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GENETIC SURVEY OF *PINUS RADIATA*.
3: VARIANCE STRUCTURES AND NARROW-SENSE HERITABILITIES FOR GROWTH VARIABLES AND MORPHOLOGICAL TRAITS IN SEEDLINGS

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

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

ABSTRACT

Within-population variances (σ^2) and narrow-sense heritabilities (h^2) were estimated in a *Pinus radiata* D.Don provenance-progeny trial. Samples from the five natural populations and two New Zealand "land-race" populations were included, each as 50 wind-pollinated progenies, on two sites in Kaingaroa Forest in the central North Island of New Zealand. Assessments were made to around 8 years throughout and to 11–12 years in a sample. Estimates of heritabilities provisionally assumed random mating to give "apparent" heritabilities, but a basis was developed for revising estimates in the light of information or assumptions on departures from random mating.

Natural populations usually gave higher apparent h^2 than New Zealand plantation material, especially for growth traits in island material and when the trees were younger. Population differences in apparent h^2 mainly reflected differences in between-family $\hat{\sigma}^2$, but the New Zealand material also showed less within-family $\hat{\sigma}^2$ for growth traits. These higher estimates of heritabilities and variances in natural populations appear to reflect appreciable non-randomness of mating, including significant inbreeding, and presumably associated contributions of non-additive gene effects. Allowing for likely biases arising from population differences in mating patterns, the different populations appeared to have generally similar variances (or coefficients of variation) and heritabilities for individual traits.

Genotype-site interaction appeared unimportant for the two sites, but there was some obscure family-block interaction which tended to erode the overall heritabilities for the less heritable traits, notably early heights. Pooling subpopulations within natural populations was usually immaterial to h^2 and $\hat{\sigma}^2$.

The results indicated the following h^2 values around age 8: forking and current leader dieback, 0–0.05; stem diameter (and stem volume), butt sweep score, and current retarded leader, 0.1; branch habit quality score, 0.1–0.15; height, 0.1–0.2; stem straightness score, 0.2; branching angle score, 0.2; branching frequency score, 0.2–0.25; branch cluster counts, ≥ 0.4; sealed bud scores, 0.5. Coefficients of variation declined with age for height but increased for stem diameter, recent increments tended to be less heritable than cumulative values for height but more so for diameter, and various heritabilities

* Present address: Acacia Road, Lake Okareka, R.D.5, Rotorua, New Zealand

appeared to rise with age. Although experimental conditions were not ideal the 7–9 year h^2 values concur well with those in other reports, particularly in respect of comparative heritabilities among traits. Heritabilities in select material thus appear to have been similar to those in both native populations and the New Zealand land races that have served as base populations.

INTRODUCTION

The *Pinus radiata* Genetic Survey experiment, which has been described by Burdon, Bannister, Madgwick & Low (1992) in the first paper of this series, was designed partly to provide a usable and broadly based collection of genetic material and partly to study as many aspects of the species' genetic variation as possible. The second paper in the series (Burdon, Bannister & Low 1992a) covered population (provenance) differences revealed by the experiment for growth variables, some disease resistances, and morphological traits.

This paper covers for most of the same traits the narrow-sense heritabilities and the variation within populations, although the variation is addressed largely in terms of coefficients of variation rather than variances as such.

A knowledge of variances and heritabilities within populations is important for various breeding decisions, which include whether to try to breed for a trait, and how best to breed for it. In addition to revealing the scope for genetic gain in individual traits, a study of variances can shed light on variation in heritabilities according to the age of trees, or according to population, as well as reflecting the comparative importance of genetic variation between main population units, between local subdivisions within populations, and from tree to tree. Such information can show *inter alia* whether improvement is best sought by breeding from within the population(s) to hand or by drawing on additional populations. Other information, which can be important in deciding how to breed for individual traits and extremely important in ascertaining which breeding objectives are mutually compatible, involves intercorrelations among traits, especially genetic correlations. Such intercorrelations are addressed in the fifth paper of the series (Burdon, Bannister & Low 1992c).

Other studies of variances and heritabilities have been undertaken with *P. radiata* (e.g., Bannister 1969, 1979, 1980[1,2,3]; Burdon 1971[4]; Cotterill & Zed 1980[5]; Shelbourne & Low 1980[6]; Guinon *et al.* 1982[7]; Dean *et al.* 1983[8]; Carson 1986[9]; Cotterill *et al.* 1987[10]; Cotterill & Dean 1988[11], 1990[12—a review]; Johnson 1990[13]), some beginning well before this one, some running essentially in parallel, and some postdating it, but all having one or more limitations in scope. These limitations include: small samples in terms of numbers of parents and/or of individuals within genetic groups (all except [5,6,7,9]), which make estimates imprecise; the use of a single population (all except [7]), which does not guarantee generality of results; the study population being a mixture/hybrid swarm involving more than one natural population (probably all except [7]), so it might show more genetic variability and therefore higher heritabilities than any natural population; the parents being highly select (exceptions being [1,2,3,4,7,8]), which would bias estimates of variances and heritabilities downwards; choosing parents that were phenotypic oddities or drawn from some undefined mix of populations, which would cause the opposite bias; or using clonal

material [4,7], which creates an upward bias in estimates of additive genetic variances and narrow-sense heritabilities through non-additive gene effects, and potential complications through expression of genetic differences being different in the clonal material compared with seedlings.

This study avoided most of the above limitations. Being based on both native and cultivated populations, and being complemented by a study of clonal material that was intermixed with part of the experiment (Burdon, Bannister & Low 1992b), it could also be used to shed light on the respective mating patterns in native and cultivated stands and on the comparative importance of non-additive v. additive gene effects. This knowledge could in turn be used to refine the estimates of heritabilities and variances that had to be made from open-pollinated progenies (families).

MATERIALS AND METHODS
The Experiment

Details of the experiment have been given by Burdon, Bannister, Madgwick & Low (1992). Briefly, each of the five natural populations (from Año Nuevo, Monterey, and Cambria in mainland California, and from Guadalupe and Cedros Islands) plus two New Zealand "land-race" populations (Kaingaroa and Nelson) were represented as 50 wind-pollinated progenies (families). Planting was spread over 3 years (stages) on two sites in Kaingaroa Forest, giving six site/stage blocks containing a total over all blocks of about 40 trees per progeny, with virtually complete randomisation of these trees within each block.

Basic Statistical Analysis

The principles adopted for statistical analysis and the basis for estimating variance components have also been set out by Burdon, Bannister, Madgwick & Low (1992), but it may be noted here that the effect of sites, stages, and site × stage interaction could be absorbed into a single main effect, blocks, which showed random interactions with the hierarchy of genotypic effects, viz populations (pops), subpopulations (subpops) (if differentiated), and families.

Provisional Estimates of Narrow-Sense Heritabilities

Heritability estimates were calculated from the variance component estimates derived from various ANOVA models of Burdon, Bannister, Madgwick & Low (1992, Table 6), on the provisional assumption that random mating had occurred in all populations, such that the progenies would be half-sib families. Such estimates are called "apparent" heritabilities; implications of likely departures from this assumption are addressed later.

The bases of the various estimates (Table 1) differed principally in whether they applied:

• Within single populations (cases 1, 2, 5, 6, 9), or were pooled within-population estimates over the two or three populations within a group ([Californian] mainland or New Zealand) (cases 3, 4, 7, 8, 10).

• Within a single block (cases 1–4), or were either pooled (cases 5–8) within-block values, or else averaged (cases 9–10) over blocks.

TABLE 1–Alternative forms of narrow-sense heritability.

Case No.	Designation	ANOVA*	Basis			
			Block(s)	Subpops (where applicable)	Pop(s)	Estimation
1	$h^2_{(b)}$	4	Single	Bulked	Single	$\dfrac{k^{-1}\hat{\sigma}^2_f}{(\hat{\sigma}^2_f + \hat{\sigma}^2_w)}$
2	$h^2_{(b)(sp)}$	3	Single	Pooled within	Single	$\dfrac{k^{-1}\hat{\sigma}^2_{f(sp)}}{(\hat{\sigma}^2_{f(sp)} + \hat{\sigma}^2_w)}$
3	$h^2_{(b)(p)}$	2†	Single	Bulked	Pooled	$\dfrac{k^{-1}\hat{\sigma}^2_{f(p)}}{(\hat{\sigma}^2_{f(p)} + \hat{\sigma}^2_w)}$
4	$h^2_{(b)(sp(p))}$	1†	Single	Pooled within	Pooled	$\dfrac{k^{-1}\hat{\sigma}^2_{f(sp(p))}}{(\hat{\sigma}^2_{f(sp(p))} + \hat{\sigma}^2_w)}$
5	h^2	4‡	Overall	Bulked	Single	$\dfrac{k^{-1}\hat{\sigma}^2_f}{(\hat{\sigma}^2_f + \hat{\sigma}^2_{fb} + \hat{\sigma}^2_w)}$
6	$h^2_{(sp)}$	3‡	Overall	Pooled within	Single	$\dfrac{k^{-1}\hat{\sigma}^2_{f(sp)}}{(\hat{\sigma}^2_{f(sp)} + \hat{\sigma}^2_{f(sp)b} + \hat{\sigma}^2_w)}$
7	$h^2_{(p)}$	2†‡	Overall	Bulked	Pooled	$\dfrac{k^{-1}\hat{\sigma}^2_{f(p)}}{(\hat{\sigma}^2_{f(p)} + \hat{\sigma}^2_{f(p)b} + \hat{\sigma}^2_w)}$
8	$h^2_{(sp(p))}$§	1†‡	Overall	Pooled within	Pooled	$\dfrac{k^{-1}\hat{\sigma}^2_{f(sp(p))}}{(\hat{\sigma}^2_{f(sp(p))} + \hat{\sigma}^2_{f(sp(p))b} + \hat{\sigma}^2_w)}$
9	$\bar{h}^2_{(b)}$	–	Averaged	Bulked	Single	$\sum_b \hat{h}^2_{(b)} / N_b$
10	$\bar{h}^2_{(b)(p)}$	–	Averaged	Bulked	Pooled	$\sum_b \hat{h}^2_{(b)(p)} / N_b$

*	Burdon, Bannister, Madgwick & Low (1992)
†	Or New Zealand counterpart thereof (1 d.f. for populations, etc.)
‡	Extended to include blocks as a random main effect
§	Not used in finally tabulated results or intermediate steps thereof
σ^2_w	Variance within family/block subclasses, which may be pooled in various combinations of populations and/or blocks.
σ^2_f	Variance between families (with any subpops bulked) in one population.
$\sigma^2_{f(sp)}$	Variance between families within subpops in one population.
$\sigma^2_{f(p)}$	Pooled variance between families within pops.
$\sigma^2_{f(sp(p))}$	Pooled variance between families within subpops within pops.
σ^2_{fb}	Interaction variance between blocks and families within one population, etc.
k	Coefficient of relationships in families, provisionally assumed to be $^1/_4$ (see later)
N_b	Number of blocks involved (≤ 6)

• Within subpopulations (cases 2, 4, 6, 8) or with subpopulations bulked (cases 1, 3, 5, 7, 9).

Further alternatives existed, and were explored, in whether or not to include some of the genotype × block interactions in the ANOVA models, in other words, whether to pool the interactions with residuals.

Conditions for expected discrepancies between different forms of heritability (Table 1) are summarised in Table 2. They centre around whether there is differentiation between subpopulations within populations (mainland and Cedros) and whether there is appreciable family $\times$ block interaction. The estimates, $\widetilde{h}^2_{(b)}$ and $\widetilde{h}^2_{(b)(p)}$ (Table 1, cases 9 and 10), being arithmetic averages rather than based on pooled sums of squares, are admittedly crude approximations, but they were a practical means of obtaining a general picture for the traits that had not been assessed in all blocks. For those traits that had been assessed in all blocks it was possible to compare $\widetilde{h}^2_{(b)}$ with $\hat{h}^2$, the discrepancy reflecting primarily the contribution of block $\times$ family interaction, on the basis that $\sigma^2_{f(b)} = \sigma^2_f + \sigma^2_{bf}$, etc.

The statistical significance of an estimated heritability is given by the test for the significance of the families effect contributing to the numerator (Table 1). The precision of a heritability estimate is indicated to a large degree by its statistical significance of the families effect. Confidence limits for heritability estimates, while they can be calculated, do not reflect the extent to which a heritability is specific to the circumstances of an individual experiment, especially for weakly heritable traits.

TABLE 2–Summary of conditions expected to generate specific inequalities between alternative narrow-sense heritabilities (*see* Table 1 for definition of notation).

Inequality(ies)		Cause	
$h^2_{(sp)}$	$< h^2$	σ^2_{sp}	> 0
$h^2_{(b)(sp)}$	$< h^2_{(b)}$		
$h^2_{(sp(p))}$	$< h^2_{(p)}$	$\sigma^2_{sp(p)}$	> 0
$h^2_{(b)(sp(p))}$	$< h^2_{(b)(p)}$		
h^2	$< h^2_{(b)}, \overline{h}^2_{(b)}$	σ^2_{fb}	> 0
$h^2_{(sp)}$	$< h^2_{(b)(sp)}$	$\sigma^2_{f(sp)b}$	> 0
$h^2_{(p)}$	$< h^2_{(b)(p)}, \overline{h}^2_{(b)(p)}$	$\sigma^2_{f(p)b}$	> 0
$h^2_{(sp(p))}$	$< h_{(b)(sp(p))}$	$\sigma^2_{f(sp(p))b}$	> 0

Comparisons of Variances Among Populations

Comparisons of variances among populations and between ages within a population are complicated, when considering growth variables, by a tendency for variances to be related to means. It was appropriate to study such relationships, and deemed more informative to express the variation in terms of coefficients of variation. Where traits were measured by subjective ratings using scales with set bounds, variances were smaller when the means were near the bounds of the scale. While this feature can be accommodated in order to express meaningful coefficients of variation for traits that vary continuously between two set bounds (Burdon & Low 1992), we were dealing with a small number of discrete categories (scores). It was deemed more appropriate, where means sometimes fell close to the bounds, as sometimes happened with sealed-bud scores, to plot population variances against means, in order to ascertain whether individual means departed materially from the overall curvilinear relationships between variances and means. For scores that clustered around mid-scale, direct comparisons of within-population variances were satisfactory.

Adjustment of Parameter Estimates for Non-randomness of Mating

Background

Some departures from random mating undoubtedly occurred, which must have led to upward biases in estimates of additive genetic variance and narrow-sense heritability. These departures were conveniently addressed in terms of two components, inbreeding and "full-sibbing". The impacts of inbreeding and full-sibbing, on expected composition of among-family and within-family variances, are covered in the Appendix. These expectations reveal the expected biases in estimates, based on the assumption of a perfect half-sib family structure, of additive genetic variances and narrow-sense heritabilities. In turn, this affords a basis for adjusting such "provisional" estimates for the non-random components of the mating patterns, provided that acceptable estimates are available for mating parameters and the relative importance of certain non-additive genetic variances.

The inbreeding can include various forms of related matings, although in the New Zealand land-race populations, with their population structures, selfing is likely to be very much the main form. The approach to addressing inbreeding is based on the key proposition (*see* Appendix) that the parents were non-inbred, with F, the inbreeding coefficient, or fixation index, equalling zero. Inbreeding can thus be quantified, for present purposes, as an equivalent selfing rate, z, which equals 2F. Full-sibbing represents the presence of a finite number of unrelated pollinators, and is defined here as the reciprocal of the effective number of unrelated pollinators.

While both the designated components of non-random mating will presumably be represented in certain matings, particularly within natural stands, it still appears appropriate to treat them as separate mating parameters for deriving expected variances.

Extension of genetic model

Considering an additivity plus dominance genetic model, with no epistasis, the following expectations were adopted to account for non-randomness of mating (*see* Appendix, Eqn A1, A2 for further detail):

Between-families variance $(\sigma^2_f) \quad = \frac{1}{4}h^2\sigma^2_P [(1 + z)^2 + y(1 - z) + (y + z - yz)D]$ (1)

Within-families variance $\quad (\sigma^2_w) \quad = h^2[(\frac{3}{4} + D - \frac{1}{4}z - \frac{1}{2}zD - \frac{1}{4}z^2 + \frac{1}{4}yz +$

$$\frac{1}{4}yzD) + (1 - h^2)] \sigma^2_P \qquad (2)$$

$$\sigma^2_f + \sigma^2_w = \{h^2[1 + \frac{1}{2}z + (1 - \frac{1}{4}z)D] + (1 - h^2)\} \sigma^2_P \qquad (3)$$

where $D \quad = \quad \sigma^2_D/\sigma^2_A$ i.e., the ratio of dominance genetic variance to additive genetic variance

$\quad$ y $\quad = \quad$ rate of full-sibbing, = (effective No. of unrelated pollinators)$^{-1}$

$\quad$ z $\quad = \quad$ equivalent rate of selfing, i.e., 2F for parental F = 0

$\quad \sigma^2_P = (1 + D) \sigma^2_A + \sigma^2_e$

$\quad \sigma^2_e \quad = $ environmental variance $= [1 - (1 + D)h^2] \sigma^2_P$

Upward biases in $4\hat{\sigma}^2_f$ as an estimate of σ^2_A, and $4\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_w)$ as an estimate of h^2, are obvious.

Solving for h^2, with available estimates or assumed values for y, z, and D, gives $\hat{h}^2$ adjusted for non-random mating. The factor, Q, for adjusting the provisional $\hat{h}^2$ obtained as $4\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_w)$, is given by

$$Q = 1/[(1 + z)^2 + y(1 - z) + (y + z + yz)D] \qquad (4)$$

(cf. Appendix, Eqn A3).

This factor, which under the specified genetic model is the unbiased adjustment of $4\hat{\sigma}^2_f$ as an estimate of σ^2_A, is a good approximation unless both z and h^2 are high, in which case it can represent an overcorrection of the provisional $\hat{h}^2$ (Appendix, Eqn A3; also Burdon & Low 1992).

Adjustments based on more elaborate genetic models (Appendix 1C), which could include epistasis or inbreeding depression as such, may be more realistic, but appear intractable.

Application to present case

The relevant considerations for adjusting the genetic parameter estimates for non-randomness of mating are:

- Comparisons of estimates of narrow-sense heritability, assuming half-sib families, between New Zealand material (in which non-randomness of mating was evidently less and therefore expected to generate little upward bias in the estimates) and natural populations (in which non-randomness of mating was evidently greater and therefore expected to generate greater upward bias)—material presented in this paper.

- Inbreeding (F) statistics based on isozyme studies (Moran *et al.* 1988; also Plessas & Strauss 1986) which are available in the most relevant forms for parents ($F \approx 0$) and seed embryos ($F \approx 0.1$, 0.225, and 0.175 for Californian mainland, Guadalupe, and Cedros respectively).

- Comparative percentages, of chlorophyll-defective germinants (between New Zealand populations and their Californian progenitors), assuming no changes in allele frequencies since introduction to New Zealand—Burdon & Bannister (1973, and unpubl.) observed in the New Zealand land-race material an incidence about one-tenth of that in the samples from the progenitor populations.

- Likely rate of self-fertilisation in dense plantations, assumed to be 2% or less (cf. Friedman & Adams 1981), which accords with the comparative incidences of chlorophyll defectives (*see* above), in conjunction with the F statistic of 0.1 (suggesting a "selfing equivalent" rate of 0.2) in seeds from the Californian mainland.

- Likely degree of selective elimination of inbreds, which will include germination failure and some other losses until pricking out into the planting-stock containers (unrecorded), plus field losses (totals recorded but selectivity could only be guessed).

- Comparisons of estimates of narrow-sense heritability (this paper) and broad-sense heritability (Burdon, Bannister & Low 1992b), applying the provisional assumption that systematic discrepancies will stem almost entirely from non-additive gene effects, which in turn were assumed to reflect dominance variance (σ^2_D), at least in the New Zealand material. Also considered were empirical findings that the ratio of non-additive to additive genetic variance tends to decline with age (Dean *et al.* in press; Burdon, Low &

A. Firth unpubl.; Low unpubl.), and which sorts of traits have so far shown evidence of relatively greater specific combining ability (Carson 1986; Cotterill *et al.* 1987; Johnson 1990; Burdon unpubl.) and inbreeding depression (Wilcox 1983).

• Comparisons of estimates of genotypic variances between families and between clones within families, in different population groups (Burdon, Bannister & Low 1992b).

The effective values of mating parameters that were finally assumed in connection with this paper are listed in Table 3. The assumptions were based on a combination of available evidence and plausibility.

In practice there is no explicit and convenient algorithm to combine the various items of information—some of the items were based on several alternative comparisons between statistics, and so unique iterative solutions could not readily be made, and some had to be based largely on "educated guesswork". Rather, it was a matter of judging which set of parameter values best account for the observed statistics. In particular there were the dual uncertainties as to the comparative mating patterns represented in the different populations or population groups and the comparative heritabilities, since heritability estimates depended on assumptions.

TABLE 3–Assumed values (%) of mating-pattern parameters represented in surviving samples assessed for the respective populations

Parameter (or estimate)	Population group			
	Mainland	New Zealand	Guadalupe	Cedros
Self-fertilisation equivalent*	20	2	45	35
Field mortality etc.	6	3.4	18	28
Likely selective loss of inbreds*	10	>1	27.5	20
Residual selfing† (= z = F/2)	10	<1	17.5	15
Full-sibbing (y) a)‡	20	10	25	20
b)§	10	5	20	10

* *See* main text for explanation.

† Equivalent selfing rate represented in surviving trees for which data were analysed for traits in question.

‡ Values used for presented results. That for New Zealand is compromise between 20% indicated by Burdon, Bannister & Low (1992b, Tables 8 and 9) and almost zero indicated by Burdon & Low (1992) and < 10% by Burdon, Gaskin, Zabkiewicz & Low (1992).

§ Alternative set of values, which were also considered, giving more weight to observations for *P. sylvestris* (*see* Müller 1977; Yazdani *et al.* 1989)

RESULTS

Heritabilities

Assuming random mating

Estimates of between-family variances and heritabilities ($\sigma^2_{f(b)}$ and $h^2_{(b)}$ respectively) within blocks tended to vary erratically, reflecting the small within-family samples, and in general are not presented. However, heritability estimates overall ($\hat{h}^2$) (Table 4) and arithmetically averaged over blocks ($\hat{h}^2_{(b)}$ or $\hat{h}^2_{(b)(p)}$) (Table 5) showed much more coherent patterns.

TABLE 4–Estimates of narrow-sense heritability (h^2, *see* Table 1, case 5) over all blocks, by populations, for individual variables. Any subpopulations were bulked within populations, and family × [site/stage] block interaction treated as a random effect.

Population	Variable†						
	~2.5 yrs	~8 yrs					
	HT	HT	DIAM	BUTT	STR	BR QU	FORK
A Assuming random mating (i.e., "apparent" heritabilities)							
Año Nuevo	0.11***	0.32***	0.21***	0.23***	0.49***	0.18***	0.16***
	(0.05*)‡		(0.14***)‡				(0.11***)‡
Monterey	0.12***	0.22***	0.14***	0.14***	0.25***	0.20***	0.12**
Cambria	0.11***	0.23***	0.16***	0.16***	0.12**	0.26***	0.055**
Kaingaroa	0.054 NS	0.19***	0.11***	0.11***	0.15***	0.11***	0.013 NS
Nelson	0.076**	0.074**	0.087***	0.080**	0.21***	0.15***	0.055*
Guadalupe	0.095**	0.40***	0.34***	0.12***	0.18***	0.22***	0.057*

B. Adjusting Eqn 4 for assumed non-randomness of mating (Table 3)

Inferred σ^2_D/σ^2_A§

	1	0.75	1	1	1	1	1
Año Nuevo	0.07	0.20	0.13	0.14	0.29	0.11	0.10
Monterey	0.07	0.14	0.08	0.08	0.15	0.12	0.07
Cambria	0.07	0.14	0.10	0.10	0.07	0.16	0.03
Kaingaroa	0.04	0.16	0.09	0.09	0.12	0.09	0.01
Nelson	0.07	0.06	0.07	0.07	0.17	0.12	0.04
Guadalupe	0.07	0.21	0.17	0.06	0.11	0.11	0.03

† HT = height; DIAM = dbhob; BUTT = butt straightness score; STR = stem straightness score; BR QU = branch habit quality score; FORK = forking (0 or 1). For fuller definition of variables *see* Burdon, Bannister, Madgwick & Low 1992).

‡ With subpopulations not pooled ($\hat{h}^2_{(sp)}$, *see* Table 1, case 6), resulting in appreciably lower $\hat{h}^2$ for the particular cases concerned.

§ *See* Burdon, Bannister & Low (1992b)

NS = p>0.05
*   = p<0.05
** = p<0.01
*** = p<0.001

Comparing two classes of heritability estimate (Table 5), the estimates over all blocks ($\hat{h}^2$ or $\hat{h}^2_{(p)}$) were almost always less than the average within-block values ($\bar{\hat{h}}^2_{(b)}$ or $\bar{\hat{h}}^2_{(b)(p)}$) respectively), but the discrepancies varied markedly according to the trait. The discrepancies were greatest for early height (HT), but tended to be less for stem diameter (DIAM) and forking (FORK), and were least for "8-year" height and the other tree-form variables (BR CLUS, BR FR, BR QU, BR ANG, BUTT, STR). Estimates of h^2 were not sensitive to whether or not family × block interaction was included in the ANOVA model; pooling the interaction sums of squares with the residual generally inflated $\hat{h}^2$ only very slightly, even when such interaction was appreciable. On the other hand, the presence of interaction readily reduced both $\hat{h}^2$ compared with $\hat{h}^2_{(b)}$ and the statistical significance of $\hat{h}^2$. Even so, the large majority of the $\hat{h}^2$ values (Table 4), and all but one of the available estimates over all blocks and pooled over populations within groups ($\hat{h}^2_{(p)}$, Table 5), were very highly significant (p < 0.001).

TABLE 5–Average within-population within-block narrow-sense heritability estimates ("apparent" heritabilities assuming random mating), by population groups, for different variables, with subpopulations bulked; based on pooled within-population estimates in the (Californian) mainland and New Zealand material. Figures in brackets are corresponding overall narrow-sense heritability estimates over all blocks for the traits concerned.

Variable		Population group						
Trait*	Year(s)	Mainland		New Zealand		Guadalupe		Cedros
		$\bar{h}^2_{(b)(p)}$†	($\hat{h}^2_p$)†	$\bar{h}^2_{(b)(p)}$†	($\hat{h}^2_p$)†	$\bar{h}^2_{(b)}$†	($\hat{h}^2$)†	$\bar{h}^2_{(b)}$†
HT	1	0.28		0.15		0.32		0.36
	~2.5	0.20	(0.12)	0.14	(0.07)	0.25	(0.09)	0.49
	~4	0.19		0.12		0.43		0.47
	~8	0.29	(0.26)	0.18	(0.13)	0.67	(0.40)	0.48
	~11.5	0.30		0.36		0.66		0.24
DIAM	~8	0.26	(0.18)	0.19‡	(0.10)	0.60	(0.34)	0.48
	~11.5	0.34		0.29‡		0.56		0.11§
BARK	~8.5	0.37		0.31		0.29		0.09
	~11.5	0.38		0.39		0.50		0§
BR CLUS	1	0.33		0.20		0.25		0.18
	~4	0.65		0.44		0.72		0.47
	~7	0.64	(0.74)	0.55	(0.46)	0.88		0.46
BR FR	~8	0.41		0.26		0.39		0.33
	~11.5	0.38		0.40		0.70		0.44§
BR QU	~8	0.24	(0.23)	0.12‡	(0.13)	0.25‡	(0.22)	0.27‡
	~11.5	0.31		0.32		0.46		0.30§
BR ANG	~8	0.27		0.23		0.32		0.42
BUTT	~8	0.25	(0.20)	0.10‡	(0.09)	0.20	(0.12)	0.19
STR	~8	0.34	(0.30)	0.21‡	(0.19)	0.28	(0.18)	0.26
	~11.5	0.56		0.28‡		0.42		0.50§
FORK	~8	0.21	(0.13)	0.03‡	(0.03)	0.10‡	(0.06)	0.08
	~11.5	0.16‡		0.03‡		0.12		0.30§
BUDS	~3	0.59		0.56		0.75		0.35
RLDR	~1.5	0.02‡		0.05		0.05		0.12
	~4	0.13		0.16‡		0.12‡		0.39
AP ABORT	2	0.16		0.09‡		0.13		–
CROWN	~10	0.41		0.25		0.63		0.15
DBK	~8	0.11		0		0.20‡		0.03

* BARK = bark thickness; BR CLUS = no. of branch clusters on main stem; BR FR = branch cluster frequency score; BR ANG = branch angle score; BUDS = sealed buds score; RLDR = retarded leader (0 or 1); AP ABORT = apical abortion (thrip damage) score; CROWN = crown retention (Cyclaneusma resistance) score; DBK = leader dieback; otherwise as defined for Table 1. For definition of remaining traits *see* Table 4. For fuller description of variables *see* Burdon, Bannister, Madgwick & Low (1992).

† *See* Table 1 for definition.

‡ Subject to some upward bias through setting lower bound of zero for individual $\hat{h}^2_{(b)}$.

§ Very limited data available.

Among population groups, the New Zealand material tended to show the lowest apparent heritabilities, and Guadalupe the highest. In Cedros, the apparent heritabilities were generally relatively high, although the values for later (age ~ 11.5) growth variables and for foliage retention (CROWN) tended to be low.

Apparent heritabilities were not identical among populations within the Californian mainland and New Zealand groups respectively (Table 4), but the differences were generally well within likely sampling error. Apparent exceptions (i.e., material disparities) were: low $\tilde{h}^2_{(b)}$ for buds in Cambria (0.21) compared with c. 0.7 for Año Nuevo and Monterey (not tabulated); the differing $\hat{h}^2$ values for straightness scores in the Californian mainland populations (Table 4) which, however, were far less evident when $\tilde{h}^2_{(b)}$ values were compared for straightness scores at 11–12 years (not tabulated); and a higher $\tilde{h}^2_{(b)}$ for die-back in Cambria (~ 0.2, not tabulated) than in Año Nuevo and Monterey (~ 0.05). While $\hat{h}^2$ was somewhat higher for several variables in Año Nuevo compared with Cambria and Monterey (Table 4), this was not evident in $\tilde{h}^2_{(b)}$ values (not tabulated) for the more complete set of variables.

Bulking subpopulations appreciably raised heritability estimates compared with within-population values only with early height, stem diameter, and forking, just in Año Nuevo (Table 4), reflecting some appreciable differences among the subpopulation samples in this population.

Height growth (HT) generally showed marked increases in $\hat{h}^2$ between age 2–3 (from planting) and around age 8 (Table 4); time trends for $\hat{h}^2_{(b)}$, however, were not so clear, being apparently inconsistent among population groups (Table 5). Diameter (DIAM) showed apparent within-block heritabilities ($\hat{h}^2_{(b)}$ or $\hat{h}^2_{(b)(p)}$) similar to height, but lower overall apparent heritabilities ($\hat{h}^2$ or $\tilde{h}^2_{(b)}$) than height (Table 5). Heritability estimates for stem volume (assuming constant form factor) were virtually identical to those for diameters, and so are not tabulated. Periodic increments in diameter generally showed apparent higher within-block heritabilities ($\hat{h}^2_{(b)}$ or $\hat{h}^2_{(b)(p)}$) than diameter at the ends of the periods (Table 6). The later periodic height increments, in contrast, showed much lower apparent heritabilities than the "final" heights (Table 6).

Crown retention (CROWN) scores (putatively reflecting resistance to *Cyclaneusma minus* (Butin) diCosmo et al.) showed some high apparent heritabilities ($\tilde{h}^2_{(b)} \geq 0.4$) in native populations (Table 5), except for Cedros in which scoring was complicated by appreciable crown suppression. Dieback incidence (DBK) (current rather than cumulative) showed very low heritabilities (Table 5), the highest estimates being for Guadalupe (0.2) and Cambria (0.2, not tabulated separately) which were the populations most affected. Apical abortion (AP ABORT) (putative thrip attack of the growing tip) showed low apparent heritability (Table 5).

Among the branching traits (Table 5), branch cluster (so-called branch whorl) counts (BR CLUS) from about year 4 onwards showed the highest apparent heritabilities, generally upwards of 0.5. Branching frequency scores (BR FR) showed somewhat lower values ($\hat{h}^2_{(b)}$ generally ≥ 0.3), while scores for branching angle (BR ANG) and overall branch habit quality (BR QU) generally showed even lower values. Stem straightness scores (STR) showed apparent heritabilities similar to the last-mentioned branching traits, which were rather higher than those for butt sweep scores (BUTT) (Table 5). All these tree-form traits tended to show higher heritabilities as the trees got older. Forking generally showed low to very low apparent heritabilities, while apparent heritabilities for current retarded leader (RLDR) were initially very low but were appreciably higher around age 4 (Table 5).

Bark thickness (BARK) generally showed apparent heritabilities ($\hat{h}^2_{(b)}$) of 0.3–0.4, with the exception of very low values for Cedros (Table 5). Adjusting bark thickness sums of

TABLE 6–Within-population heritability estimates, ("apparent" heritabilities, assuming random mating), for periodic increments compared with corresponding estimates for end-of-period measurements, for growth traits.

Trait	Site/Stage block	Period/ age (years)	Population group			
			Californian mainland (pooled)	New Zealand (pooled)	Guadalupe	Cedros
			-----------$h^2_{(b)(p)}$*-----------		---------$h^2_{(b)}$†---------	
DIAM	A III	7–8	0.38	0.25	0.63	0.15
		8	0.25	0.27	0.42	0.31
	B II	9–12	0.56	0.36	0.82	0.22
		12	0.50	0.33	0.67	0.08
HT	B III	3–5	0.26	0.11	0.52	–
		5	0.22	0.06	0.29	–
		5–9	0.18	0.11	0.53	–
		9	0.22	0.09	0.41	–
	A I	4–7	0.29	0.16	0.51	–
		7	0.46	0.18	0.58	–
	B I	5–12	0.37	0.21	0.35	–
		7–12	0.12	0.13	0.21	–
		12	0.43	0.24	0.46	–
	A II	4–7	0.31	0.18	0.91	–
		7	0.12	0.29	0.91	–
		7–11	0‡	0.18	0.31	–
		11	0‡	0.36	0.92	–

*   *See* Table 1, case 3
†   *See* Table 1, case 1
‡   Negative estimate revised to lower theoretical bound

squares for within-subclass covariance on stem diameter generally had very little impact on estimated heritability for bark thickness, except in the Guadalupe population where such adjusted heritabilities (not tabulated) were close to zero. Sealed bud scores (BUDS) showed consistently high apparent heritabilities, $\hat{h}^2_{(b)}$ generally exceeding 0.5 despite the subjective and relatively crude scoring scale (Table 5). Estimated between-family variances (not tabulated) within the mainland populations for BUDS were around one-quarter to one-fifth the "variance" among those populations.

Adjusting for assumed non-randomness of mating

Estimated heritabilities, after adjustment for non-random mating, were generally much more similar among population groups (Tables 4B, 7) than the unadjusted estimates (Tables 4A, 5). Considering the imprecision of point estimates even from the larger data samples, there were very few substantial discrepancies between groups. Guadalupe tended to show higher values than the mainland and New Zealand populations, for growth variables and needle retention (CROWN). With Cedros, for which the data were more limited, the values for several variables did not concur closely with those for the other populations; these included high values or the very early heights, age ~ 8 diameter, and retarded leader (RLDR),

but lower values for age ~ 11.5 height and diameter, bark thickness (BARK), sealed bud scores, and crown retention scores.

Despite some indications of lower heritabilities in New Zealand material, compared with the Californian mainland and Guadalupe Island populations (Table 4B), such a pattern was not clearly evident for the larger set of variables (Table 7).

TABLE 7–Average within-population within-block heritability estimates as for Table 5, but adjusted (Eqn 4) for assumed non-randomness of mating (Table 3).

Variable		Assumed	Population group			
Trait	Year(s)	σ_D^2 / σ_A^2 *	Mainland	New Zealand	Guadalupe	Cedros
HT	1	1	0.17	0.12	0.16	0.20
	~2.5	1	0.12 (0.07)	0.11 (0.06)	0.13 (0.05)	0.27
	~4	1	0.11	0.10	0.22	0.26
	~8	0.75	0.18 (0.16)	0.15 (0.11)	0.36 (0.21)	0.28
	~11.5	0.5	0.19	0.31	0.36	0.14
DIAM	~8	1	0.16 (0.11)	0.15 (0.08)	0.30 (0.17)	0.27
	~11.5	0.75	0.21	0.24	0.30	[0.06]
BARK	~8.5	0.5	0.24	0.26	0.16	0.05
	~11.5	0.25	0.27	0.34	0.28	0
BR CLUS	1	0.25	0.24	0.18	0.15	0.12
	~4	0	0.46	0.39	0.45	0.31
	~7	0	0.46 (0.53)	0.49 (0.41)	0.55	0.31
BR FR	~8	0.5	0.27	0.22	0.21	0.20
	~11.5	0.25	0.21	0.35	0.41	0.28
BR QU	~8	1	0.14 (0.14)	0.10 (0.11)	0.13 (0.11)	0.15
	~11.5	0.5	0.19	0.26	0.23	0.17
BR ANG	~8	0.5	0.18	0.20	0.18	0.25
BUTT	~8	1	0.15 (0.12)	0.08 (0.07)	0.10 (0.06)	0.10
STR	~8	1	0.20 (0.18)	0.17 (0.15)	0.14 (0.09)	0.14
	~11.5	0.5	0.37	0.24	0.23	0.29
FORK	~8	1	0.13 (0.08)	0.03 (0.03)	0.05 (0.03)	0.04
	~11.5	1	0.10	0.03	0.03	0.07
BUDS	3	0	0.42	0.50	0.47	0.23
RLDR	~1.5	1	0.01	0.04	0.03	0.07
	~4	0.05	0.08	0.14	0.07	0.24
CROWN	~10	0.5	0.27	0.21	0.39	0.10
DBK	~8	1	0.07	0	0.10	0.02

* = D (see Burdon, Bannister & Low 1992b)

Variances

Coefficients of phenotypic variation ((phenotypic variance)$^{0.5}$ divided by mean) are exemplified for growth variables, by provenance groups, in Fig. 1. For height, the phenotypic coefficients (CV_P) tended to decline by nearly 50% during about the first 7–8 years, and then stabilise or rise again slightly. For diameter, however, CV_P tended to rise between the two measurements (Fig. 1), particularly in the native populations. The New Zealand material showed consistently the lowest CV values, and the island populations the highest, although
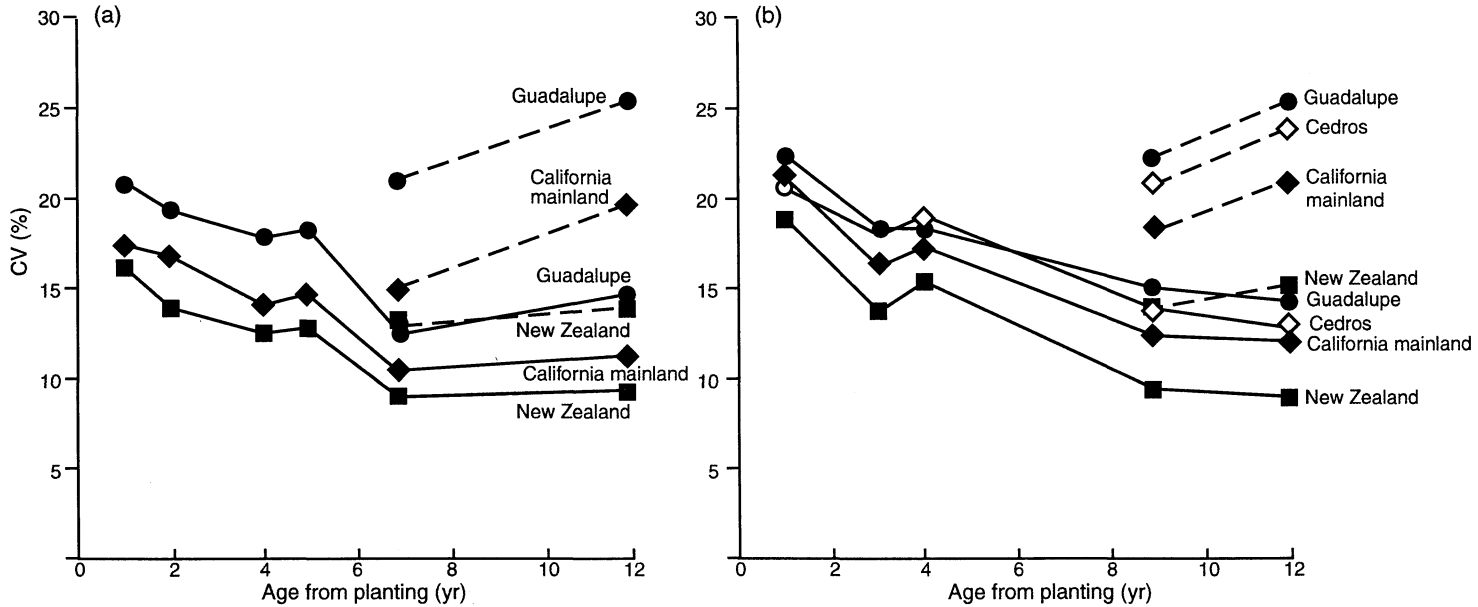
FIG. 1–Examples of within-population phenotypic coefficients of variation (%) (CV_P) for height (plottings joined by solid lines) and diameter (plottings joined by dashed lines) *v.* age, by population groups (a) in Site B Stage I, (b) in Site B Stage II.

Cedros tended to show somewhat lower values than Guadalupe. Periodic growth increments tended to show much higher CV_P values than end-of-period measurements, except when the trees were younger (Table 8).

TABLE 8–Estimated within-population phenotypic coefficients of variation (%) for periodic increments compared with corresponding estimates for end-of-period measurements, for growth traits.

Trait	Site/Stage block	Period/ age (years)	Population group			
			Californian mainland (pooled)	New Zealand (pooled)	Guadalupe	Cedros
			----------Case 3*----------		--------Case 1*-------	
HT	B III	3–5	19	18	17	–
		5	16	17	16	–
		5–9	20	18	22	–
		9	14	14	15	–
	A I	4–7	13	11	18	–
		7	11	9	17	–
	B I	5–12	13	11	17	–
		7–12	19	17	25	–
		12	11	9	14	–
	A II	4–7	14	13	14	–
		7	14	12	14	–
		7–11	20	14	23	–
		11	13	9	15	–
DIAM	A III	7–8	55	37	58	77
		8	23	18	25	29
	B II	9-12	39	25	46	44
		12	21	15	25	24

* *See* Table 1

The decline with age in the CV_P for height growth, which was accompanied by an increase in overall heritability, was reflected in a decline in the coefficients of variation within family/ block subclasses (CV_w), while the between-family coefficients (CV_f) generally appeared to remain fairly constant (Table 9). In Table 9 can also be seen how very similar the corresponding CV values were both among the three Californian mainland populations and among the two New Zealand ones, the within-group differences being far less than those between the population groups.

For straightness scores the variances are of little interest in themselves, on account of the arbitrary nature of the scales used, but population differences in apparent heritability (Tables 4A, 5) were very consistently reflected in the between-family variance estimates rather than in the phenotypic or within-family variances (details not shown). For sealed bud scores, the block-by-block plottings (not presented) of within-population variances v. means showed no consistent trend for individual populations to deviate from the general variance v. mean relationships. For threshold (presence-or-absence) traits, such as forking or dieback, variances were also not amenable to direct comparisons among populations, being subject to the relationship $\sigma_P^2 = x(1-x)$ where σ_P^2 is the phenotypic variance and x is the proportion of incidence which can range from 0 to 1.

TABLE 9–Estimates of coefficients of variation, over entire experiment (assuming random site/stage blocks), by individual populations (based on Case 5, Table 1)

Trait	Age	California mainland			New Zealand		Guadalupe
		Año Nuevo	Monterey	Cambria	Kaingaroa	Nelson	
Between families (CV$_f$)							
HT	~2.5	3.65	3.97	3.64	2.42	2.85	3.16
HT	~8	4.09	3.38	3.51	2.59	1.69	5.15
DIAM	~8	4.90	4.10	4.21	3.00	2.64	7.06
Within family/block subclasses (CV$_w$)							
HT	~2.5	21.2	22.3	21.3	20.5	20.3	23.7
HT	~8	13.9	13.7	14.3	11.7	12.3	15.6
DIAM	~8	20.7	20.5	19.9	17.7	17.7	24.1
Phenotypic (CV$_P$)							
HT	~2.5	21.5	22.7	21.6	20.6	20.5	23.9
HT	~8	14.5	14.1	14.7	12.0	12.4	16.4
DIAM	~8	21.3	20.9	20.3	18.0	17.9	25.1

CV_f = $\hat{\sigma}_f$ /(overall mean)

CV_w = $\hat{\sigma}_w^2$ /(overall mean)

CV_P = $(\hat{\sigma}_f^2 + \hat{\sigma}_w^2)^{0.5}$ /(overall mean)

$(\hat{\sigma}_f^2 + \hat{\sigma}_w^2)^{0.5} \approx (\hat{\sigma}_f^2 + \hat{\sigma}_{fb}^2 + \hat{\sigma}_w^2)^{0.5}$

Numbers of branch clusters on the main stem showed an even greater decline in CV_P with age (Fig. 2) than height, but the values appeared to stabilise after age 4. Among population groups, the Californian mainland material generally showed the highest values. Guadalupe material showed comparatively low CV_P values initially, but not later on.
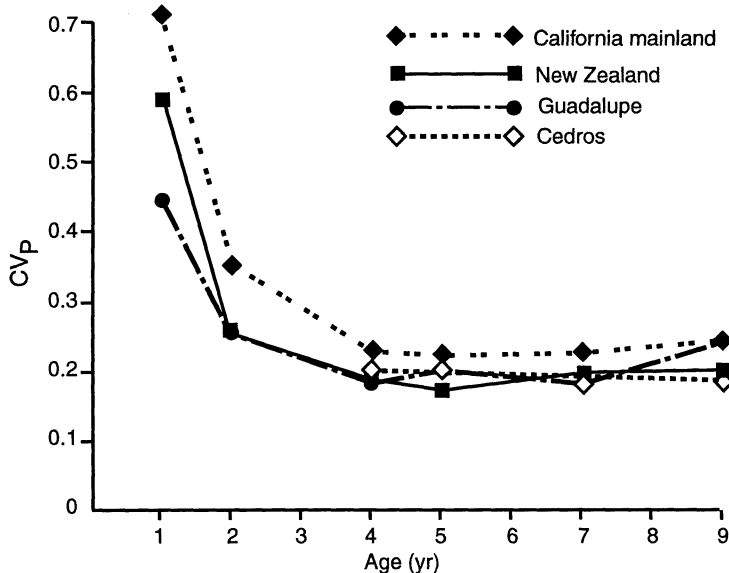

FIG. 2–Within-population phenotypic coefficients of variation for total branch clusters on stem v. age, by population groups, at Site B.

Bark thickness at around age 8 showed CV_P (within blocks) of about 35% (not tabulated) within all populations, but at around age 11 the values were 34%, 27%, 42%, and 38% for Californian mainland, New Zealand, Guadalupe, and Cedros respectively.

DISCUSSION
Overall *v.* Within-block Heritabilities

The differences between estimated overall heritabilities ($\hat{h}^2$, $\hat{h}^2_{(p)}$) and within-block heritabilities ($\overline{\hat{h}}^2_{(p)}$, $\overline{\hat{h}}^2_{(b)(p)}$) (Tables 4A, 5) were readily attributable to block × family interaction. These differences were very marked in early height and in diameter, but not in the branch-habit or straightness traits for which comparisons were available. Early height and "8-year" diameter thus showed marked block × family interaction for which no pattern could be discerned. Incidentally, this parallel in the behaviour of early height and subsequent diameter accords well with the results of Burdon, Bannister & Low (1992c) which indicate that the inheritance of diameter growth tends to reflect that of height growth with a time lag.

The obscure (apparently unpatterned) interaction shown by early height and "8-year" diameter is paralleled by the results of Hodge & White (1992) in that apparent family × site interactions for growth traits in slash pine (*Pinus elliottii* Engelm.) exhibited a much less discernible pattern when the trees were young than later on. This is somewhat analogous to observations that apparent specific combining ability generally becomes less important in *P. radiata* as the trees get older (Dean *et al.* in press; Burdon, Low & A. Firth unpubl.; Low unpubl.).

Early growth thus appears subject to certain obscure interactions between genotype and individual plantings. Some of these interactions probably reflect poorly repeatable effects that become confounded with effects of genotype. Thus individual trials seem subject in the early years to some errors that are not evident from estimates of standard errors made from within the trials. Such effects will create upward bias in heritability but downwards bias in estimates of age-age genetic correlations. The inflated heritability estimates will tend to bias downwards the apparent optimum age for advanced-generation selection, whereas the depressed age-age correlation estimates would tend to bias it upwards, but the net bias is uncertain. Some of the obscure interaction, however, may effectively stem from departures from perfect "age-age" genetic correlations (in this context, Type B correlations*), since it was not possible to standardise closely both the timing and the stage of development for early height measurements. Indeed, stages of development reflected, say, in absolute heights, may be more important than chronological age *per se* in determining patterns of so-called age-age correlations. The early assessments (up to age 3 from planting) inevitably entailed quite large relative differences in age and/or stage of development, and relative rather than absolute age differences seem paramount in generating departures from unity in Type A age-age genetic correlations (Lambeth 1980; King & Burdon 1991). Interactions arising in this way, while they may not actually inflate within-block heritabilities, would betoken very imperfect age-age genetic correlations which would largely vitiate early selection.

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* Type A genetic correlations are expressed in the same set of individuals for both variables; Type B are expressed in independent subsets, for the respective variables, of the same families (Burdon 1977).

Actual Heritabilities

The heritability estimates depended markedly on assumptions concerning mating patterns and the relative importance of non-additive gene effects. Applying plausible assumptions (Table 3) gave a set of adjusted heritability estimates that generally agreed well among the various population groups (Table 7). This approach has an element of circular argument if an essentially common set of heritability estimates is used to verify the assumptions, or if the assumptions are used to substantiate a common set of genetic parameters among the populations. Nevertheless the appeal of a comparatively simple and consistent picture is very strong.

Regarding the importance of particular assumptions, the heritability estimates (Tables 4, 5, and 7) are clearly sensitive to assumed levels of inbreeding, for which there were at least some independent data. Assumptions concerning the rate of full-sibbing (y), and the ratio of dominance to additive genetic variance (D), were generally less critical in this connection, which is important in view of contradictory evidence regarding combinations of y and D (Burdon, Bannister & Low 1992b). Accepting the alternative, lower, values of y (Table 3), the adjusted $\hat{h}^2$ values would be raised by factors of 2.5–4.5% for Guadalupe, 4.5–9% for New Zealand, and 6–12% for the remaining populations. Setting D $\leq$ 1 was arbitrary, and lower in some cases than the comparisons between $\hat{H}^2$ and unadjusted $\hat{h}^2$ (Burdon, Bannister & Low 1992b) suggested, but otherwise most of the inferred D values tended to be high relative to recent reports (Carson 1986; Dean *et al.* in press; Burdon, Low & A. Firth unpubl.; Low unpubl.) and there were suspicions that the $\hat{h}^2/\hat{H}^2$ comparisons tended to over-estimate D. If in fact the assumed values of y and D (Table 3) for deriving adjusted $\hat{h}^2$ values (Tables 4B, 7) were too high, this would tend to be offset by no account being taken of epistasis (Appendix, Eqn A4–A6) or inbreeding depression (Appendix, Eqn A12, A13). Thus the adjusted $\hat{h}^2$ values (Tables 4B, 7) are unlikely to be substantially misleading, although the failure to accommodate inbreeding depression has presumably tended to leave more of a residual upward bias in the adjusted values for natural populations.

The higher adjusted $\hat{h}^2$ values for growth variables and needle retention in Guadalupe than in other populations (Table 5) could reflect the significance of inbreeding depression in this population. Given varying rates of inbreeding among families (cf. Wilcox 1983) the between-families variance, and thence even the adjusted $\hat{h}^2$ values, could have been markedly inflated by inbreeding depression (Appendix, Eqn A13), although inbreeding depression could also inflate within-family variance (Appendix, Eqn A9) which contributes to the denominators of $\hat{h}^2$. It is also possible that in the Guadalupe material adaptational problems, in respect of the test sites, could have accentuated the resolution of genetic differences, and that this could have occurred for early heights in Cedros material.

For several traits Cedros showed relatively low heritability estimates. This may have reflected a combination of: less data, which would produce inherently less precise estimates; a greater degree of truncation selection by suppression and/or culling data according to set thresholds (although the net effects on $\hat{h}^2$ are uncertain); and some heritabilities being depressed (particularly at later ages) by the severe competition suffered by this population. The heritability for needle retention could have been depressed by the last factor, but the population may have genuinely lower heritabilities for bark thickness, branch cluster frequency, and sealed bud score.

Considering other heritabilities in more detail, the higher heritability estimates for dieback incidence (DBK) in the Cambria and Guadalupe populations could well be an effect of a much lower incidence in other populations leading to poorer resolution of family differences—such a relationship was observed by Sohn & Goddard (1978) in fusiform rust infection in *P. elliottii*. The low apparent heritability for "8-year" straightness score (STR) in Cambria may have resulted in part from difficulties in scoring associated with the incidence of dieback, but it should be noted that apparent heritabilities for the "11.5-year" scores did not differ nearly so much among the mainland populations. The low apparent heritability for sealed bud scores in Cambria could not be readily explained in terms of Cambria scores consistently clustering around the bottom end of the scale; but, with only 50 families per population, considerable sampling errors for $\hat{\sigma}_f^2$ and thence $\hat{h}^2$ are likely to occur for the occasional trait. In Guadalupe the heritability for bark thickness at age 8 appeared to reflect the heritability for stem diameter, rather than existing in its own right. The island populations thus appear to differ from the Californian mainland ones in this respect, which is not surprising in view of how different their bark was at that age.

Sealed bud scores are of special interest, being the one trait in this study for which Año Nuevo and Monterey, the ancestral populations of the New Zealand material, differed strongly. Higher variances and heritabilities might therefore have been expected in the New Zealand populations, through genetic segregation in a more broadly-based hybrid swarm or, conceivably, through New Zealand populations containing pure-strain trees of both ancestral populations, but there was no evidence of higher values—adjusted heritability estimates for the New Zealand progenitor populations, Año Nuevo and Monterey (not tabulated), concurred almost exactly with that for the New Zealand material.

Variances and Coefficients of Variation

The coefficients of variation for growth variables (Fig. 1) differed among population groups roughly in step with the between-group differences in apparent heritabilities, which would be expected with some inbreeding in native populations. Differences between seed parents in the rates of inbreeding among the viable seeds that are produced, and differences between those parents in susceptibility to inbreeding depression (cf. Wilcox 1983), can also be expected to increase open-pollinated family differences beyond the true half-sib values, although there was no firm basis for attempting quantitative adjustments for these factors. Inbreeding depression, affecting only some of the individuals within families, would likewise be expected to inflate within-family variances (Appendix, Eqn A9). However, some factors other than straightforward inbreeding effects may have influenced the coefficients of variation. The rise with time in CV_P for diameter presumably reflected competitional effects, and indeed CV_P was almost invariably least in the New Zealand material which must have suffered least from competition. Also, it is likely that the native population material that was less well-adapted to the sites would show more phenotypic "noise" variation, either through inherently less developmental homoeostasis or through growth disturbances arising from a higher incidence of dieback or other diseases. The higher within-family coefficients shown in Table 9 are consistent with this possibility as well as with a more direct effect of increased epistatic variances associated with inbreeding (Appendix, Eqn A7). Phenotypic coefficients of variation for numbers of branch clusters, however, did not differ among population groups in quite the same way as those for growth-rate variables, in that the island populations did

not show higher coefficients, which suggests a pattern of lower coefficients in more "multinodal" populations. Variances for tree-form trait scores are subject to reservations, but the fact that phenotypic variances did not differ obviously between New Zealand and native populations does not suggest that actual inbreeding was generally a major factor, which accords with the comparatively low inbreeding depression generally shown by such traits (Wilcox 1983).

The possibility that a narrow genetic base had markedly reduced genetic variances in the New Zealand land-race populations cannot be discounted, although the size of known early seed introductions (Shepherd 1990) makes this unlikely. A minor caveat, which also attaches to the assumption that the New Zealand parents and families were essentially non-inbred, stems from the possibility that a few Monterey ancestors may have made substantial genetic contributions to the New Zealand population (Burdon 1992).

Comparison with Results from Other Studies

In comparing results with those from other experiments, heritability estimates offer perhaps the most convenient statistics for cross-reference, even though a heritability is in principle specific to the study populations and the experimental conditions. Rigorous comparisons of variances, while they may be possible, are not straightforward, and variances can show the same specificities as heritabilities do.

For comparing heritability estimates with those from other studies, based on plantation-grown stocks, the estimates for the New Zealand populations are the logical benchmark, although this choice of benchmark generally matters little in view of the extent of agreement among population groups in the adjusted estimates (Tables 4A, 7). In general, they agree well with estimates reviewed by Cotterill & Dean (1990, Table 6). Also, the results generally agree very well with those of C.J.A. Shelbourne, A. Firth & C.B. Low (unpubl.) from work in Kaingaroa Forest. Our heritability estimates for forking were generally lower than the estimates for malformation, which may well reflect the fact that we usually treated forking as an all-or-nothing trait (cf. van Vleck 1972) rather than scoring on a multi-point scale. Bannister (1979) reported a much higher apparent heritability for straightness (or crookedness) but, after allowing for the fact that he combined scores from several observers, thereby eliminating most of the random assessment error, the disparity was much less.

Overall, the heritability estimates obtained for select and base-population material were mostly in close agreement, particularly when the different sample population sizes and ages at assessment are considered. This accords with the expectation (cf. Finney 1956) that a combination of high effective heritability and quite intensive selection are needed to achieve a major truncation of between-family variance and thus a large downwards bias in heritability estimates.

In this study there were several factors that would have tended to depress heritabilities below potential values. Site preparation was less intensive than it might have been, and there were some problems of animal damage, while the large block units would have militated against optimal partitioning of environmental effects. The high incidence of stem malformation, particularly in some native-population material, would have created problems in assigning scores for tree-form traits, which would also tend to depress heritabilities. Nevertheless the comparisons with results from other studies do not suggest major downwards bias from these factors.

The high within-population heritability for sealed bud scores appears to be a novel finding. It may have some significance for vegetative propagation because the development of sealed buds is a manifestation of maturation ("physiological aging"), and maturation affects both the ease of vegetative propagation and the growth and form of the propagules.

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APPENDIX

EXPECTED IMPACTS OF NON-RANDOM MATING
ON COMPARISON OF VARIANCE COMPONENTS

A: The Basic Approach

The approach used for addressing expected genotypic variances, in relation to the variable mating patterns, differed from Malécot's widely used coefficient of relationship. Our approach was to express the expected value of each variance component, for a specified mating pattern, as a fraction (which could be greater or less than 1) of its value for a large set of non-inbred parents within a deme (any definable, locally differentiated population or subpopulation unit). This approach was adopted because of the evidence that, even in natural populations of *P. radiata*, the parents were non-inbred (Plessas & Strauss 1986; Moran *et al.* 1988), evidently through selective elimination of inbred offspring. Indeed, this situation appears to be more the rule than the exception in forest trees (Bush & Smouse 1992), whereas previous theoretical work (*see* Squillace 1964; Namkoong 1966) has focused largely on accommodating inbreeding in the parents.

There are several advantages to our approach, given parental F = 0:

(1) It expresses the expected genetic variances in terms of baseline values that would recur each generation (except under very strong directional selection), even with fluctuating levels of inbreeding;

(2) It provides an extremely convenient basis for expressing, in common terms, the genetic variance components of populations with different mating patterns, by specifying their respective mating parameters (or estimates thereof);

(3) It takes advantage of the simple relationship, when parental F = 0, of F = $^1/_2$z, so that F and $^1/_2$z can be used interchangeably to specify inbreeding in terms of an equivalent rate of self-fertilisation.

(4) It also provides a convenient framework for accommodating non-additive gene effects in formulating expectations.

While $\hat{F}$ is often slightly less than zero for parent trees (Plessas & Strauss 1986; Bush & Smouse 1992) it is assumed that such departures from zero are unimportant in this connection.

The ensuing development of expectations of genetic variance components begins with an additivity plus dominance (no epistasis) model, which was applied in the main paper. This was theoretically tractable, and while undoubtedly an oversimplification had the advantage that there was experimental evidence for setting reasonable ranges for the parameters involved.

Further developments included incorporation in the genetic model of:

(1) Epistasis

(2) Inbreeding depression

    (a) Assuming common rates, among all parents, of inbreeding and inbreeding depression;

    (b) Assuming variation, among parents, in levels of inbreeding and susceptibility to inbreeding depression.

In the absence of worthwhile information on the additional parameters involved, these more elaborate models were not applied to the observed genetic statistics, but instead serve to indicate the biases that could arise through using the simplified genetic model.

B: Additivity plus Dominance Genetic Model

Basic conditions

- All genetic parameters are expressed in terms of values applicable to non-inbred parental populations with $F = 0$.

- y = proportion of full-sibbing, defined as the reciprocal of the effective number of unrelated pollen parents per seed parent ($0 \le y \le 1$).

- z = selfing-equivalent rate, defined as $2F$ ($0 \le y \le 1$).

- For simplicity of formulation, σ_P^2 for parental genotypes $= 1$, $\therefore \sigma_A^2 = h^2$

- D = σ_D^2 / σ_A^2 ($\le (1 - h^2) / h^2$)

- H^2/h^2 = $(1 + D)\sigma_A^2$ —*see* Burdon, Bannister & Low (1992b)

Expectations

$$\sigma^2_f = (1+z)^2 \tfrac{1}{4}\sigma_A^2 + y(1-z)\tfrac{1}{4}\sigma_A^2 + \left[z + y(1-z)\right]\tfrac{1}{4}D\sigma_A^2 \tag{A1}$$

where the respective right-hand side (RHS) terms relate to: the impact of inbreeding on contribution of σ_A^2; the marginal impact of full-sibbing, compared with random mating on contribution of σ_A^2; and the contribution of σ_D^2, which derives entirely from the non-randomness of mating.

The first RHS term can be derived as follows (assuming a large population):

Δf (a family effect) $= z\Delta A + (1 - z)^{1}/_{2}\Delta A + f(y, z, \text{dominance effects}) + \varepsilon$, ε being a sampling error item

$$= {}^{1}/_{2}(1 + z)\Delta A + f(y, z, \text{dominance effects}) + \varepsilon,$$

and under the expectation that $s^2\Delta f = \sigma_f^2 + \sigma_\varepsilon^2$, $s^2\Delta f$ being the variance of family effects and σ_ε^2 the error component of $s^2\Delta f$,

$$\sigma_f^2 = \tfrac{1}{4}(1 + z)^2 \sigma_A^2 + f(y, z, \sigma_D^2)$$

Regarding $f(y, z, \sigma_D^2)$ *see* explanation (below) of composition of third RHS term.

In the second RHS term, $y(1 - z)$ denotes the rate of full-sibbing after allowing for the inbreeding component, while $^{1}/_{4}\sigma_A^2$ represents the difference between $^{1}/_{2}\sigma_A^2$ (the additive genetic variance among full-sib families) and $^{1}/_{4}\sigma_A^2$ (the additive genetic variance among half-sib families).

In the third RHS term, $z + y(1 - z)$ denotes the total component of non-random mating, while $^{1}/_{4}\sigma_D^2$ denotes the expected component of dominance variance among self- and full-sib families alike.

$$\sigma_w^2 = z(\tfrac{1}{2}+\tfrac{1}{2}D)\sigma_A^2 + y(1-z)(\tfrac{1}{2}+\tfrac{3}{4}D)\sigma_A^2 + (1-y-z+yz)(\tfrac{3}{4}+D)\sigma_A^2 + z(1-z)\tfrac{1}{4}\sigma_A^2 + \sigma_e^2 \tag{A2}$$

where the respective terms relate to: the genotypic variance among "selfs"; the genotypic variance among full-sibs; the genotypic variance among half-sibs; the

average difference between selfs and outcrosses; and environmental variance $(\sigma_e^2)\,(= \sigma_P^2 - (1+D)\sigma_A^2)$.

Simplifying the above, and assuming $\sigma_P = \sigma_A^2 + \sigma_D^2 + \sigma_e^2 = 1$ (*see* earlier), we arrive at Eqn 1–3.

It may be noted that, in respect of F (=2z), Eqn 3 agrees with well-known expectations. Given $\hat{h}^2$, assuming random mating, $= 4\hat{\sigma}^2{}_f / (\hat{\sigma}_f + \hat{\sigma}_w^2)$

and $\quad \hat{\sigma}_A^2$, assuming random mating, $= 4\sigma^2{}_f$,

if $\quad z = 0$, we have the expectation

$$\hat{h}^2 / h^2 = \hat{\sigma}_A^2 / \sigma_A^2 \tag{A3}$$

which can be expanded into the reciprocal of the RHS of Eqn 4,

but if $\quad z > 0$

$$\hat{h}^2 / h^2 < \hat{\sigma}_A^2 / \sigma_A^2$$

the limiting case being when $z = 1$, $h^2 \to 1$ $(\therefore D \to 0)$, $\hat{h}^2/h^2 \to 2.6$, $\hat{\sigma}_A^2 \geq 4\hat{\sigma}_A^2$, although the difference is usually minor unless under h^2 and z are both high.

Equations A1 and A3 lead to Q (Eqn 4).

C: Epistasis and Inbreeding Depression

Epistasis

In naturally outbreeding species, provided outbreeding is maintained, only a small fraction of the epistatic variance is expected to contribute to among-family variances. Indeed, the expected composition of half-sib family variances ($\sigma_{f.hs}^2$), is (Kempthorne 1957, p.423):

$$\sigma_{f.hs}^2 = \tfrac{1}{4}\sigma_A^2 + \tfrac{1}{16}\sigma_{AA}^2 + \tfrac{1}{64}\sigma_{AA}^2 \text{ etc.} \tag{A4}$$

where σ_{AA}^2 etc. represent increasing orders of additive $\times$ additive epistatic variances and for full-sib family variances ($\sigma_{f.fs}^2$):

$$\sigma_{f.fs}^2 = \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{4}\sigma_D^2 + \tfrac{1}{4}\sigma_{AA}^2 + \tfrac{1}{8}\sigma_{AD}^2 + \tfrac{1}{16}\sigma_{DD}^2 + \tfrac{1}{8}\sigma_{AAA}^2 \text{ etc.} \tag{A5}$$

For self-family variances ($\sigma_{f.s}^2$) the corresponding expectation is (cf. Mather 1974):

$$\sigma_{f.s}^2 = \sigma_A^2 + \tfrac{1}{4}\sigma_D^2 + \sigma_{AA}^2 + \tfrac{1}{4}\sigma_{AD}^2 + \tfrac{1}{16}\sigma_{DD}^2 + \sigma_{AAA}^2 \text{ etc.} \tag{A6}$$

and for variance within self families ($\sigma_{w.s}^2$) the expectation is:

$$\sigma_{w.s}^2 = \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{2}\sigma_D^2 + \tfrac{5}{4}\sigma_{AA}^2 + \tfrac{7}{8}\sigma_{AD}^2 + \tfrac{1}{2}\sigma_{DD}^2 + \tfrac{19}{8}\sigma_{AAA}^2 \text{ etc.} \tag{A7}$$

so for phenotypic variances of selfed offspring ($\sigma_{P.s}^2 [= \sigma_{f.s}^2 + \sigma_{w.s}^2]$)

$$\sigma_{P.s}^2 = \tfrac{2}{3}\sigma_A^2 + \tfrac{3}{4}\sigma_D^2 + \tfrac{9}{4}\sigma_{AA}^2 + \tfrac{9}{8}\sigma_{AD}^2 + \tfrac{9}{16}\sigma_{DD}^2 + \tfrac{27}{8}\sigma_{AAA}^2 \text{ etc.} \tag{A8}$$

It can be seen that in addition to σ_A^2 being greater in the inbred offspring, when between- and within-family expectations are summed, various epistatic variances become exaggerated, notably the increased contribution of the various orders of additive $\times$ additive genetic variances.

The above expectations, however, cannot readily be applied to actual data. This full genetic model is unmanageably complex, and it cannot readily address the feature of the undirectional nature of inbreeding depression effects. Furthermore, it assumes intermediate allele frequencies (cf. Namkoong 1966).

Inbreeding depression

Inbreeding depression arises from a class of alleles that are presumably present at a large number of loci but at very low frequencies. While their effects, both additive and non-additive, may be drastic their low frequencies mean that they make very minor contributions to the variance structures in large, essentially panmictic, populations. Inbreeding, however, creates local concentrations of such genes, whereby they contribute substantially to means and variances (cf. Robertson 1952. Rather than trying to construct detailed models of gene action an alternative approach is to address the impacts of selfing on variance structures in terms of inbreeding depression superimposed on additive gene effects.

To address the impact of inbreeding depression, assume that the inbreeding depression, per unit of F (F = $^1/_2$ for selfing), equals q, and that non-random mating consists entirely of an effective selfing rate of z. Assume, for simplicity, that D = 0, except insofar as it contributes to q. If z and q are the same in all families we have the expectation:

$\sigma_f^2 = (1+z)^2 \frac{1}{4}\sigma_A^2$, as in Eqn 4 and Eqn A1.

$$\sigma_w^2 = z\frac{1}{2}\sigma_A^2 + (1-z)\frac{3}{4}\sigma_A^2 + z(1-z)\frac{1}{4}\sigma_A^2 + z(1-z)\frac{1}{4}q^2 + \sigma_e^2 \qquad (A9)$$

the respective RHS terms relating to: variance among selfs, variance among half-sibs, additive genetic differences between selfs and outcrosses, the effect of the differences between selfs and outcrosses arising from inbreeding depression, and environmental variance.

Simplifying,

$$\sigma_w^2 = (\frac{3}{4} - \frac{1}{4}z)\sigma_A^2 + z(1-z)\frac{1}{4}q^2 + \sigma_e^2 \qquad (A10)$$

$$\sigma_w^2 + \sigma_f^2 = \sigma_A^2(1 + \frac{1}{2}z) + z(1-z)q^2 + \sigma_e^2 \qquad (A11)$$

$$\therefore \quad \hat{h}^2 = \frac{(1+z)^2 \sigma_A^2}{\sigma_A^2(1+\frac{1}{2}z) + z(1-z)q^2 + \sigma_e^2} \qquad (A12)$$

In practice, z is likely to vary markedly between families, and q has been shown to do so (Wilcox 1983). This will affect σ_f^2, but should not affect σ_w^2 which is an average within-family parameter.

It is therefore suggested that the expression for σ_f^2 could be extended, to take account of these factors:

$$\sigma_f^2 = (1+z)^2 \frac{1}{4}\sigma_A^2 + [z^2 \frac{1}{4}\sigma_q^2 + \frac{1}{4}q^2\sigma_z^2] \qquad (A13)$$

where σ_z^2 and σ_q^2 are the variances of z and q respectively, the second RHS term reflecting the variance of the product zq which represents inbreeding depression (for zero covariance between z and q)—note that σ_z^2 and σ_q^2 will be constrained by the relationships $\sigma_z^2 \le z(1-z), \sigma_q^2 \le q(1-q)$. It can be seen that this RHS term could substantially inflate $\hat{\sigma}_f^2$, but there are virtually no quantitative data to proceed from this point.