GENETIC SURVEY OF *PINUS RADIATA*. 2: POPULATION COMPARISONS FOR GROWTH RATE, DISEASE RESISTANCE, AND MORPHOLOGY

R.D.BURDON, M.H.BANNISTER*, and C.B.LOW

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

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ABSTRACT

Pinus radiata D.Don provenances (populations) were compared to age 12 years on two contrasting sites in Kaingaroa Forest in the central North Island of New Zealand. Differences between populations were detected in most traits, including growth rate, tree-form variables, other morphological traits, and susceptibility to fungal diseases, but variation in economic traits overlapped strongly among almost all populations.

The Californian mainland populations (Año Nuevo, Monterey, and Cambria) showed very similar growth, although for diameter Monterey had evidently begun to draw ahead and Cambria to fall behind. Trees of the Guadalupe Island population were on average about 10% shorter than Monterey; Cedros Island averaged about 30% shorter, and could not compete. The New Zealand populations (Kaingaroa and Nelson) grew more uniformly and averaged about 10% taller and 20% greater diameter than Monterey; Kaingaroa slightly outgrew Nelson. Resistances to dieback and needle-casts were highest in the New Zealand populations, followed by Año Nuevo and Monterey. Cedros appeared to be the worst adapted to local conditions.

Año Nuevo generally showed the worst tree form in stem crookedness, branching, and forking. Kaingaroa was superior, particularly as the trees got older. Cambria had relatively straight butts and boles, but became otherwise inferior. Guadalupe tended initially to have straight stems and tidy "multinodal" branching, but this superiority declined with age. In Cedros, the competition masked an inherently squat growth habit. Population rankings for branch-cluster frequency changed appreciably with age.

Population-site interaction as such was mostly negligible, the main interactions evidently reflecting specific establishment conditions. Local differentiation within mainland populations was usually minuscule. Variation among natural populations was complex and multidimensional, resemblances between populations differing among traits. The Monterey and Año Nuevo populations appeared the most similar, while the island ones, especially Cedros, appeared quite distinct. The island populations were distinguished by thin unfissured bark and binate fascicles. The New Zealand populations evidently derived from Año Nuevo and Monterey, Kaingaroa showing a clearer preponderance of Año Nuevo ancestry than Nelson. Possible reasons for the superiority

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* Present address: Acacia Road, Lake Okareka, RD 5, Rotorua, New Zealand

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of New Zealand material included a release from the "neighbourhood inbreeding" of natural stands.

Keywords: provenance; gene resource; growth rate; site tolerance; disease resistance; morphology; tree form; maturation; physiological age; *Pinus radiata.*

INTRODUCTION

Details of the *Pinus radiata* Genetic Survey experiment in Kaingaroa Forest have been given in the first paper of this series (Burdon, Bannister, Madgwick & Low 1992). A major objective of the experiment was to compare material from virtually the entire natural range, along with suitable examples of domesticated stocks.

When it was decided to mount an intensive breeding programme with *P. radiata* in New Zealand soon after 1950 the significance of provenance variation in the species was untested. In an unreplicated trial planted in Australia in 1950 (Fielding 1961), on just one high-altitude site, Cambria material performed poorly in comparison with material from Año Nuevo and Monterey and local stock. In New Zealand, weakly-replicated provenance trials containing material from Monterey and Cambria plus two local plus-tree progenies were planted on two sites in 1955 (Shelbourne *et al.* 1979), and Guadalupe Island material was planted in a pilot trial at Rotorua in 1958.

The Genetic Survey experiment was planted in 1964, 1965, and 1967, and preliminary results comparing provenances were published by Burdon & Bannister (1973a). Provenance differences were already evident in respect of: growth rate (although interpretation was complicated by different levels of inbreeding); tree-form variables (stem crookedness, malformation rate, branching pattern); rate of appearance of adult characteristics; other morphological features; wood density; certain site tolerances; and incidence of Dothistroma needle blight, adelgid attack, and animal browsing. The results, however, were only from very young trees, and represented only limited samples of the experiment.

This paper covers provenance (population) comparisons for the full experiment, up to about 12 years from planting, and for a wider range of variables. It also addresses differences between subpopulations (localities within natural populations). Population comparisons for wood properties and monoterpene composition are covered in other papers in this series (Burdon & Low 1992; Burdon, Gaskin, Zabkiewicz & Low 1992; and Burdon, Zabkiewicz & Andrew 1992). The final paper of the series (Burdon 1992) discusses population differences in the light of results for the full range of variables studied. Of interest are the advantages and disadvantages of the various populations, and comparisons between native populations and local stocks. The latter comparisons are used to infer both the Californian ancestry of the local stocks and the genetic changes that have occurred since they were introduced to New Zealand. All this information gives pointers to what benefits infusions of native-population material into the breeding programme are likely to confer.

MATERIAL AND METHODS

A detailed description of the genetic sampling, raising, planting, and tending of the material, field design, assessments, data manipulation, and principles of statistical analysis, has been given by Burdon, Bannister, Madgwick & Low (1992).

Experimental

Briefly, the material represented the entire natural range of the species, with the five natural populations Año Nuevo, Monterey, and Cambria from mainland California, and Guadalupe Island and Cedros Island off the coast of Baja California. Also included were two New Zealand "land-race" populations (Kaingaroa and Nelson). Each population was represented basically as 50 wind-pollinated progenies which were planted during 3 years (Stages I, II, III) on two contrasting sites in Kaingaroa Forest (Sites A and B), giving six site/stage blocks. Within each of the six blocks randomisation was for all practical purposes complete. The three Californian mainland populations were each divided into five subpopulations (according to localities) (Table 1) and the Cedros population into two subpopulations (North and South). A subsample of the progenies was also represented as clonally replicated material (cuttings) in the last planting stage (Stage III).

TABLE 1–Particulars of subpopulations within Californian mainland populations (*see* Forde 1964a, 1966)

Population	Sub-population	Locality
Año Nuevo	I	Between Año Nuevo Creek and Finney Creek, near northern limit
	II	Stand interior, south of Elliot Creek, northern mid-range
	III	Straddling Waddell Creek, near mid-range
	IV	Southernmost stands on coastal ridge
	V	Swanton area, inland near southern limit, between Scott Creek and Mill Creek
Monterey	I	Seaward margin, north-west part of peninsula, between Cypress Point and Point Joe
	II	Directly south of Monterey, approaching Loma Alta Ridge
	III	Dry, south-facing slopes, Carmel Valley
	IV	Inland margin from Point Lobos, ridge between San José Creek and Gibson Creek
	V	Malpaso Canyon, near southern limit
Cambria	I	Stand margins, 1 km south of Leffingwell Creek, near northern limit of main stands
	II	Coastal margin, west of Cambria township
	III	South-facing slopes, above Cambria township
	IV	Coastal margin, south of Cambria
	V	Near inland margin south of Cambria township

Statistics and Expression of Results

Differences between subpopulations, if present, were of interest both in themselves and for drawing inferences about the nature of population differences. In testing for population differences it was appropriate to consider any between-subpopulation variance, along with variances attributable to families within subpopulations and genotype-block interactions, although this implied treatment of subpopulations as a random effect would make the tests over-stringent.

In practice, tests for population differences were not usually made according to formal analysis of variance models, for several reasons. Firstly, it appeared that subpopulation differences generally did not need to be taken into account; secondly, the data properties often differed for a trait from block to block; thirdly, for all but seven variables data were not available from all six blocks, which severely complicated the computing; and finally, formal tests were inherently cumbersome. Accordingly, the emphasis was placed on expressing population means in terms of relative performances within each block. Averaging relative performances over blocks appeared to give robust measures of overall performance, and to give a convenient if *ad hoc* basis for inferring whether pairwise differences could be accepted as genuine.

Thus, the usual basis for comparing populations across all six blocks was:

(1) Convert population means, block by block, to relative scores (Monterey mean = 100 for each block). For metric traits such as height and diameter the relative score was a simple ratio. For traits that were measured on visual rating scales, or if 0 or 1 denoted absence or presence of a feature, the following measure was adopted (cf. Burdon & Bannister 1985):

$$\text{Relative performance} = 100\sqrt{\frac{(Y_X - Y_{min})\,(Y_{max} - Y_M)}{(Y_M - Y_{min})\,(Y_{max} - Y_X)}} \qquad (1)$$

where Y_X and Y_M are the means for the population in question and Monterey respectively.

and Y_{max} and Y_{min} are the upper (ideal) and lower (worst value) bounds respectively of the closed-ended scale.

The measure of performance in Eqn 1 is independent of convention; for example, it accommodates the fact that 1%:3% of forking represents the same situation as 99%:97% of unforked trees. It also gives a comparative measure that is reasonably stable with respect to wide departures of average scores from the midpoints of the scales.

(2) Relative performance values were averaged, for each trait in each population, over all the site/stage blocks in which the trait was assessed for the particular age bracket. For the seven variables that were assessed in all six blocks the relative performance values (Monterey = 100) could also be calculated directly from the overall means across all blocks, for each provenance. The resulting figures, however, generally differed very little from the averages over blocks of the within-block relative performance values.

(3) Any two populations were deemed to differ significantly for a trait if relative scores differed, in the same direction, within all four to six blocks where the trait was assessed ($p = 0.5^{[\geq 4]}$). The difference was always significant ($p < 0.05$, protected t-test, cf. Burdon, Bannister, Madgwick & Low 1992, ANOVA 1 or ANOVA 2, as appropriate) within at least one such block, meeting a second condition that had been set *a priori*. This procedure was robust with respect to differences between blocks in data properties. Where data were available from less than four blocks the criterion adopted was for relative scores to differ not only in the same direction but also significantly (as above), or else to differ significantly (t-test, $p < 0.05$) in combined analyses of data over all blocks represented (cf. Burdon, Bannister, Madgwick & Low 1992, Table 7).

RESULTS

Comparisons among Subpopulations within Populations

Local differentiation within populations was generally very slight, so subpopulation effects could usually be disregarded in statistical tests for population differences. Within blocks few of the tests for differences between subpopulations within populations were statistically significant ($p < 0.05$), and in most of those the pattern of subpopulation differences was not consistent among blocks. Overall, nearly 50% of such tests gave F ratios ≤ 1. Where meaningful subpopulation differences appeared to exist, they tended to involve groups of traits that were developmentally interrelated. Presentation of detailed results is accordingly focused on such traits and the populations for which there appeared to be appreciable subpopulation differences.

For the Californian mainland populations, subpopulation means are shown in Table 2 for five of the seven variables that were assessed over all six blocks, there being no evidence of significant local differentiation for the other two variables, butt straightness (or sweep) and stem straightness (or crookedness). The most noteworthy feature was the performance of subpopulation V within Año Nuevo, which showed relatively poor growth and a high incidence of forking. The only other significant ($p < 0.05$) subpopulation differences involved the desirable branching pattern of subpopulation V within Monterey, and "8-year" height among subpopulations of Cambria.

Estimates of variances between subpopulations within mainland populations were necessarily very imprecise relative to their small but presumably non-zero values. Very approximate ratios of $\hat{\sigma}^2_{sp(p)}/\hat{\sigma}^2_{A(sp)}$ (estimates of variances over all six site/stage blocks between subpopulations within populations and of additive genetic variances between trees within subpopulations, respectively—cf. Burdon, Bannister, Madgwick & Low 1992, Table 6, ANOVAs 1 and 4) were as follows: 8-year height and dbhob—10%; 2- to 3-year height—17.5%; 8-year forking—12.5%; 8-year scores for stem straightness, butt sweep, and branch

TABLE 2–Means over all blocks for Californian mainland subpopulations, with significance tests (p values) for subpopulation differences within each population

Population	Sub-population	Height (cm)		Dbhob (mm)	Branch habit quality (1–9)	Forking (0–1)
		~2.5 yr	~8 yr	~8 yr	~8 yr	~8 yr
Año Nuevo	I	135	991	159	4.5	0.41
	II	130	948	152	4.4	0.40
	III	130	963	150	4.4	0.29
	IV	132	983	155	4.4	0.35
	V	123	937	145	4.5	0.48
	p	<0.01	<0.05	<0.05	>0.5	<0.01
Monterey	I	135	979	161	4.6	0.32
	II	133	983	161	4.8	0.30
	III	135	960	162	4.5	0.38
	IV	135	978	161	4.9	0.26
	V	128	944	153	5.3	0.31
	p	<0.2	<0.2	<0.2	<0.05	>0.1
Cambria	I	141	957	160	4.4	0.35
	II	138	981	158	4.8	0.36
	III	135	939	155	4.6	0.33
	IV	135	934	155	4.4	0.37
	V	140	974	160	5.1	0.28
	p	<0.2	<0.05	>0.5	<0.1	<0.2

habit quality—0–8%. These ratios were based on assumptions (Burdon, Bannister & Low 1992a, Table 3 and Eqn 4) that could produce conservative estimates of $\sigma^2_{A(sp)}$.

Within the Guadalupe population the high-altitude outlier progenies were clearly less vigorous overall than the rest of the population, showing relative performance values (main population = 100) overall of 50 for effective survival (*see* Eqn 1) and 84, 91, 87, and 81 for 1-year height, 2- to 3-year height, 8-year height, and 8-year diameter respectively. No clinal variation nor any other pattern of local differentiation was evident within the main population.

The only appreciable differences that were evident between the Cedros subpopulations (Table 3) involved incidence of retarded leader and several tree-form variables that would be expected to reflect the incidence of retarded leader, the North subpopulation sample being better in this respect.

TABLE 3–Relative performance values of Cedros subpopulations (Cedros mean = 100) averaged over all blocks. Number of blocks represented in parentheses.

Sub-population	Retarded leader		Branch angle	Branch habit quality		Forking	
	2 yrs (1)	4 yrs (3)	~8 yrs (3)	~8 yrs (3)	~12 yrs (2)	~8 yrs (3)	~12 yrs (2)
North	119	118	104	105	105	106	112
South	84	85	96	95	95	94	89

Note: Higher values represent more desirable situation, viz lack of retarded leader and forking and less steep branch angles.

Comparisons among Populations

Growth rate and survival

For growth-rate variables, the New Zealand populations were the fastest, followed by those from the Californian mainland, with Guadalupe appreciably slower and Cedros considerably slower still (Table 4). Among the New Zealand populations, Kaingaroa tended to draw ahead with time, significantly ($p < 0.05$) excelling Nelson after about 8 years from planting. Among the Californian mainland populations height growth differences were minuscule, a slight early advantage in Cambria disappearing with time. Diameter growth in Cambria fell appreciably behind that of Monterey by 12 years, while Año Nuevo was only marginally behind but with appreciably lower periodic increments. This pattern did not differ materially between over-bark and inside-bark diameters despite some population differences in bark thickness (*see* later).

The growth advantage of New Zealand material over that from the Californian mainland and Guadalupe Island was less marked, however, in the top percentiles than it was in the population means (cf. Burdon & Bannister 1973a). This is reflected in greater phenotypic variances (details not shown), or at least larger coefficients of variation (Burdon, Bannister & Low 1992a), in native-population material.

The island populations, while they did not appear to fall back further with time in relative performances for growth rate among final samples of trees assessed, showed greater attrition of numbers of surviving unsuppressed stems. Such losses were generally less than 5% for

Californian mainland and New Zealand material, except in the Stage III block on Site B where they were about 10% for New Zealand trees and nearly 20% for mainland trees. The losses were generally 10–15% in Guadalupe trees and 15–35% in Cedros trees, but in the Site B Stage III block they were nearly 50% and over 95% for seedlings of Guadalupe and Cedros respectively.

Incidence of disease and pests

The populations differed markedly in levels of all three fungal diseases studied (Table 5); Cedros, Cambria, and Guadalupe were the worst, and the two New Zealand populations were generally the best. For Dothistroma incidence there were some important changes in ranking with increasing age, Monterey improving greatly relative to the other populations, and Guadalupe showing a sharp decline between 1 year and 5 years after planting.

The incidence of apical abortion (Burdon & Bannister 1973b) which represents putative thrip damage (Ray & Vanner 1988) varied markedly among populations. At age 2, the Monterey and Cambria populations had average scores around 0.75–0.8 per tree (counting 2 for a definite occurrence and 1 for a suspected occurrence), while the Año Nuevo, Guadalupe, and New Zealand populations had much lower average scores, all around 0.4. At age 4, however, Cambria showed a markedly higher incidence than Monterey (Burdon & Bannister 1973b).

Tree form variables

Butt straightness scores (Table 6) were best in the two island populations, followed by Cambria, differing little among the remaining populations. For stem straightness scores, the island populations, especially Guadalupe, excelled around age 8, followed by Cambria, with Año Nuevo the worst, but by about age 12 when the trees were larger and taller, the scores of Cedros, Guadalupe, and Cambria had declined appreciably relative to those of other populations, while those of Kaingaroa had improved markedly. Incidence of forking (Table 6) was least in Kaingaroa and greatest in Año Nuevo around age 8, but around age 12 years Año Nuevo was no worse than Cambria and the island populations.

Branching characteristics varied between populations (Table 7), but the rankings for frequency of branch clusters changed markedly with age. Cambria initially had the lowest frequency (counts), but later Año Nuevo and the island populations showed the lowest frequencies (scores). These later frequencies were reflected inversely in internode lengths (population averages at around 8 years ranging from 51 to 59 cm), and directly in numbers of branch clusters on the bole (corresponding averages ranging from 16 to 19.5).

Branch habit quality scores were largely paralleled by branch cluster counts, scores for branch cluster frequency, branch angle scores, and freedom from forking and, inversely, by mean internode lengths (Table 7). (This pattern reflects the tendency for long internodes, although desirable in themselves, to be associated with otherwise undesirable branching characteristics and forking.) The most consistent feature was the high branching frequency (with relatively short internodes) and generally desirable branching characteristics of the Kaingaroa population, which were accentuated with time. The Año Nuevo population showed comparatively undesirable branching characteristics, and mean branching frequency scores became lower relative to other mainland populations as the trees got older. Cambria,

TABLE 4–Relative performance overall of provenances (Monterey = 100) for growth variables. Figures in parentheses denote numbers of blocks on which figures are based.

Population	Height				Dbhob		Diam. increment
	1 yr (5)	~3 yr (6)	~8 yr (6)	~12 yr (4)	~8 yr (6)	~12 yr (4)	~8–12 yr (4)
Año Nuevo	99.4 b	97.8 b	99.8 c	100.0 c	95.7 b	96.0 cd	92.2 d
Monterey	100.0 b	100.0 b	100 c	100 c	100 b	100 c	100 c
Cambria	105.0 ab	103.3 ab	99.3 c	98.2 c	99.7 b	93.8 d	81.8 e
Kaingaroa	103.2 ab	104.3 a	108.8 a	110.2 a	107.8 a	111.0 a	119.8 a
Nelson	106.6 a	105.2 a	104.7 b	105.5 b	105.5 a	106.8 b	109.6 b
Guadalupe	83.0 c	89.8 c	90.8 de	88.2 d	75.3 c	72.5 e	66.8 f
Cedros	~60 d	~70 d	~72 e	~70 e	~55 d	~55 f	~50 g

Values in a column that are suffixed with a letter in common are deemed not to differ significantly (*see* Materials and Methods).

TABLE 5–Relative performances overall of populations (Monterey = 100) for disease resistances. Figures in parentheses denote numbers of blocks involved.

	Diplodia dieback		Cyclaneusma needle-cast		Dothistroma needle blight			
	Seedlings (4)	Cuttings (1)	Seedlings (4)	Cuttings (1)	Seedlings			Cuttings
					2 yr* (1)	5 yr* (1)	7 yr (1)	7 yr (1)
Año Nuevo	98 c	91 abc	99 cd	91 b	134 a	104 a	89 a	78 b
Monterey	100 c	100 ab	100 c	100 a	100 b	100 a	100 a	100 a
Cambria	70 e	58 d	79 de	85 b	90 b	77 b	67 b	74 bc
Kaingaroa	148 a	153 a	114 a	106 ab	147 a	113 a	99 a	101 a
Nelson	128 b	104 ab	107 b	104 a	125 a	113 a	103 a	96 a
Guadalupe	67 c	71 cd	88 d	101 b	158 a	75 b	72 b	60 c
Cedros	86 d	–	~70 e	–	–	64 c	60 b	–
Nature of test	Standard†	Tukey	Standard	Tukey	Tukey	Tukey	Tukey	Tukey

Values within a column that are suffixed with a letter in common are deemed not to differ significantly (*see* Materials and Methods).

* Adapted from Burdon & Bannister (1973a).

† See Materials and Methods

TABLE 6–Relative performance overall of populations (Monterey = 100) for straightness variables and forking. Figures in parentheses denote numbers of blocks on which figures are based.

Population	Butt straightness	Stem straightness		Forking (lack)*	
	~8 yr (6)	~8 yr (6)	~12 yr (4)	~8 yr (4)	~12 yr (2)
Año Nuevo	101 c	82 d	82 c	85 c	91 c
Monterey	100 c	100 c	100 b	100 b	100 bc
Cambria	117 b	112 b	104 b	92+ bc	88+ bc
Kaingaroa	106 bc	104 bc	115 a	122+ a	127 a
Nelson	99 c	96 c	102 b	99+ b	104 b
Guadalupe	130 ab	134 a	119 a	96+ bc	86+ bc
Cedros	138 a	125 a	106 b	105 bc	88 bc

Values in a column that are suffixed with a letter in common are deemed not to differ significantly (*see* Materials and Methods).

* Figures calculated from blocks (number in parentheses) where forking was analysed as 0–1 data allowing use of Eqn 1.

\+ Pluses indicate where results of open-ended counts in two additional blocks show populations in a more favourable light relative to Monterey.

TABLE 7–Relative performances overall of populations (Monterey = 100) for branching variables. Figures in parentheses denote number of blocks represented.

Population	Branch cluster* number		Internode* length	Branching* frequency score		Branch habit quality score		Branch angle† score	
	~3 yr (5)	~8 yr (4)	~8 yr (4)	~8 yr (4)	~12 yr (4)	~8 yr (6)	~12 yr (4)	~8 yr (5)	~12 yr (1)
Año Nuevo	98 b	94 c	106 a	85 c	86 c	90 c	94 c	95 c	89 c
Monterey	100 b	100 b	100 bc	100 ab	100 ab	100 b	100 bc	100 bc	100 bc
Cambria	79 c	92 c	107 a	96 b	99 ab	96 bc	93 c	98 c	103 b
Kaingaroa	108 a	115 a	96 c	104 a	107 a	116 a	116 a	111 a	120 a
Nelson	101 b	103 b	103 b	95 b	97 b	101 b	104 b	102 b	105 b
Guadalupe	101 b	99 b	93 c	88 bc	83 c	113 a	98 bc	109 a	112 ab
Cedros	102 b	92 c	~80 d	84 bc	73 c	104 b	95 bc	109 a	116 ab

Values within a column that are suffixed with a letter in common are deemed not to differ significantly (*see* Materials and Methods).

* Relating to numerical values and not *per se* to any scale of desirability.

† Lower values denoting less-desirable steeper angles.

by contrast, started with the lowest branch cluster frequency, but eventually came into line with Monterey, although its branch habit quality scores declined, if anything, towards age 12. The island populations initially had a relatively high frequency of branching, which carried through into relatively short internodes, but as the trees got older they dropped in the rankings for branch cluster frequency and branch habit quality scores, despite having relatively wide-angled branching.

Onset of formation of sealed buds

The progression from having green apical tufts to producing scarious sealed buds as the trees got taller is illustrated in Fig. 1, which shows consistent population rankings. Guadalupe was the most advanced throughout. Cedros was the next most advanced relative to tree height, but not necessarily in absolute scores. Kaingaroa, Año Nuevo, and Nelson had similar average scores, but with Nelson consistently behind Kaingaroa and Año Nuevo. Monterey had appreciably lower scores again, with Cambria clearly the lowest.

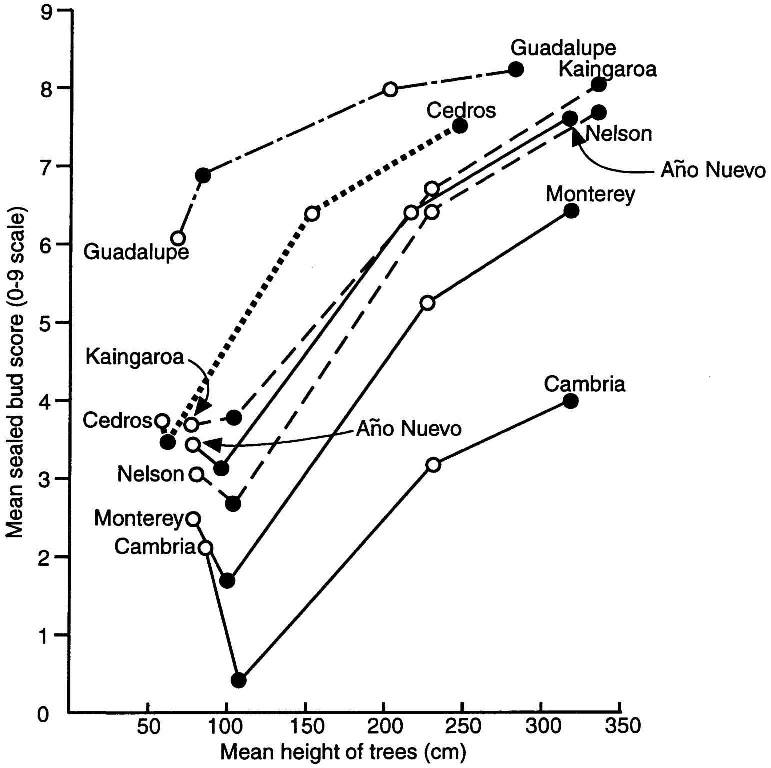

FIG. 1–Mean bud scores (0–9 scale), by populations, *v*. mean height at 2 years and 4 years from planting (Site A — ●, Site B —○).

Corresponding to the relationship shown in Fig. 1 between mean sealed bud scores and mean height was a consistent relationship between sealed bud scores and individual-tree heights within blocks at given ages (r within populations ≥ 0.2). Given the faster growth of the New Zealand material this complicated comparisons of scores among Año Nuevo, Monterey, Kaingaroa, and Nelson. Accordingly, sealed bud scores in these populations were adjusted for covariance on individual heights, and relative performance values were computed (Eqn 1) on the adjusted bud scores. The means of these performance values are listed by population in Table 8, which shows higher scores for Kaingaroa than for Año Nuevo even after the adjustment, but somewhat lower scores for Nelson.

The population differences in sealed bud production were paralleled by differences in the seasonal pattern of height growth. A subsidiary experiment at Rotorua, involving 2- to 3-year-old trees, showed Guadalupe to have the most pronounced spring maximum in its height growth and Cambria the least (Burdon unpubl.).

TABLE 8–Relative performance values overall of populations (Monterey = 100) for progression towards producing fully sealed buds, based on bud scores adjusted for covariances on individual tree height to the Monterey mean height.

Population	Seedlings (6 blocks)	Cuttings (2 blocks)
Año Nuevo	138 b	151 a
Monterey	100 d	100 c
Kaingaroa	151 a	156 a
Nelson	128 c	126 b

Values within a column that are suffixed with a letter in common do not differ significantly (*see* Materials and Methods).

Retarded leader

The incidence of retarded leader is plotted by provenance *v.* tree height in Fig. 2. Despite much "noise" variation certain trends are evident. In seedlings the incidence increased until tree height reached 1.5–2 m, the initial incidence being lowest in the populations showing the slowest onset of sealed bud formation, namely Cambria followed by Monterey. In cuttings the incidence built up much sooner (cf. Burdon & Bannister 1985). Later, after the incidence (but not the general significance of individual cases) apparently peaked, the Kaingaroa population showed a consistently lower incidence than Año Nuevo which also showed a higher incidence than Monterey and Cambria. Results for Guadalupe were erratic, and those for Cedros less complete.

Bark thickness

Bark thickness differed strikingly among populations (Table 9), being by far the least in the island populations, especially at around 12 years when it had become thicker and more strongly fissured in the mainland populations while still being quite smooth in island material. Monterey had the thickest bark among the native populations, but the ranking reversed among Año Nuevo and Cambria between the two measurement ages. The New Zealand populations showed the thickest bark of all after 12 years, but this clearly reflected the greater size of the trees. Bark thicknesses (transformed) were accordingly adjusted for

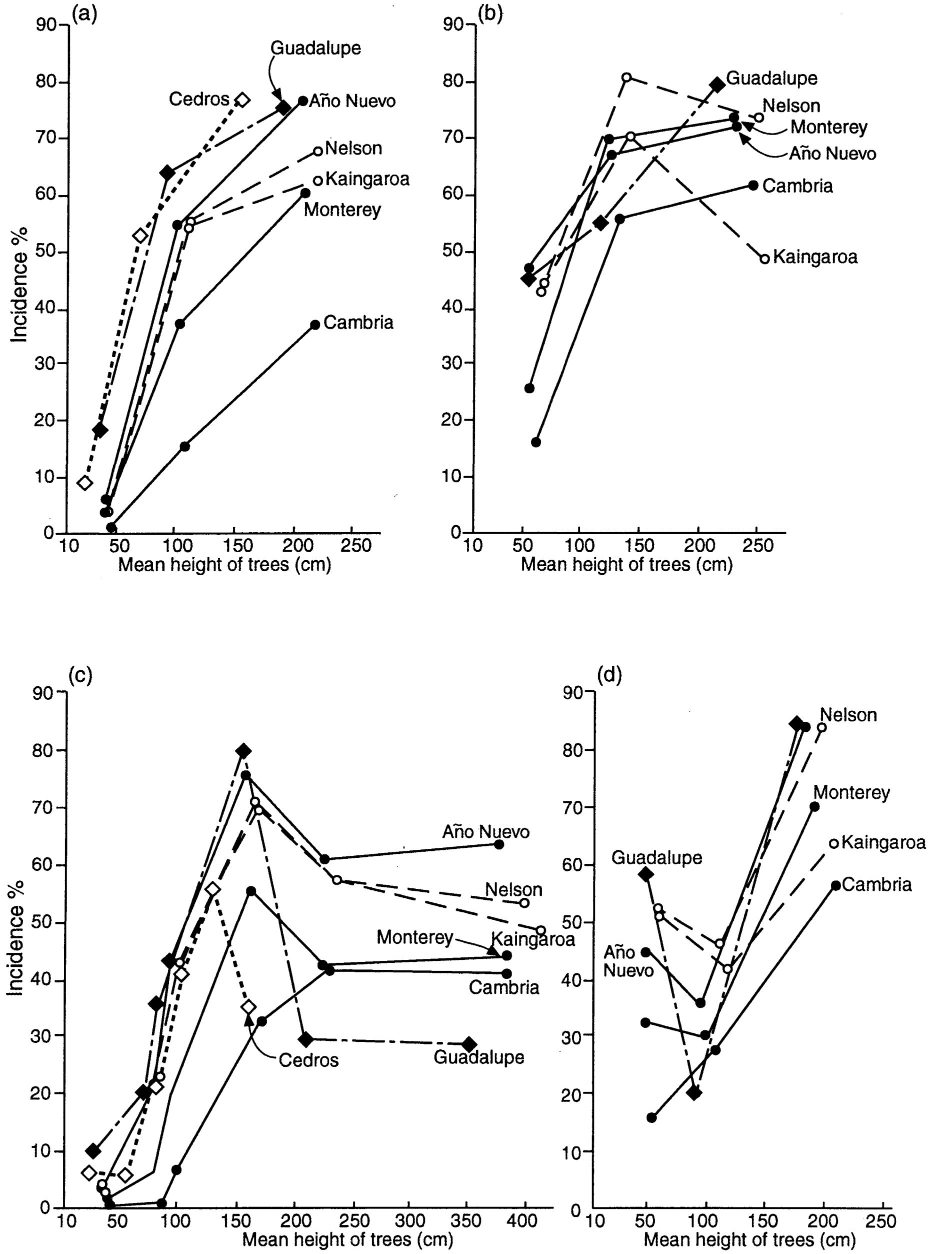

FIG. 2–Current incidence of retarded leader (percentage of trees affected) by populations, *v.* mean height.

(a) Site A, Stage III seedlings at 1, 2, and 3 years from planting.

(b) Site A cuttings at 1, 2, and 3 years from planting.

(c) Site B seedlings—consecutive plottings for: Stage III, 1 year from planting; Stage III, 2 years; Stage I, 2 years; Stage III, 3 years; Stage II, 4 years; Stage III, 5 years.

(d) Site B cuttings at 1, 2, and 3 years from planting.

individual covariance on dbhob ($r \geq 0.7$ within populations at individual assessments) for the Año Nuevo, Monterey, and New Zealand populations. The adjusted values for Kaingaroa fell well below those for Monterey and close to those for Año Nuevo, while those for Nelson fell to figures almost exactly intermediate between Año Nuevo and Monterey.

TABLE 9–Relative performance values, averaged over several blocks, of populations (Monterey = 100) for bark thickness: (A) unadjusted; (B) adjusted for individual covariance on dbhob about the Monterey mean for dbhob. Figures in brackets denote numbers of assessments involved.

Population	(A) Unadjusted			(B) Adjusted*		
	Seedlings		Cuttings	Seedlings		Cuttings
	~8 yrs (5)	~12 yrs (4)	~8 yrs (2)	~8 yrs (5)	~12 yrs (4)	~8 yrs (2)
Año Nuevo	76 c	88 b	80 c	84.6	92.6	87.0
Monterey	100 a	100 a	100 a	100	100	100
Cambria	88 b	85 b	92 b	–	–	–
Kaingaroa	96 a	108 a	104 a	87.6	93.6	92.2
Nelson	98 a	109 a	104 a	92.0	95.9	94.0
Guadalupe	45 d	28 c	45 d	–	–	–
Cedros	42 d	28 c	–	–	–	–

Values in a column suffixed by a letter in common are deemed not to differ significantly (*see* Materials and Methods).

* Relative performance values based on reverse transformation of population means for $\sqrt{}$-transformed thicknesses adjusted for covariance on dbhob.

Miscellaneous Notes

In addition to the differences evident from formally analysed data, various other population differences could readily be observed, particularly in the early stages.

The seed from Guadalupe was distinctive in the straggle of its germination unless it was stratified for about 4 weeks at 4°C. The stratification requirement has also been observed in Guadalupe seed by K.G.Eldridge (pers. comm.) and in New Zealand × Guadalupe seed (A.Firth, pers. comm.).

The populations showed obvious differences in size of seedlings and number of cotyledons, which could be readily related to difference in seed size, mean seed weight for the experiment being 41, 23, 48, 31, 29, 37, and 37 mg for Año Nuevo, Monterey, Cambria, Guadalupe, Cedros, Kaingaroa, and Nelson respectively (Burdon & Bannister unpubl.). Anthocyanin occurred in the hypocotyls, and in the cotyledons where it was generally concentrated near the tips. Occurrence at these two positions was clearly very imperfectly correlated among progenies and individuals within progenies. Anthocyanin was most abundant in the Monterey population, followed by Año Nuevo and Guadalupe, and was least so in Cambria and Cedros. Morphologically post-germinant seedlings of the island populations were distinctive; Guadalupe showed long, shaft-like hypocotyls in relation to seedling sizes, and the early primary leaves were long and slender with a slight glaucous bloom (Burdon &Bannister unpubl.). By contrast, Cedros seedlings had short hypocotyls, and the early primary leaves were relatively short and thick, tending to become horizontal or slightly recurved, and showing deep green, glossy, upper surfaces (Burdon & Bannister unpubl.).

In older seedlings in nursery beds the differences in appearance tended to reflect differences in the rate of onset of adult characteristics, becoming pronounced when they reached about 40 cm tall. Guadalupe was the first to produce sealed buds in place of the green apical tufts of primary leaves, followed by Año Nuevo, Cedros, and New Zealand material, then Monterey, and finally Cambria. Correspondingly, Cambria seedlings also produced far more small laterals from the axils of primary leaves in the zone immediately above the cotyledons, to give a conspicuous bunch of very juvenile-looking branches towards the base. Guadalupe seedlings in the early spring of the second season in the nursery tended to show delayed shoot elongation which was associated with a distinctive rosette-like configuration at the tops.

By this stage, the colour and set of foliage differed appreciably among populations. Cedros and, to a lesser extent, Guadalupe tended to look more yellowish than the others, and Guadalupe acquired a slight "chimney-brush" set to the foliage. Cedros often showed white flecks of dried resin on foliage. Monterey and Cambria were a very vivid green, Cambria evidently having the longer foliage, while Año Nuevo was a less vivid green, and was closely resembled by the New Zealand populations. These differences remained evident for a few years in the field, and so during the first 4–5 years or so it was possible on visual examination to place a high proportion of trees according to their natural populations.

As trees got older, however, the pattern of differences tended to change. Guadalupe foliage, for instance, appeared relatively grey and lost the "chimney brush" set, while Monterey foliage was no longer shorter than that of Año Nuevo (Burdon & Low 1977). Another feature was the tendency for young trees of the Guadalupe population to develop relatively long branches from near the base of the stem; this presumably tended to lower the centres of gravity in seedlings, which in turn should be conducive to less toppling caused by wind. Monterey trees, in particular, tended to retain dead foliage that hung up on suppressed branches, with Guadalupe showing the least tendency to do this.

DISCUSSION

Subpopulation Differences

Within the Californian mainland populations, subpopulation differences were very slight overall, despite the deliberate sampling from diverse sites within populations. This accords with several earlier reports for field performance (Hood & Libby 1980; Guinon & Libby 1982; Falkenhagen 1991) and with the very weak subpopulation differences observed for isozymes by Moran *et al.* (1988) and for monoterpenes by Burdon, Zabkiewicz & Andrew (1992). Some differences might be expected through sampling effects, or through differential inbreeding resulting from local variations in patterns of regeneration after past disasters. The one convincing difference was the relatively poor growth of the Año Nuevo subpopulation V, from the Swanton locality. Not only was it pronounced in itself, but it has also been corroborated by poor growth of a later collection from that locality (Falkenhagen 1991; Burdon, M.A.Miller, Low, A.Firth & T.G.Vincent unpubl.). The pines have been sparse in the area (Forde 1966), which created obvious scope for inbreeding and consequent inbreeding depression. Alternatively, the sparseness of the pines could have led to weaker natural selection for rapid height growth.

The two trial sites, while appreciably different from each other, were both far from marginal. As such, they might not be expected to give sharp resolution of any subpopulation differences in site tolerance that might exist. Against that, sites on the New Zealand volcanic plateau tend to give very good resolution of progeny differences within *P. radiata* (*see* Carson 1991). The strongest evidence of ecological differentiation within Californian mainland populations appears to be a finding of Cromer *et al.* (1982) who showed differences in tolerance of salinity; paradoxically, the coastal dune material from Monterey was less tolerant, which was attributed to greater dilution of salinity by more intense fog drip on free-draining sands near the coast. Inbreeding depression, however, could also have affected salinity tolerance; greater inbreeding might be expected in the coastal dune area, with the scattered trees and windward location, and the isozyme study of Moran *et al.* (1988) indicated that it had occurred.

The poorer survival and growth of the high-altitude Guadalupe outlier progenies may be due to greater inbreeding, although a harsher environment could have selected for a more conservative growth rate. Chlorophyll defectives, which were presumably homozygotes for deleterious recessive genes (cf. Franklin 1969), occurred among the germinants in at least one of these progenies; yet Moran *et al.* (1988) found no evidence of more inbreeding (F statistics) than in the main stand.

The differences between the two Cedros subpopulations, while involving several observed variables, presumably all stemmed from differing percentages of retarded leader, which may well have been a fortuitous sampling effect.

Population Differences

For almost all traits the populations showed considerable overlap in variation. The main exceptions involved the island populations, in which the persistently thin smooth bark and the binate fascicles on older and less vigorous shoots were essentially qualitative differences from the mainland populations.

In general, population differences were very consistent over blocks. Site B could be expected to be very unfavourable for the Cedros population because it was the cooler site whereas Cedros is presumably much the warmest of the natural habitats, and while Cedros failed badly there in Stage III it did not fail in the same way in Stage II. Thus there appeared to have been little population × site interaction as such, even though the higher levels of Dothistroma blight on Site B would not have favoured the more susceptible populations there. This accords with other evidence of minimal genotype-site interaction in *P. radiata* on the volcanic plateau (Johnson & Burdon 1990; Carson 1991).

There were some minor anomalies among blocks in population rankings for some visually rated traits, which could reflect various factors such as observer × population interactions and complications arising from timing of assessments within blocks in relation to disease outbreaks or wind damage.

Survival and growth

Initial mortality, which was made good by blanking, was not high and was dominated by frost damage (Burdon & Bannister 1973a). Subsequent effective survival basically reflected competitive ability which in turn must have reflected growth potential and resistance to disease.

The Californian mainland populations appeared to have very similar growth potential, the later fall-off in the performance of Cambria being readily attributable to effects of needle-cast diseases. There were also indications that Monterey was beginning to draw away from the Año Nuevo in stem diameter, and in a selection operation at age 20 years (Burdon unpubl.) many more vigorous, healthy, well-formed trees could be chosen in the Monterey material than in that from Año Nuevo and Cambria. In the first few years Cambria was marginally taller than Año Nuevo and Monterey, but in subsequent experiments using a fresh seed collection (Eldridge 1978) Cambria consistently lagged slightly in early height growth (Eldridge 1986; Falkenhagen 1991; Burdon unpubl.). The reasons for this anomaly are not clear, but the wrenching of nursery stock for the later trials may have more effectively erased effects of heavier seeds in Cambria.

The growth advantage of the New Zealand material increased with age. While later population differences in growth and effective survival were doubtless inflated by the competitional patterns resulting from the single-tree-plot layout, there is no reason to believe that the rankings were spurious. As discussed by Burdon & Bannister (1973a) there were three possible reasons for the superiority of New Zealand material: elimination of the "neighbourhood inbreeding" of natural stands, adaptive responses to natural and silvicultural selective pressures in New Zealand environments, and heterosis (hybrid vigour) from crossing between the Año Nuevo and Monterey populations which were clearly the progenitors. The first of these possibilities was almost certainly significant—the partial inbreeding in natural stands, with consequent inbreeding depression, would both depress means and inflate variability for growth rate, and thus account for the observed patterns—but the relative importance of the other two possibilities is uncertain. The eventual advantage of Kaingaroa over Nelson, however, suggests an effect of local selective pressures.

The slower average growth of Guadalupe would be partly due to considerable inbreeding (Moran *et al.* 1988). Nutrient deficiencies, in the forms of boron deficiency (Burdon & Bannister 1973a) and a few instances of needle fusion which is often but not always associated with phosphorus deficiency, may have contributed but they may themselves have largely reflected inbreeding; in Stage III where the boron deficiency was corrected before symptoms appeared this population did not fare materially better. Cedros showed similar levels of boron deficiency symptoms to Guadalupe, and both populations were much affected by needle-cast diseases, but only after their slower growth had become evident. In both Guadalupe and the even slower-growing Cedros population, wood density was appreciably higher (Burdon & Bannister 1973a; Burdon & Low 1992) and the tap-root development was stronger, especially in Cedros. These particular differences suggest that these populations may differ appreciably from the others in biomass allocations. It is clear, though, that pure Cedros has much slower height growth. Nevertheless, F1 hybrids between each island population and New Zealand material closely resemble the New Zealand parents in growth rate (Burdon 1988, and unpubl.; A.Firth & C.J.A.Shelbourne unpubl.; P.J.Simmons unpubl.).

Disease resistance

The preliminary results for Diplodia-associated dieback (Burdon & Bannister 1973a) were confirmed. The population differences in scores for Cyclaneusma-associated needle cast, which became evident only 4–5 years after planting, roughly paralleled the differences in Dothistroma blight scores after 5 years. The Monterey population continued to improve its ranking for Dothistroma resistance, which was not paralleled exactly by the results of Ades & Simpson (1991). Reasons for this progressive change in ranking are uncertain. The poor early ranking of Monterey can be readily attributed to a slow acquisition of adult characteristics, but that does not explain the sharp decline in ranking of Guadalupe between 2 years and 5 years. Questions arise concerning interactions between Cyclaneusma and Dothistroma—these two forms of needle cast are not always easily distinguished in a closed canopy, and synergisms between the two diseases are suspected. There is also the tenuous possibility that over time Dothistroma in New Zealand has shown a genetic shift in the direction of greater aggressiveness towards New Zealand and Año Nuevo material. A further complication is suspected in that trees appeared to go through 2- to 3-year cycles of defoliation (heavy defoliation being followed by a recovery period before another heavy defoliation) which were not fully synchronised among populations, some of the rankings for Cyclaneusma being inconsistent between assessments. Moreover, the Cyclaneusma scoring, being based on the duration of foliage retention, assumed a common norm among all material for the longevity of foliage.

Tree form

Early comparisons for tree form and branching characteristics (Burdon & Bannister 1973a) were largely confirmed. However, the general superiority and strongly multinodal branching pattern of the Kaingaroa population became increasingly marked. The decline in relative performance for straightness of island material and Cambria probably reflected, in varying degrees, the impacts of leader dieback (despite efforts to disregard this factor in scoring straightness) and less infilling of sinuosity because of slower growth. Branching frequency rankings showed some other changes, with a reversal between Año Nuevo and Cambria. The tidy, strongly multinodal branching initially shown by the island populations compared with the rest became less evident with time, but tree form in both Guadalupe and Cambria had probably become affected by relatively high levels of leader dieback. Other plantings of Cedros revealed an inherently squat growth habit on such sites, which was not manifested in mixture with faster-growing populations. The incidence of retarded leader, although showing some complex trends, appeared to have also influenced branch habit quality scores and the rate of forking.

The superior tree form with the strongly polycyclic branching in the Kaingaroa population affords perhaps the strongest evidence of a genetic shift resulting specifically from natural and silvicultural selection in New Zealand. Branching frequency is not appreciably affected by inbreeding (Wilcox 1983) and on the volcanic plateau from where the population was drawn it shows strong favourable genetic correlations with growth rate (at least in young trees), straightness, and lack of malformation (e.g., Shelbourne & Low 1980; Bannister 1980; Burdon, Bannister & Low 1992b). Moreover, a higher branching frequency has been observed in some other New Zealand control material in follow-up provenance trials (Burdon in prep.).

Of much interest is the superior butt straightness (involving the lowermost 2 m of the bole) of the island populations, which was especially evident in the Stage III block of the experiment on Site B, where considerable toppling of trees occurred after the "Wahine" storm in 1968. The superiority of Cedros, however, is less convincing because the trees were so overtopped. Another feature of butt form was observed, although it was not formally scored; Cambria, at one extreme, was highly cylindrical right to ground level while Guadalupe, at the other extreme, generally showed a relatively pronounced root "pedestal". This root pedestal, which was not associated with obvious butt flare or fluting, resembled that of *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir).

Other morphological differences

Populations differ strongly in the rate at which certain adult characteristics appear. This was particularly marked in the development of sealed buds, but it was also evident in the occurrence of apical abortion and the onset of retarded leader which both appear to be features of juvenile to semi-juvenile material, and in reproductive activity. The onset of strobilus production (Burdon & Bannister 1973a) largely paralleled sealed bud formation, except for a slowish onset of pollen production in Guadalupe. However, although the adult growth habit is associated with a considerable improvement in tree form, this effect clearly did not dominate population comparisons for tree form. In the Guadalupe population the early onset of adult characteristics does not appear to reduce the longevity or the ultimate size to which trees can grow (Libby *et al.* 1968).

Bark thickness differences were major, but their practical significance for domesticated crops is not clear; there is presumably a trade-off between allocation of biomass to stemwood and vulnerability to physical damage. The populations also differed in other bark features. Among the mainland populations unfissured bark was very scurfy (with very small, thin, loose flakes) in Cambria (cf. Fielding 1961) and least so in Año Nuevo. Later on Monterey tended to have a strongly vertical pattern of fissuring in the bark. While the island populations both retained thin, smooth, unfissured bark on the butts, the Cedros trees showed far more numerous resin blisters.

Bark thickness and the sealed bud scores appeared to be useful bases for comparing the New Zealand populations with their Californian progenitors, Año Nuevo and Monterey. Covariance adjustments for tree size were clearly indicated, correcting for a size-related bias towards Año Nuevo in sealed bud scores and a similar bias towards Monterey in bark thickness. Since neither bark thickness nor the progress towards producing fully sealed buds would have been measured without error, the regressions would tend to be biased downwards with consequent under-corrections, and the results were consistent with this having occurred. The implications of the results for inferring the ancestry of the New Zealand populations are discussed along with those of the results from oleoresin analyses (Burdon, Gaskin, Zabkiewicz & Low 1992; Burdon, Zabkiewicz & Andrew 1992) in the final paper of this series (Burdon 1992).

CONCLUSION

Adaptive profiles of the various natural populations, as revealed in this experiment, are summarised in Table 10. Overall, Año Nuevo and Monterey were the best adapted to local conditions, and the New Zealand material generally showed the best adaptive features of these two native populations. The two sites, however, did not provide a comprehensive test of edaphic tolerances, or of resistances to a broad spectrum of diseases, or of tolerance of exposure or extreme winds. Considering performance in other environments, both physical

TABLE 10–Patterns of natural-population differences revealed by this experiment for growth rate, survival, site tolerances, and resistances to certain pathogens and pests. Pluses denote superiority, minuses inferiority, zeros essentially average.

Feature	Provenance				
	Año Nuevo	Monterey	Cambria	Guadalupe	Cedros
Growth rate	+	+	+	–	– –
Ease of transplanting*	+	0	–	++	– –
Resistance to/tolerance of:					
Frost	++	+	–	–†	– –
Boron deficiency	+	+	+	– –	– –
Needle fusion	0	0	0	–	0
Toppling (in wind)	–	–	–	+	+
Dothistroma pini	++	++	– –	0	– –
Cyclaneusma minus	+	++	– –	–	– –?
Diplodia pinea	++	++	– –	– –	–
Pineus pini	0	+	+	– –	+
Deer/rabbit browse	0	0	0	–	+

* From subsidiary plantings using spare blanking stocks (Shelbourne *et al.* 1979).

† In two trials in the United States this population showed the greatest frost tolerance (W.J. Libby pers. comm.)

and biotic, a much more complex picture emerges, with each population having its own adaptive advantages and limitations. For instance, Butcher & Stukely (1986) observed superior resistance to *Phytophthora cinnamomi* Rands in Cambria seedlings, in contrast to Año Nuevo, among the mainland material. Resistance to western gall rust (*Endocronartium* (syn. *Peridermium*) *harknessii* (J.P.Moore) Y.Hirat.) in California has proved greatest in Guadalupe material and least in Monterey and Cambria (e.g., Old *et al.* 1986), in close relationship to the ages of acquiring adult characteristics. Cromer *et al.* (1982) obtained indications of superior tolerance of salinity in the Cambria population. A New Zealand-wide series of provenance trials planted in 1980 (Burdon in prep.) showed that, among the Californian mainland populations, Monterey performed relatively better in the north of the country particularly on phosphorus-deficient clays where Cambria also fared well, and Año Nuevo excelled in the far south.

The morphological differences revealed in this experiment are summarised in Table 11 (note that the rankings for some of the tree-form variables could have been influenced by levels of leader dieback). Bark thickness, along with number of needles per fascicle, showed virtually no overlap in variation between the island populations and the rest. The rate of assuming adult characteristics, along with cone sizes, showed sharp differences between populations at the extremes of the scale of variation. For most other traits, the variation overlapped strongly between populations.

The observed population differences, not all of which are covered in this paper, are complex and multidimensional. Some are easily interpreted as adaptations to the respective natural habitats. For example, the browse palatability of Guadalupe, in contrast to that of Cedros, can readily be attributed to biotic differences between various natural habitats, while the thin bark without resin blisters may also reflect a previous original lack of browsing animals on Guadalupe Island, and the long hypocotyls of Guadalupe seedlings may be an adaptation to less trampling and compaction of the forest litter than elsewhere. Similarly, the contrast in frost resistance between Año Nuevo at one extreme and Cedros at the other is

TABLE 11–Summary of population differences revealed in this experiment for tree-form variables and other morphological traits. Pluses denote superiority, minuses inferiority, zeros average, dots no satisfactory data.

Feature		Population						
		Año Nuevo	Monterey	Cambria	Guadalupe	Cedros	Kaingaroa	Nelson
Tree form								
Overall		– –	0	+	+	– – –§	++	+
Stem straightness		– –	0	+	++	+	++	0
Forking (lack):	early	– –	0	–	0	++	++	0
	later	–	~+	–	~0	–	++	~+
Branch habit	early	– –	0	0	++	+	++	0
quality:	later	–	+	+	–	–	++	+
Butt straightness		– –	– –	+	++	++	+	–
Maturation rate*								
Sealed buds†		+	– –	– – –	+++	++	++	+
♂ strobili‡		++	–	– –	–	•	++	++
♀ strobili‡		+	–	– –	++	•	++	++
Bark thickness*								
Early		0	++	+	– –	– –	++	++
Later		+	++	0	– – –	– – –	++	++

* Not implying preference for either high or low values.

† Unadjusted for tree heights.

‡ From Burdon & Bannister (1973a).

§ Taking into account form observed in neighbouring pure stand of Cedros material.

presumably adaptive, as is the prominent tap-root or sinker-root development in the Cedros population (Burdon & Bannister 1973a). Some other features, however, are very hard to explain convincingly in adaptive terms, e.g., the major differences among the mainland populations in the onset of producing sealed buds, despite the large and very heritable variation within populations (Burdon, Bannister & Low 1992a) which would allow rapid shifts under any directional selection. Cone size differs strongly among populations (Axelrod 1980) and, while Axelrod argued strongly that large cones are an adaptation to drought, he did not address the possible biotic selection imposed by squirrel predation of cones and he did not appear to explain why cones were smallest in Cedros which was the driest habitat. Moreover, cone size also shows great variability within populations (Forde 1964b) and a high heritability has been demonstrated, albeit in the broad sense (Burdon & Low 1973), which should make cone size also very responsive to any directional selection. The comparative fire ecology of the various populations is not well known. Although not evident from this experiment, Cedros material has shown profuse and relatively precocious cone production on some other sites; this feature along with the thin bark could betoken less dependence on trees surviving fires and more on regeneration after each fire.

Founder effects, as well as local selective pressures, were presumably important in shaping the population differences, because there must have been various local extinctions and colonisations associated with climatic changes and associated eustatic changes in sea level since the late Tertiary. These founder effects would reflect both the immediate source populations and the genetic samples that colonised from those sources.

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