PROVENANCE VARIATION IN THE NEW ZEALAND SPECIES OF *NOTHOFAGUS*

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SUMMARY: Provenance variation was studied in the growth and morphology of seedlings of silver beech *(Nothofagus menziesii),* red beech *(N. fusca),* hard beech *(N. truncata),* black beech *(N. solandri* var. *solandri),* and mountain beech *(N. solandri* var. *cliffortioides)*. Seedlings were grown for 2½ years in replicated provenance experiments at Rangiora and Rotorua.

Silver beech was shown to be a genetically variable species, with strong differentiation into regional ecotypes and possibly altitudinal clines. North Island provenances from lower altitudes grew the fastest and had the biggest leaves. Exceptionally small leaves, which turned a claret red in winter, were a feature of two low-elevation provenances from Westland.

Red beech seemed a comparatively uniform species, with only minor genetic variation apparent in the growth rate and appearance of seedlings from a comprehensive range of provenances. Hybridism with N. *solandri* was prevalent in several seedlots.

Hard beech was poorly represented in the study. At Rotorua, the local Mamaku Plateau provenance was the most vigorous, but was the slowest-growing at Rangiora.

In the black beech - mountain beech complex there was considerable provenance variation in the size, shape, colour, and arrangement of leaves, as well as in the branching habit and growth rate of seedlings. Clinal genetic variation in seedling growth rate was demonstrated in a series of altitudinal provenances of mountain beech from the Craigieburn Range, Canterbury. Seedlings of black beech grew faster than those of mountain beech, had a characteristic interlacing habit, with distant, orbicular leaves, and were partially deciduous in winter.

A third form of N. *solandri* was recognised, with seedlings in many ways intermediate between those of mountain beech and black beech. These undifferentiated populations of N. *solandri* occur on well-drained, low-altitude sites in the South Island. The seedlings are of erect habit, have relatively large leaves, and are among the fastest-growing of all the New Zealand beeches.

KEYWORDS: provenance; ecotype; genetic variants; morphology; growth rate; beech; Nothofagus; Fagaceae Nothofagus fusca; Nothofagus menziesii; Nothofagus truncata; Nothofagus solandri; New Zealand.

INTRODUCTION

The ecology of the beeches *(Nothofagus)* in New Zealand has been widely investigated (e.g. Cockayne, 1926; Wardle (J.), 1970a, 1970b) but genetic variation in the species has not been experimentally studied before. It is well recognised that all five beeches in the field exhibit phenotypic variation from stand to stand in tree stature and size of leaves that often seems associated with changes in site. Reduction in tree height with altitude is perhaps the most obvious example. However, the genetic component of this phenotypic variation cannot be assessed properly unless progenies from different populations are grown together and compared in common environments.

This experimental survey of the broad genetic variability in the beeches, associated with geographic origin or provenance, was undertaken primarily to give guidelines for defining zones for seed collection and transfer. Should the beeches ever be planted extensively for production forestry, the identification of superior seed sources could be of considerable practical significance. The study was also expected to reveal something about the evolution of the beeches, especially their genetic differentiation into geographic faces, ecotypes, and subspecies, as a consequence of isolation and of adaptation to different climates. It was also hoped that knowledge of provenance variation in the growth and morphology of seedlings would contribute to a better understanding of the taxonomy and ecology of the species

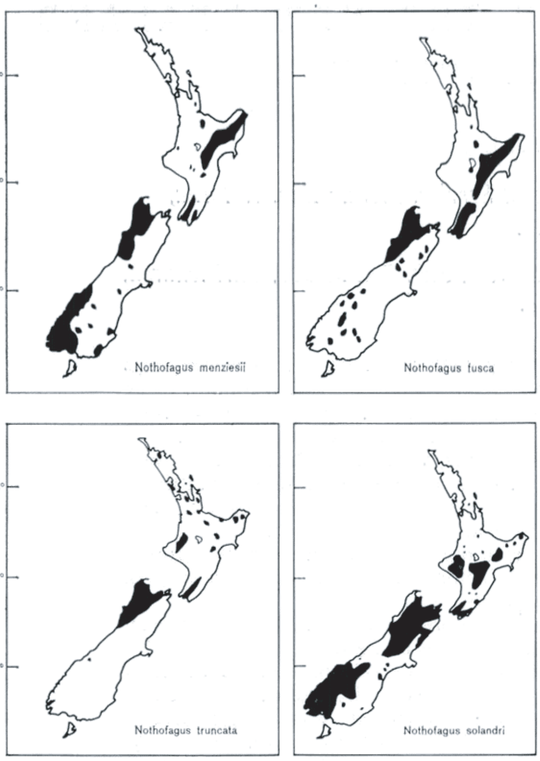

FIGURE 1. *Natural distribution of the New Zealand beeches.*

METHODS AND MATERIALS

Sampling procedure

Approximate distribution maps (Fig. 1) of silver beech *(Nothofagus menziesii* (Hook.f.) Oerst), red beech *(N. fusca* (Hook.f.) Oerst), hard beech *(N. truncata* (Col.) Ckn.), black beech *(N. solandri* (Hook.f.) Oerst. var. *solandri),* and mountain beech *(N. solandri* (Hook. f.) Oerst var. *cliffortioides* (Hook. f.) Poole) were broadly adapted from published sources (Entrican, Hinds and Reid, 1957; June, 1977; Wardle (J.), 1970a; Wardle (P), 1967). Provenances were chosen in each species to represent major areas of beech forest and to cover broadly their latitudinal and altitudinal ranges.

Specific sites for seed collection (Appendix 1) were determined variously by the whims of seed collectors, road access, and the availability of easily-collected seed crops. Except in the mountain beech forests of the Craigieburn Range, Canterbury, no seed collections were made along altitudinal transects. An average of eight (range 1-12) seed trees spaced 100 m or more apart were sampled per provenance. The seed trees were chosen only for the presence of a good crop of seed. Eighty-three seedlots were collected from 50 sites. There were 17 provenances sampled of silver beech, 27 of red beech, 3 of hard beech, 9 of black beech, and 27 of mountain beech (Fig. 2 and Appendix 1).

Seed collection

The seedlots were collected by Forest Service employees in 1979 from late February to early May. It was a good seed year for all beeches in most districts. Depending on the ripeness of the seed, and the terrain, the various methods used for collecting the seed were climbing, shooting off branches with a rifle, breaking off branches with a rope thrown up from the ground, shaking seed down on to a canvas sheet, seed traps on the ground, and sifting through leaf litter by hand on the forest floor. By far the most productive method was to work along a forest edge from a roadside or boundary with grassland, where the trees had low branches. After a suitable branch was secured with a throwing rope, the clean

FIGURE 2. *The locations at which seeds of New Zealand beeches were collected.*

seed could be readily shaken down (if ripe, and the wind not too strong) and caught on a sheet spread out beneath the tree.

Approximately equal amounts of seed from individual trees were bulked to form provenance seedlots, with the total target for each provenance being 50 g.

Nursery experiments

Nursery provenance tests were established at two *sites.*

Rotorua: Forest Research Institute nursery, Whakarewarewa. Lat. 38∞ 10'; Long. 1760 16'; Alt. 307 m; soil-friable dark loam derived from rhyolitic ash deposits. The total rainfaIl recorded over the 33-month duration of the experiment, from 1 November 1979 to 31 July 1982 was 3900 mm.

Rangiora: Forest Research Institute nursery. Lat. 43° 19'; Long. 172° 34'; Alt. 46 m; soil-stony silt-loam. Rainfall for experiment period was 1622 mm.

The seed was stratified for eight weeks under moist conditions at 4°C to break dormancy and to give uniform germination (see Bibby, 1953). The stratified seed was sown in October 1979 in seed boxes (Rangiora) or directly in the nursery (Rotorua). Seedlings were lined out into replicated experimental plots in January 1980 (Rangiora) and October 1980 (Rotorua). Individual seedlings were spaced at 30 x 30 cm.

A randomised block design was employed in each species. At Rotorua there Were four block replicates and 6 to 15 plants per provenance per plot. At Rangiora there were five block replicates with 10 to 25 plants per provenance per plot. In both nurseries several seedlots did not germinate well, resulting in shortages as well as imbalance in the numbers of seedlings in experimental plots. Poor or nil seed germination meant a few provenances had to be excluded altogether from the study, though all seedlots collected are listed in Appendix 1.

Growing conditions included fertiliser dressings to the lining-out beds, mulching with pine bark (at Rotorua) to reduce summer temperatures at the soil surface, overhead shade during the first few months afte:r lining out. and regular weeding. No root pruning or other conditioning treatments that would interfere with the free growth of the seedlings were carried out. though at Rotorua the roots were undercut after measurement!' had been completed to prepare the seedlings for planting out.

Assessment and statistical analysis

The height (cm) and basal *stem* diameter (mm) of each seedling was measured in April 1982 when the trees were 2 1/2 years old from seed germination. Analyses of variance were made for each species at each nursery, and F-tests were performed to gauge the significance of differences between provenance means. The correlation between seedling height and altitude of seed source was calculated for the altitudinal series of mountain beech provenances from the Craigieburn Range.

In June 1982 a leaf was randomly sampled from each silver beech seedling at Rotorua, and measurements taken of its length and width. Mean dimensions of the leaves were calculated for each provenance. As well, each silver beech provenance was classified as having leaves in the winter that were coloured red (R), green (G), or a mixture of red and green (R/G).

In July 1982, a lower branch was removed from a sample of ten seedlings in each provenance of black and mountain beech at Rangiora. Measurements were made of 'branchiness' (number of branches per dm of branch) and 'leafiness' (number of leaves per dm of branchlet), and provenance means calculated. Descriptions were made of the seedlings in each provenance under the categories of habit (erect or interlacing), leaf colour (green or reddish/bronze), leaf shape (triangular or oval/ orbicular), leaf arrangement (distichous / overlapping or distant), and leaf margins (rolled or flat).

Foliage specimens of most provenances were collected and lodged in the herbarium of the Forest Research Institute, Rotorua.

Measurements and descriptions of foliage were not made in red or hard beech since there were no obvious differences between provenances.

RESULTS

Silver beech

There were marked differences between some provenances in growth rate, leaf size and shape, and development of red pigmentation (presumably anthocyanin) in the winter (Table 1, 2). At Rotorua the biggest seedlings were from provenances near the lower end (550-660 m) of the species' altitudinal range in the North Island-Mamaku Plateau, Moanui (between Opotiki and Gisborne), and Karioi near Ohakune, and certain low-altitude South Island provenances- Totara Flat (north Westland), Catlins (eastern Southland), and Rowallan (western Southland). Slowest growth was shown by a high-altitude provenance (I 100 m) from the Huiarau Range in the Urewera country, and by various South Island provenances, particularly those from the Nelson region (Cobb River, Brown River, Branch River), and from certain southern localities (Pisa Range, Milford Sound, and Mid Dome).

Results at Rangiora were much the same as at Rotorua (Table 1) except that there the Mamaku and Rowallan provenances were relatively slower

TABLE 1. *Growth of* Nothofagus menziesii *provenances at Rotorua and Rangiora at age 2½ years after sowing, ranked in order of mean height at Rotorua. The average sample sizes were 49 seedlings/provenance at Rotorua and 30 seedlings/provenance at Rangiora. Significance level:* ** $P \leq 0.01$

Rank	Seedlot	Origin	Height (cm)		Basal diameter (mm)	
			Rotorua	Rangiora	Rotorua	Rangiora
1	51	Mamaku Plateau	82	94	11	12
2	54	Moanui	79	102	11	15
3	42	Totara Flat	77	97	10	13
4	49	Karioi	75	106	10	15
5	55	Rowallan	66	92	10	15
6	45	Catlins	65	106	9	15
7	57	Totara Flat	65	101	9	14
8	53	N. Kaimanawa Rg.	64	101	9	14
9	48	Golden Downs	64	-	9	-
10	44	Branch River	63	-	9	-
11	52	Mt Te Aroha	58	93	8	13
12	40	Mid Dome	56	85	8	13
13	56	Milford Sound	56	79	7	12
14	46	Huiarau Range	53	84	9	14
15	43	Brown River	50	-	7	-
16	50	Pisa Range	49	75	8	12
17	41	Cobb River	42	73	7	12
	General Mean		63	92	9	14
	Least significant difference (.05)		9	9	2	1
	F-test (seedlots)		12.15**	7.54**	3.97**	3.36**

TABLE 2. *Leaf characteristics of* Nothofagus menziesii *provenances assessed on 2½ year-old seedlings ranked* in *order of leaf length at Rotorua. Winter leaf colour: R=red, G=green, RIG= mixture of red and green seedlings.*

Rank	Seedlot	Origin	Length (mm)		Width (mm)		Winter leaf colour
			Rotorua	Rangiora	Rotorua	Rangiora	
1	51	Mamaku Plateau	17	12	14	11	R/G
2	49	Karioi	16	12	14	12	R/G
3	54	Moanui	16	12	14	11	R/G
4	52	Mt Te Aroha	14	11	12	11	R/G
5	44	Branch River	13	-	11	-	G
6	53	N. Kaimanawa Rg.	13	10	11	10	R/G
7	48	Golden Downs	12	-	11	-	R/G
8	43	Brown River	12	10	10	10	R/G
9	46	Huiarau Range	12	10	10	10	R/G
10	45	Catlins	11	10	11	10	R/G
11	40	Mid Dome	11	10	11	10	G
12	56	Milford Sound	11	10	9	9	G
13	50	Pisa Range	11	10	10	9	R/G
14	55	Rowallan	11	10	10	10	R/G
15	41	Cobb River	10	9	10	10	R/G
16	57	Totara Flat	9	9	8	9	R
17	42	Totara Flat	9	8	8	8	R
	General Mean		12	10	11	10	
	Least significant difference (.05)		1	1	1	1	

growing, and the Catlins provenance relatively faster growing. There is thus a suggestion that provenance x site interaction might be important in this species. Provenance variation was pronounced in the length, width, and length/width ratio of seedling leaves (Table 2). Four of the northernmost provenances-Mamaku Plateau, Moanui, Mt Te Arona (extreme northern limit of species), and Karioi-had the biggest leaves at both nurseries (only by inspection at Rangiora).

The Mamaku Plateau provenance had exceptionally big leaves for silver beech. At Rotorua its mean dimensions were 17 x 14 mm, with individual leaves not uncommonly exceeding 20 mm in length. The longest (28 mm) and widest (20 mm) individual leaves recorded on silver beech seedlings in the study were from this provenance. Very small leaves were characteristic of provenances from Totara Flat and Cobb River, the lowest mean dimensions being 9 x 8 mm at Rotorua and 8 x 8 mm at Rangiora in a Totara Flat seedlot (Fig. 3). Average leaf size was greater at Rotorua (12 x 11 mm) than at Rangiora (10 x 10 mm), though correlations of provenance means between the two nurseries were very high for length ($r = 0.96$) and width ($r = 0.88$).

At Rotorua, the most elongated leaves were possessed by the provenances from Milford Sound (L/W = 1.27), Mamaku Plateau (1.21), and north Kaimanawa Range (1.17). Provenances with the most

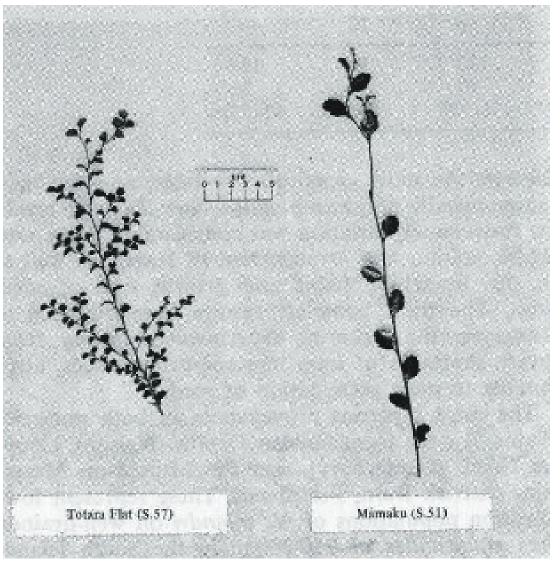

FIGURE 3. *Seedling leaves of two contrasting provenances of silver beech,* Nothofagus menziesii.

orbicular leaves at Rotorua were Rowallan (1.05), Pisa Range (1.06), Catlins (1.06), and Mid Dome (1.07). Similar trends in leaf shape were evident at Rangiora, though differences between provenances there were less. Leaves were generally less elongate at Rangiora than at Rotorua.

The seedlings experienced a series of severe ground frosts to -8ºC at both nurseries in July 1982, but without significant damage to foliage in any of the provenances. However, an apparent striking reaction to winter cold was that all the leaves on some seedlings turned a deep claret red, presumably due to development of anthocyanins. Other seedlings reo mained a normal green colour. Most provenances were polymorphic, containing a mixture of green and red seedlings. However, three provenances-Branch River, Mid Dome, and Milford Sound-had almost 100% green seedlings, while the two Totara Flat seedlots had almost 100% red seedlings. The Totara Flat seedlings, with their very small, deeply-toothed, red leaves, were especially noticeable in the Rotorua nursery and appealed as a possible commercial horticultural cultivar for use by florists.

Red beech

Red beech proved to be a comparatively uniform species, with only minor genetic variation apparent between provenances in the growth rate and appearance of seedlings from a considerable range of latitudes and altitudes. Differences between provenances in height growth were neither strong within nurseries nor consistent between nurseries. One exception was the Mamaku Plateau provenance which was among the leaders in both nurseries (Table 3). Much of the variation in height growth of red beech in this study seemed to arise from provenance x site interaction, expressed in erratic fluctuations in the rank of provenances between the two nurseries (Table 3).

Few provenances looked distinctive in the nursery. The Mt Grey and Eglinton Valley provenances had somewhat larger leaves than most and remained a vivid green colour before turning bronze in midwinter, Most other provenances assumed a reddish colour during the winter months.

Hybridism with *N. solandri* was prevalent in several provenances of red beech (see Cockayne, 1926), even though all seed trees sampled were positively identified as typical red beech. The greatest incidence of hybrids occurred in the provenances from the Branch River, Mt Grey, Panekirikiri (near Lake Waikaremoana), and Kaimanawa Range. Hybrid seedlings were easily distinguished from red beech by their smaller, often toothless leaves. Hybrid vigour was not apparent, though no detailed study was made of the performance of hybrid seedlings.

TABLE 3. *Growth of* Nothofagus fusca *provenances at Rotorua and Rangiora at age 2 1/2 years after sowing ranked in order of mean height at Rotorua. The last Jour seedlots listed are unranked because of inadequate seedling numbers. Average sample sizes were* 38 *seedlings/provenance at Rotorua and* 29 *seedlings/provenance at Rangiora. Significance level:* *p≤0. 05, **p ≤ 0.01.

Rank	Seedlot	Origin	Height (cm)		Basal diameter (mm)	
			Rotorua	Rangiora	Rotorua	Rangiora
1	33	Mamaku Plateau	93	135	12	18
2	18	Moanui	90	116	11	15
3	20	Mawhera	90	122	10	17
4	39	Kaweka Range	87	128	10	16
5	32	Karioi	85	115	10	15
6	13	Cobb River	84	-	10	-
7	31	Golden Downs	83	124	11	17
8	28	Kaimanawa Range	83	127	10	16
9	14	Kaweka Range	83	123	10	15
10	15	Kaweka Range	82	114	10	17
11	21	Marui	82	117	10	16
12	22	Banks Peninsula	82	-	11	-
13	16	Branch River	82	114	11	16
14	30	Big Bush	82	121	11	16
15	24	Lake Sumner	80	124	10	17
16	25	Eglinton Valley	80	125	10	17
17	19	Brown River	80	118	10	18
18	27	Garvie Mountains	80	-	11	-
19	23	Panekirikiri	79	-	10	-
20	29	Rahu Saddle	76	122	9	16
21	17	Mt Grey	76	120	10	16
22	26	Eglinton Valley	74	120	9	18
-	34	Mt Te Aroha	99	103	10	14
-	36	Tararua Range	95	-	14	-
-	37	Kaimanawa Range	80	138	9	17
-	38	Gwavas	86	-	12	-
		General Mean	82	122	10	16
		Least significant difference	9	10	2	2
		F-test (seedlots)	2.27**	1.75*	1.42ns	1.27ns

Hard beech

No conclusive results were obtained on provenance variation in hard beech because not enough provenances were sampled, and too few seedlings were grown owing to poor germination of seeds. The Mamaku Plateau provenance was clearly the fastest-growing lot at Rotorua (Table 4), but was much slower growing at Rangiora than provenances from north Westland. Seedlings of all provenances suffered damage at Rotorua and Rangiora from winter frosts. The seedling leaves in hard beech are flat, and readily distinguishable from the leaves of red beech, which have undulating margins. Some seedlings in each provenance of hard beech tested turned an impressive red colour in winter.

Black beech and mountain beech

This complex constitutes the most ecologically diverse, the most genetically variable, and the most taxonomically perplexing of the New Zealand beeches. Provenance variation was considerable in the size, shape, colour, and arrangement of leaves, as well as in the branching habit and growth rate of seedlings. The most complete results were obtained at Rangiora, the Rotorua experiment suffering from severe shortages of trees in some provenances, attributable to poor germination of seed.

The most vigorous provenances in both nurseries (Table 5) were from Golden Downs (Nelson), Coopers Creek (Canterbury), and the Murchison Mountains (Ettrick Burn, Fiordland). These represent low-elevation populations of *N. solandri;* on well-drained sites at altitudes of 250-300 m in the South Island. Slowest growth was shown by montane and subalpine provenances such as those sampled from the Craigieburn Range (Canterbury), Lake Ohau, and

TABLE 4. *Growth of* Nothofagus truncata *provenances at Rotorua and Rangiora at age* 21 *years after sowing ranked in order of mean height at Rotorua.*

Rank	Seedlot	Origin	Height (cm)		Basal diameter (mm)	
			Rotorua	Rangiora	Rotorua	Rangiora
1	10	Mamaku Plateau	82	35	10	8
2	11	Garvey Creek	65	64	7	11
3	12	Ahaura	64	101	5	15

TABLE 5. *Growth of* Nothofagus solandri *provenances at Rangiora and Rotorua at age* 2 1⁄2 *years after sowing ranked in order of mean height at Rangiora. The last four seedlots listed are unranked since they were not present at Rangiora. Average sample sizes were 21 seedlings/provenance at Rotorua and 42 seedlings/provenance at Rangiora. Variety B=black beech (var.* solandri); *M=mountain beech (var.* cliffortioides); *B* & *M=a mixture of both varieties; U=undifferentiated* N. solandri.
Significance level: ** P≤0.01

Rank	Seedlot	Variety	Origin	Height (cm)		Basal diameter (mm)	
				Rotorua	Rangiora	Rotorua	Rangiora
1	8	U	Golden Downs	95	146	12	20
2	6	U	Coopers Creek	83	143	10	19
3	5	U	Branch River	71	136	9	19
4	61	U	Murchison Mts	90	136	13	19
5	2	U	Hundalee Hills	77	134	9	17
6	64	U	Rowallan	-	127	-	17
7	9	B	Gwavas	-	125	-	16
8	4	B	Panekirikiri	88	118	10	15
9	77	B & M	Desert Road	70	118	8	17
10	71	M	Lake Ohau	54	106	7	16
11	59B	M	Craigieburn Range	-	103	-	16
12	75	M	Craigieburn Range	38	100	7	16
13	67	M	Mavora Lakes	78	98	10	15
14	65	M	Harper River	-	96	-	16
15	59A	M	Craigieburn Range	-	95	-	16
16	68A	M	Craigieburn Range	35	86	7	15
17	66	M	Craigieburn Range	76	84	8	14
18	78	M	Ada Pass	-	75	-	13
19	68C	M	Craigieburn Range	30	75	5	13
20	68D	M	Craigieburn Range	-	72	-	14
21	80	M	Totara Flat	-	67	-	10
22	73	M	Craigieburn Range	66	66	10	14
-	70	M	Eyre Mts	77	-	10	-
-	76	M	Karioi	67	-	7	-
-	7	B	Rai Valley	84	-	9	-
-	3	U	Mt Grey	78	-	9	-
			General mean	68	105	9	16
			LSD	12	9	3	2
			F-test, lots	9. 86**	15.53**	3.54**	6.76**

Ada Pass, and by a low-elevation provenance from a poorly drained site at Totara Flat in the Grey Valley, Westland. All these slower-growing provenances were typical mountain beech. Of intermediate vigour were typical black beech provenance~ such as those from Panekirikiri and Gwavas (Hawkes Bay), and Rai Valley (Nelson).

Based on the size, shape, colour, and arrangement of the seedling leaves, and on the branching habit and vigour of the seedlings, the provenances could be broadly classified into three groups.

Group 1. "Mountain beech": Erect habit, leaves green, triangular in shape with rolled margins, overlapping in a close, distichous arrangement, giving

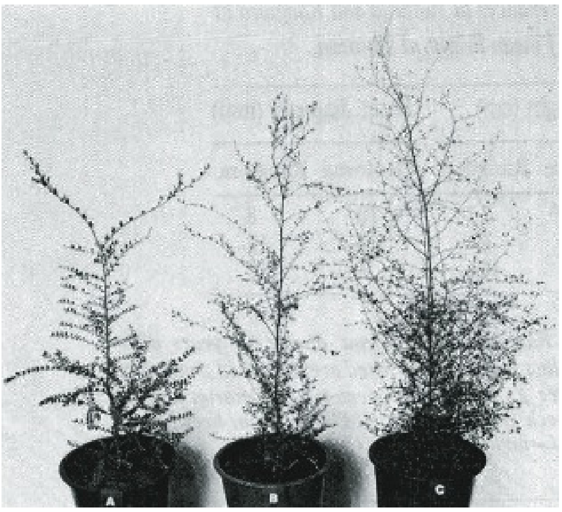

FIGURE 4. *Seedlings of the three forms of* Nothofagus solandri: *A-mountain beech (var.* cliffortioides), *Mavora Lakes (Lot* 67); *B-undifferentiated* N. solandri: *A-mountain beech (var.* cliffortioides), *(var.* solandri), *Panekirikiri (Lot* 4).

the branches a flattened appearance. Relatively slow growth rate (see Table 5). Typically 16 branchlets per dm of branch, and 60 leaves per dm of branchlet.

Examples: Karioi (Mt Ruapehu), Douglas Range (NW Nelson), Craigieburn Range (Canterbury), Mavora Lakes (Southland). Usually at high altitudes (e.g. 800 - 1300 m) on mountain sides, or at lower altitudes on poorly drained-sites (e.g., 200 m at Totara Flat).

Group 2. "Black beech": Interlacing habit, with tendency to zig-zag, tangled branching. Partially deciduous. Leaves bronze or reddish (in winter), oval or orbicular in shape, flat, distant on the branchlets. Moderate to fast growth rate. Typically 6 branchlets per dm of branch and 15 leaves per dm of branchlet.

Examples: Panekirikiri (Lake Waikaremoana), Gwavas (Hawkes Bay), Bainham (NW Nelson), Rai Valley (Nelson). Usually at low altitudes (e.g. 100-600 m), and commonly on ridges and spurs.

Group 3. Undifferentiated *N. solandri:* Erect habit, but with some tendency for lower branches to be interlaced. Leaves mainly green, oval, apiculate, flat, and usually of large size. Rapid height growth. Typically 10 branchlets per dm of branch and 30 leaves per dm of branchlet. Not distichous.

Examples: Golden Downs (Motueka Valley), Coopers Creek (Canterbury), Mt Grey (Canterbury), Murchison Mountains (Fiordland), Rowallan (Tuatap ere, western Southland), and Branch River (Nelson). Sites more mesic' than those typical of "mountain beech" and "black beech". These fast-growing, low-altitude provenances of *N. solandri* with erect seedlings were classified by seed collectors variously as var. *solandri* or var. *cliffortioides*. They do not fit readily into either, although as a group they are perhaps more like black beech than mountain beech. The adult trees in these populations are often large and of good form, and their identity has long been baffling (e.g., Poole, 1958; Wardle, (J.), 1970a).

Seedlings from each of the three groups are illustrated in Figure 4, and seedling foliage of typical mountain and black beech is contrasted in Figure 5.

Altitudinal provenances of mountain beech from the Craigieburn Range, Canterbury, showed a strong clinal variation in the height growth of seedlings at Rangiora, with a correlation of -0.85 between height of seedlings and altitude of seed source (Fig. 6). Thus the altitudinal gradient in the size of adult trees evident in the field is likely to have a strong genetic component. A phenotypic cline in the cold-hardiness of mountain beech has been demonstrated by Sakai and Wardle (1978).

General comparison of the species

The height growth of all species was greater at Rangiora than at Rotorua though Rangiora had by far the lower rainfall. We think that transplanting

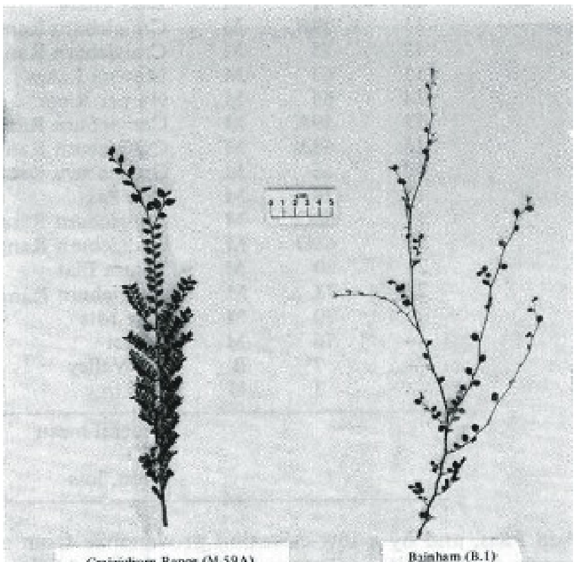

FIGURE 5. *Seedling leaves of typical mountain beech.* N. solandri *var.* cliffortioides *(left) and black beech,* N. solandri *var.* solandri *(right).*

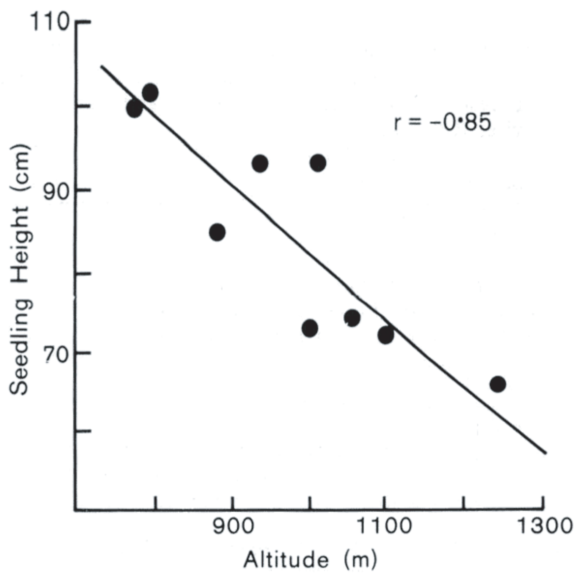

FIGURE 6. *Plot of seedling height versus altitude of seed source in altitudinal provenances of mountain beech from the Craigieburn Range, Canterbury. Seedlings were grown and assessed in a common-garden experiment at Rangiora.*

shock occasioned by delaying the lining-out until October caused the trees to grow less well at Rotorua. Differences between species, based on the tallest provenance, were similar at the two nurseries. The tallest individual seedlot was No.8, a provenance of undifferentiated *N. solandri* from Golden Downs, Nelson. Red beech generally grew taller than either silver beech or hard beech, and was faster growing than most mountain beech.

DISCUSSION AND CONCLUSIONS

Results of a genetic survey like this can be misinterpreted because of critical gaps in the provenance sampling. In *N. solandri,* several important populations in the North Island were missed, notably those from eastern Taranaki, and from the main axial ranges (Wardle (1.), 1970a, 1970b). Furthermore, no seedlots were collected from isolated northern occurrences of black beech such as the small stand on the Mamaku Plateau near Rotorua, or the population recently discovered by employees of the Wildlife Service on a remote ridge top of Little Barrier Island (E. Cameron, pers. comm.). Thus, it is not known if the interlacing bronze-leaved habit typical of black beech seedlings from east of the main ranges also occurs in the extensive Taranaki populations, and northern outliers. Nor is it known if undifferentiated *N. solandri* occurs in the North Island. Though generally noncommittal about these intermediate populations, we have been struck by their resemblance in some features to *N. fusca*. Perhaps they are ancient, stable, *N. solandri* x *N. fusca* hybrids, now occupying sites between mountain beech and red beech. Genetic studies with isozymes could be rewarding in checking this hypothesis.

Our survey of *N. solandri* was too incomplete for us to reach any firm conclusions on the taxonomic status and genetic affinities of the three forms. We can say, however, that *N. solandri* exhibits considerable genetic variation due to provenance. Provenance samples from transects which encompass the *full* altitudinal range of *N. solandri* within a region should be given high priority in any future genecological studies in this species.

An adequate coverage of provenances was obtained in red beech. The results suggest that, in keeping with its rather narrow ecological range, this species has only weakly evolved into genetically distinct populations. There were no consistent trends in growth rates of provenances, regardless of altitude or latitude, and it was not possible to firmly categorise provenances by leaf colour or size. However, variation *within* provenances in the nursery plots of this species was perhaps more evident than in the other beeches.

Only a token sample was obtained of hard beech, with correspondingly inconclusive results. Nevertheless, on seedling morphology and frost hardiness, there was no doubt from the three provenances studied that hard beech is distinct from red beech.

Except for the Tararua Range, a broad geographic coverage of provenances was sampled in silver beech. The species has a wide altitudinal and latitudinal range, and grows on a variety of soils (Wardle, (P.), 1967). In accordance with its considerable ecological tolerances, it was shown in this study to be a genetically variable species, as reflected in seedling growth and morphology. Differentiation into altitudinal races was apparent, although no systematic altitudinal transect of provenances was studied in any locality. Some North Island provenances had very large seedling leaves, but there was no evidence in any seedlot of hybridisation with other beech species (also see Cockayne, 1926).

Genetic differences between provenances of forest tree species are often most evident in seedlings. Thus, the genecological results presented here from seedling tests should be valid and useful.

The study thus far has limited direct application to the planting of beech for forest regeneration. Neither nursery site was in a region where beech forests are now managed for wood production, and the practical importance of apparent provenance x nursery interactions, especially in red beech, is therefore difficult to gauge. In addition, differences between provenances in growth rate can be expected to be associated with differences in adaptive traits such as tolerance of drought or frost, though no opportunity arose in this study to examine this aspect.

A field test of a range of provenances in each species was planted in the Whakarewarewa State Forest Park in September 1982 for long-term observation and assessment of provenance variation. Unfortunately, no field tests were established in important beech management areas such as western Southland, and the Reef ton district (Kirkland, 1973).

In planting or seeding programmes with the beeches, we advise using local provenances wherever possible. This will minimise the risk of planting trees ill-adapted to the site, and will avoid indiscriminate mixing of provenances from different ecological regions. It is suggested that the recently-instituted series of ecological districts in New Zealand (Simpson, 1982) could be a useful basis for limiting and controlling the transfer of genetic material in *Nothofagus*.

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APPENDIX 1

Details of Nothofagus *seedlots*

Code	Seedlot	Provenance	Collection site	Conservancy	Latitude (S)	Longitude (E)	Altitude (m)	Seed trees
			I BLACK BEECH					
1	9/0/79/582	Bainham	15 Mile Creek	Nelson	40° 49′	172° 31′	180	2
2	9/0/79/542	Hundalee Hills	Hundalee Hills	Canterbury	42° 50′	173° 20′	200	8
3	9/0/79/555	Mt Grey	J. Elder	Canterbury	43° 05′	172° 32′	325	9
4	9/0/79/554	Panekirikiri	Panekirikiri State Forest	Rotorua	38° 50′	177° 04′	600	6
5	9/0/79/545	Branch River	May's Creek, Leatham S.F.	Nelson	41° 47′	173° 07′	520	10
6	9/0/79/553	Coopers Creek	Oxford S.F.	Canterbury	43° 16′	172° 04′	300	8
7	9/0/79/556	Rai Valley	Collins Valley, Compartment 21, Rai S.F.	Nelson	41° 11′	173° 33′	120	4
8	9/0/79/552	Golden Downs	Pretty Bridge area, Cpt. 154, Golden Downs S.F.	Nelson	41° 25′	172° 55′	240	8
9	3/0/79/023	Gwavas	Compartment 113, Gwavas S.F.	Wellington	39° 43′	176° 17′	520	10
			II HARD BEECH					
10	9/0/79/2336	Mamaku Plateau	Mamaku S.F., Utuhina Stream, Mangorewa S.F.	Rotorua	38° 00′	176° 00′	500	6
11	9/0/79/616	Garvey Creek	Waitahu S.F.	Westland	42° 10′	171° 57′	520	4
12	5/0/79/008	Ahaura	Ahaura, Kopara Rd	Westland	42° 23′	171° 40′	180	10
			III RED BEECH					
13	9/0/79/584	Cobb River	North-West Nelson State Forest Park	Nelson	41° 08′	172° 37′	820	6
14	9/0/79/579	Kaweka Range	Kaweka S.F. Park	Wellington	39° 17′	176° 27′	730	6
15	9/0/79/574	Kaweka Range	Makahu Saddle	Wellington	39° 17′	176° 23′	1050	10
16	9/0/79/547	Branch River	May's Creek, Leatham S.F.	Nelson	41° 47′	173° 07′	520	10
17	9/0/79/587	Mt Grey	J. Elder	Canterbury	43° 05′	172° 32′	335	2
18	9/0/79/573	Moanui	Moanui S.F.	Rotorua	38° 25′	177° 25′	600	10
19	9/0/79/580	Brown River	North-West Nelson State Forest Park	Nelson	40°51′	172° 27′	120	3
20	9/0/79/588	Mawhera	Kangaroo Creek, Mawhera S.F.	Westland	42° 27′	171° 31′	150	8
21	9/0/79/589	Maruia	Station Creek, Maruia S.F.	Westland	42°12′	172° 15′	400	10
22	9/0/79/572	Banks Peninsula	Armstrong Reserve, Akaroa	Canterbury	43° 50′	173° 00′	600	5
23	9/0/79/591	Panekirikiri	Panekirikiri S.F.	Rotorua	38° 51′	177° 04′	600	9
24	9/0/79/598	Lake Sumner	Hurunui, Lake Sumner State Forest Park	Canterbury	42° 42′	172° 07′	580	8
25	9/0/79/570	Eglinton Valley	Te Anau – Milford Road, Fiordland National Park	Southland	45° 06′	167° 57′	290	9
26	9/0/79/601	Eglinton Valley	Te Anau – Milford Road, Fiordland National Park	Southland	45° 06′	167° 57′	290	10
27	9/0/79/602	Garvie Mountains	Waikaia S.F.	Southland	45° 33′	169° 02′	210	9

APPENDIX 1 (*continued*)

Code	Seedlot	Provenance	Collection site	Conservancy	Latitude (S)	Longitude (E)	Altitude (m)	Seed trees
29	9/0/79/2333	Kaimanawa Range	Access Roads 10 and 13, Kaimanawa S.F. Park	Wellington	39° 09′	175° 49′	800	11
29	9/0/79/569	Rahu Saddle	Waitahu S.F.	Westland	42° 11′	171° 56′	275	8
30	9/0/79/600	Big Bush	Tophouse, Big Bush S.F.	Nelson	41° 46′	172° 56′	750	10
31	9/0/79/603	Golden Downs	Golden Downs S.F.	Nelson	41° 31′	172° 51′	460	7
32	9/0/79/2332	Karioi	Karioi–Rangataua, near Ohakune	Wellington	39° 09′	175° 31′	660	11
33	9/0/79/2331	Mamaku	Airstrip Road, Mamaku S.F.	Rotorua	38° 01′	176° 06′	550	11
34	9/0/79/2330	Mt Te Aroha	Mt Te Aroha, Coromandel S.F. Park	Auckland	37° 32′	175° 45′	900	3
35	3/0/79/082	Tararua Range	Kiriwhakapapa, Tararua S.F. Park	Wellington	40° 49′	175° 33′	335	10
36	3/0/79/078	Tararua Range	Holdsworth, Tararua S.F. Park	Wellington	40° 54′	175° 26′	335	10
37	3/0/79/043	Kaimanawa Range	Kaimanawa S.F. Park	Wellington	39° 09′	175° 49′	750	10
38	3/0/79/021	Gwavas	Gwavas S.F.	Wellington	39° 43′	176° 17′	520	10
39	3/0/79/022	Kaweka Range	Kaweka S.F. Park	Wellington	39° 17′	176° 23′	730	10
			IV SILVER BEECH					
40	9/0/79/490	Mid Dome	Mid Dome	Southland	45° 35′	168° 32′	550	6
41	9/0/79/585	Cobb River	Lake Sylvester ,North-West Nelson S.F. Park	Nelson	41° 06′	172° 41′	800	8
42	9/0/79/541	Totara Flat	Caledonian Creek, Paparoa S.F.	Westland	42° 19′	171° 30′	60	7
43	9/0/79/581	Brown River	North-West Nelson S.F. Park	Nelson	40°51′	172° 27′	120	3
44	9/0/79/548	Branch River	May's Creek, Leatham S.F.	Nelson	41° 47′	173° 07′	550	3
45	9/0/79/599	Catlins	Catlins S.F. Park	Southland	46° 26′	169° 27′	300	10
46	9/0/79/2385	Huiarau Range	Maungapohatu Road, Urewera National Park	Rotorua	38° 37′	177° 04′	1100	12
48	9/0/79/604	Golden Downs	Cpts. 110, 112 Golden Downs S.F.	Nelson	41° 31′	172° 51′	460	8
49	9/0/79/2328	Karioi	Karioi—Rangataua, near Ohakune	Wellington	39° 29′	175° 31′	660	12
50	9/0/79/559	Pisa Range	Luggate Creek	Southland	44° 47′	169° 10′	800	5
51	9/0/79/2327	Mamaku Plateau	Airstrip Road, Mamaku S.F.	Rotorua	38° 01′	176° 06′	550	11
52	9/0/79/2326	Mt Te Aroha	Summit of Mt Te Aroha, Coromandel S.F. Park	Auckland	37° 32′	175° 45′	930	8
53	9/0/79/2329	Northern Kaimanawa Range	Clements Road, Kaimanawa S.F. Park	Wellington	38° 57′	176° 12′	730	5
54	9/0/79/619	Moanui	Moanui S.F.	Rotorua	38° 25′	177° 25′	600	9
55	9/0/79/557	Rowallan	Rowallan S.F.	Southland	46° 01′	167° 36′	220	11
56	9/0/79/620	Milford Sound	Milford Sound, Fiordland N.P.	Southland	44° 41′	167° 57′	20	10
57	5/0/79/006	Totara Flat	B. Kennedy, Totara Flat	Westland	42° 17′	171° 35′	90	10

			V MOUNTAIN BEECH					
58	9/0/79/578	Ruahine Range	Ruahine Hut, Ruahine S.F. Park	Wellington	39° 33′	176° 19′	940	11
59A	9/0/79/586a	Craigieburn Range	Hut Creek, Carigieburn S.F. Park	Canterbury	43° 09′	171° 43′	950	5
59B	9/0/79/586b	Craigieburn Range	Lyndon Hut, Craigieburn S.F. Park	Canterbury	43° 09′	171° 44′	800	2
60	9/0/79/583	Cobb River	North-West Nelson S.F. Park	Nelson	41° 08′	172° 38′	820	8
61	9/0/79/575	Murchison Mountains	Ettrick Burn, Fiordland N.P.	Southland	45° 16′	167° 43′	250	8
62	9/0/79/568	Lake Chalice	Richmond Range	Nelson	41° 34′	173° 20′	1100	9
63	9/0/79/567	Beebys Range	Mt Richmond S.F. Park	Nelson	41° 41′	172° 56′	1310	10
64	9/0/79/566	Rowallan	Elder Road, Rowallan S.F.	Southland	46° 05′	167° 36′	220	9
65	9/0/79/565	Harper River	Harper–Avoca S.F.	Canterbury	43° 10′	171° 35′	880	9
66	9/0/79/564	Craigieburn Range	Headquarters, Craigieburn S.F. Park	Canterbury	43° 09′	171° 43′	880	2
67	9/0/79/563	Mavora Lakes	Lands and Survey Dept. Picnic Area, Mavora Lakes	Southland	45° 17′	168° 12′	680	8
68A	9/0/79/562a	Craigieburn Range	Lower Car Park, Craigieburn S.F. Park	Canterbury	43° 08′	171° 41′	1000	3
68B	9/0/79/562b	Craigieburn Range	Lower Car Park, Craigieburn S.F. Park	Canterbury	43° 08′	171° 41′	1020	2
68C	9/0/79/562c	Craigieburn Range	Lower Car Park, Craigieburn S.F. Park	Canterbury	43° 08′	171° 41′	1080	3
68D	9/0/79/562d	Craigieburn Range	Lower Car Park Craigieburn S.F. Park	Canterbury	43° 08′	171° 41′	1100	1
69	9/0/79/546	Raglan Range	Raglan Range	Nelson	41° 46′	173° 04′	1340	10
70	9/0/79/530	Eyre Mountains	Mt Bee Road, Irthing River	Southland	45° 33′	168° 25′	330	90
71	9/0/79/561	Lake Ohau	"Nordy's Crib", along stream	Southland	44° 16′	169° 49′	550	10
72	9/0/79/489	Mid Dome	Creek from Red Duster	Southland	45° 35′	168° 32′	550	1
73	9/0/79/560	Craigieburn Range	Camp Stream, Craigieburn S.F. Park	Canterbury	43° 07′	171° 42′	1250	9
74	9/0/79/590	Douglas Range	Adelaide Tarn, North-West Nelson S.F. Park	Nelson	40° 56′	172° 33′	1220	1
75	9/0/79/597	Craigieburn Range	Enys Flat, Craigieburn S.F. Park	Canterbury	43° 12′	171° 43′	770	12
76	9/0/79/2334	Karioi	Karioi S.F.	Wellington	39° 22′	175° 35′	1100	12
77	9/0/79/2335	Desert Road	Tongariro National Park	Wellington	39° 10′	175° 46′	760	10
78	9/0/79/624	Ada Pass	Ada Pass, Maruia S.F.	Westland	42° 18′	172° 28′	980	1
79	4/0/79/027	Reefton	D. Cross	Westland	42° 07′	171° 51′	240	10
80	5/0/79/007	Totara Flat	Ahaura Sawmill	Westland	42° 23′	171° 39′	330	10