate- to un-infected South Island sites were significantly greater than the corresponding means for the four heavily-infected North Island sites.

Table 9: Mean needle retention by site¹

Site	Overall		1-year foliage		2-year foliage		3-year foliage	
Hanmer	72.6	a	85.0	a	80.9	a	75.1	a
Golden Downs	60.7	b	75.6	ab	72.2	ab	61.5	b
Rankleburn	52.4	c	65.1	b	63.8	b	51.8	b
Patunamu	50.5	cd	81.8	a	63.7	b	30.6	c
Rapanui	44.6	de	75.1	ab	53.7	c	27.0	c
Maramarua	41.9	ef	84.7	a	51.9	cd	9.6	d
Kaingaroa	24.8	f	45.1	b	28.7	d	12.6	cd

¹ Values in the same column followed by the same letter do not differ significantly ($p=0.05$)

Provenances mean needle retention scores are presented separately for North Island stands, with heavy infection (Table 10), and the two southernmost South Island stands (Table 11), where infection was still negligible (overall provenance means across all sites are given in Appendix 1). In the infected North Island stands, provenances can be separated statistically into three or four groups. Provenances 636 (Deadwood, Oregon), 530 (Kaingaroa, NZ, originally from Washington) and 586 (Pe Ell, Washington.) all showed high needle retention, while 647 from Mad River and 603 from Eel River, northern coastal California were intermediate, and 660 from Santa Cruz, the southernmost coastal provenance, was slightly lower. Provenance 653, Inskip, a poorly-grown provenance from the interior Sierra Nevada, was much lower still. Provenances generally ranked similarly for different foliage ages, but there were some differences. For example, in Provenance 603, needle retention became more sharply reduced with needle age than in the other provenances (Tables 6, 10). In the better-foliated South Island stands with negligible infection, there were few significant differences between provenances (Table 11). However, means appeared to follow a similar trend to that in the North Island, and on 3-year shoots Provenances 603, and 653 retained significantly less foliage than 636 and 530.

Table 10: Mean needle retention by provenance across the four North Island sites¹

Provenance	Overall		1-year foliage		2-year foliage		3-year foliage	
636 Deadwood, Ore.	50.6	a	81.6	a	64.0	a	31.0	a
530 Kaingaroa, NZ	51.3	a	81.8	a	63.9	a	34.0	a
586 Pe Ell, Wa.	49.7	a	79.5	a	63.4	a	29.9	ab
647 Mad River, Ca.	36.0	b	65.1	b	41.8	b	18.8	b
603 Eel river, Ca.	31.6	bc	65.1	b	38.7	b	6.8	cd
660 Santa Cruz, Ca.	31.9	bc	65.0	b	35.8	b	11.2	c
653 Inskip, Ca.	25.2	c	67.4	b	18.4	c	1.9	d

¹Values in the same column followed by the same letter do not differ significantly (p=0.05)

Table 11: Mean needle retention by provenance across Rankleburn and Hanmer sites¹

Provenance	Overall		1-year foliage		2-year foliage		3-year foliage	
636 Deadwood, Ore.	68.4	a	81.6	a	76.7	a	70.3	a
530 Kaingaroa, NZ.	66.0	ab	76.4	a	74.8	a	70.4	a
586 Pe El, Wa.	63.1	ab	78.4	a	72.7	a	60.2	ab
647 Mad River, Ca/	61.6	ab	73.4	a	71.2	a	64.2	ab
603 Eel River, Ca.	58.9	ab	74.6	a	70.5	a	55.2	b
660 Santa Cruz, Ca.	58.3	b	69.7	a	68.0	a	58.9	ab
653 Inskip, Ca.	60.8	ab	79.3	a	71.8	a	54.5	b

¹Values in the same column followed by the same letter do not differ significantly (p=0.05)

The interactions for needle retention between provenance and site were not significant for 1- and 3-year foliage, but were so for age class 2 years (Table 8). The site/provenance means for each age class (Appendices 2-4) as in Tables 10, 11, show that between-provenance differences were more marked for 2- and 3-year foliage than for 1-year needles. There were slight provenance differences for different age classes at Rankleburn and Golden Downs, but not Hanmer, although the provenance rankings at all three sites appeared to be consistent with those at North Island locations. Provenance 653, deliberately-selected from the California interior and poorly grown, showed the greatest provenance defoliation in the North Island and at Golden Downs, but foliage on this seedlot was still well retained at Hanmer and Rankleburn. Provenance rankings in the four North Island sites were generally similar to one another, although there was a more pronounced difference between the highest and lowest provenances at Maramarua than at the other three sites.

Discussion

Although foliage retention and infection was subjectively scored rather than counted objectively, as has been done in previously reported studies, it is believed that the values obtained were reasonably representative of true needle retention and infection. The method used for estimating needle retention has been shown to give a reliable estimate of this variable (Hood, 1982), and the scale for infection by *Phaeocryptopus gaeumannii* was selected to leave little room for ambiguity. One observer (Observer 1) assessed at nearly all sites, in order to give uniform continuity between locations. Foliage age class was readily determined from specific branch internodes because apart from an occasional burst of easily-recognised late-season growth, Douglas-fir shoot growth is consistent, with just one internode being produced per year.

The analyses were conducted to take full advantage of all data collected from every foliage age class. However, because infected needles do not generally begin shedding until after the first year, discrimination was usually greater for the 2- and 3- year age classes than for 1-year shoots. On the other hand, at four years, shoots were generally too defoliated to show any differences. Some adjustments to the analyses were made because of unbalanced sampling of the Kaingaroa site. The two observers who assessed this stand assessed no other, and although another observer assessed one provenance at Kaingaroa, it was virtually disconnected from the rest of the study. In addition, two of the selected provenances were not assessed at Kaingaroa. Because of this, the Kaingaroa site was not included in the overall comparison between provenances, and Provenances 586 and 653 were not included in the comparison between sites. However, all data were used for assessing the interactions between site and provenance. Statistical comparisons between trials relied heavily on Observer 1, but comparisons between provenance were stronger, as the same observers were used within any given trial. The observer effect in Table 7 was due largely to one assessor (Observer 6) who consistently underestimated needle retention compared with the other observers.

The assessment reported was undertaken in 1973, at a time when *P. gaeumannii* was still extending its range on Douglas fir throughout New Zealand (Hood *et al.*, 1990). Infection was at high equilibrium levels in the North Island sites, but had still not reached Rangleburn near the southern end of the South Island, and was present at trace levels only, in Hanmer Forest in mid Canterbury. At the time of the survey, the fungus had been present in Golden Downs Forest at the northern end of the South Island for about four years, but infection levels were rapidly increasing. For this reason, it was considered better to compare provenance foliage retention rankings separately for the four infected North Island sites and the two nearly uninfected southernmost sites, even though there did appear to be some relationship between rankings between both groups. The variation in mean infection on the one-year-old foliage between the four North Island sites is probably an artifact (Table 4). When assessed, ascocarps had barely matured on this needle age class, and these disparities reflect slight differences in the stages of seasonal maturation and in assessment timing between sites during the period when the survey was undertaken.

The apparent similarity between provenance needle-retention rankings, with and without infection, despite substantially greater retention on uninfected trees, is of interest. It is possible that even under optimum growth conditions healthy, infection-free Douglas fir may vary inherently in the degree to which foliage is naturally retained. Stress due to parasitism by *P. gaeumannii*, and possibly also from other causes, may simply serve to accentuate these differences, without markedly changing rankings.

As has been previously noted (Hood, 1982), infection tends to reach a high incidence in Douglas-fir plantations throughout much of New Zealand, and this was also apparent in the data from the North Island sites in this trial. The inoculum pressures generated under the conditions of comparatively high spring rainfall that prevail in this country appear to override any intrinsic resistance, which is expressed phenotypically, only while infection is still at low incidence when a stand is first invaded (Hood *et al.*, 1990). The aim of this study was therefore to investigate variation in tolerance rather than resistance to infection, and to identify seed sources showing good foliage retention despite high infection. It is perhaps unfortunate that a greater number of provenances was not selected for this study, which would have made possible a greater depth to the analyses, providing further information of value (cf. Hood and Wilcox, 1971). However, even within this small sample of provenances it was shown that seedlots may be selected having good foliage retention, despite heavy infection, yet paradoxically, these provenances, 586, 530 and 636, all originally from Washington and Oregon, did not subsequently grow as fast as

provenances 647 and 660 from coastal California. The results of the needle retention data have yet to be explored in relation to provenance growth relativities, but it is possible that there may not be a close relationship between these two factors (cf. provenance rankings for growth provided in Knowles and Kimberley, 2001). Growth will depend on a number of variables besides needle retention, and parasitism by *P. gaeumannii* of the most productive 1-year foliage complement may be a bigger influence on growth than its effect in causing premature casting of older, less productive needles. Even the best-grown provenances may grow even better if infection can be eliminated, preventing debilitating parasitism of current and older needles.

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Appendices¹

Appendix 1: Mean needle retention by provenance, all sites

Provenance	Overall		1-year foliage		2-year foliage		3-year foliage	
636	62.8	a	85.1	a	75.2	a	53.8	a
530	60.9	a	81.4	ab	74.5	a	53.2	a
586	59.4	a	83.7	ab	72.6	a	47.8	ab
647	52.9	b	77.3	bc	61.6	b	43.2	b
603	49.1	bc	79.1	abc	60.9	b	29.8	cd
660	47.0	c	73.0	c	53.8	c	35.5	c
653	39.9	d	71.7	c	41.9	d	22.9	d

Appendix 2: Mean 1-year needle retention by site and provenance

Provenance	Site													
	Maramarua		Rapanui		Kaingaroa		Patunamu		Golden Downs		Hanmer		Rankleburn	
636	91.4	ab	86.0	ab	61.3	a	86.2	a	77.8	a	90.5	a	72.6	ab
530	92.4	a	80.5	abc	64.4	a	84.2	a	72.8	a	82.8	a	69.8	ab
586	89.8	ab	91.3	a			82.7	a	75.8	a	88.1	a	68.6	ab
647	88.1	ab	63.0	c	35.1	b	79.4	a	80.9	a	81.8	a	64.9	ab
603	79.4	ab	77.6	b	27.8	b	83.2	a	79.2	a	86.5	a	62.6	ab
660	76.7	b	68.0	c	34.5	b	78.9	a	69.2	a	84.3	a	55.1	b
653	84.9	ab	71.1	bc			71.8	a	37.7	b	84.6	a	73.9	a

Appendix 3: Mean 2-year needle retention by site and provenance

Provenance	Site													
	Maramarua		Rapanui		Kaingaroa		Patunamu		Golden Downs		Hanmer		Rankleburn	
636	82.4	a	67.8	a	35.1	ab	72.2	ab	74.8	ab	85.2	a	68.1	ab
530	85.4	a	62.0	a	40.0	a	80.9	a	68.3	b	77.7	a	71.9	a
586	75.1	a	72.0	a			65.4	abc	75.7	ab	78.5	a	66.8	ab
647	51.7	b	39.6	c	25.3	b	56.9	bc	78.1	ab	78.5	a	63.8	ab
603	26.7	c	56.6	ab	13.3	c	60.5	bc	79.6	a	80.0	a	60.9	ab
660	21.9	c	42.8	bc	21.7	bc	53.4	cd	67.5	b	80.0	a	55.9	b
653	7.3	c	31.5	c			38.3	d	29.6	c	80.0	a	63.6	ab

Appendix 4: Mean 3-year needle retention by site and provenance

Provenance	Site													
	Maramarua	Rapanui	Kaingaroa		Patunamu		Golden Downs		Hanmer		Rankleburn			
636	21.7	a	39.6	abc	12.2	ab	50.5	a	70.9	a	82.0	a	58.1	ab
530	20.7	a	39.9	ab	20.3	a	55.3	a	63.0	a	72.3	a	67.9	a
586	17.7	a	48.9	a			31.3	ab	68.6	a	71.0	a	48.9	bcd
647	14.1	ab	26.1	bcd	12.9	ab	24.4	b	66.2	a	72.4	a	55.4	abc
603	0.0	b	20.7	cd	4.2	b	19.1	bc	56.0	a	74.8	a	42.6	bcd
660	0.0	b	10.1	de	5.9	b	7.1	c	54.1	a	72.2	a	37.7	d
653	0.0	b	1.1	e			14.1	bc	15.6	b	69.5	a	39.1	cd

[†]Values in the same column followed by the same letter do not differ significantly (p=0.05)