GENETIC SURVEY OF *PINUS RADIATA*. 4: VARIANCE STRUCTURES AND HERITABILITIES IN JUVENILE CLONES

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ABSTRACT

A clonal adjunct to a large *Pinus radiata* D.Don provenance-progeny trial involved six populations (all the natural populations except Cedros, plus two "land-race" populations from New Zealand) × 30 wind-pollinated progenies (families) × two clones nested within each of two sites × four ramets per clone. The clones were cuttings taken from previously hedged 3-year-old ortets at c. 55 cm height, and came from a subsample of the seedling families used in the main experiment.

Genetic parameter estimates from the clones were compared among populations and with estimates from the seedlings. The parameters estimated included broad-sense heritabilities (H^2) *v.* narrow-sense heritabilities (h^2), phenotypic variances (addressed largely as coefficients of variation), alternative estimates of genetic variances (total genetic *v.* additive genetic), and genetic variances between and within families in clonal material. Genetic correlations between performance in seedlings and cuttings of the same families were also studied.

Phenotypic variances appeared similar between the cuttings and parallel genetic samples of seedlings. Genetic correlations between seedling and clonal performances appeared to be generally high (≥0.75). These results accord with genotypic effects being very similar between the propagule classes, with important implications for selection and predicting genetic gains.

Estimates of H^2 were very similar, trait for trait, among populations. This, despite some smaller coefficients of variation in New Zealand material, suggested that genetic variance structures are similar between populations. Estimates of h^2, made under the provisional assumption of random (i.e., 100% half-sib) mating, tended to be lower in New Zealand than in native-population material, particularly for cumulative growth traits and some tree-form traits including butt straightness, stem straightness, and branch habit quality, so that $\hat{h}^2$ tended to vary much more between traits than $\hat{H}^2$. Such $\hat{h}^2$ values, however, tended to resemble $\hat{H}^2$ more in the native populations than in the New Zealand. This, and markedly higher ratios of between-family : total clonal variance ($\hat{\sigma}_f^2 : \hat{\sigma}_c^2 [\hat{\sigma}_c^2 = \hat{\sigma}_f^2 + \hat{\sigma}_{c(f)}^2]$) in cuttings of native populations, strongly indicate much greater departures from random mating in natural stands than in plantations.

Although differences between $\hat{h}^2$ (assuming random mating) and $\hat{H}^2$ in New Zealand material tended to be greater in the traits previously reported as showing

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relatively high levels of specific combining ability, they suggested a generally higher proportion of non-additive gene effects than did earlier reports. Also, the ratios of $\hat{\sigma}_f^2 / \hat{\sigma}_c^2$ in cuttings were hard to reconcile with likely mating patterns in natural stands, unless non-additive gene effects were less than suggested by comparing $\hat{h}^2$ and $\hat{H}^2$.

Keywords: clones; cuttings; vegetative propagules; broad-sense heritability; genetic architecture; quantitative genetics; mating pattern; *Pinus radiata*.

INTRODUCTION

Vegetative propagules have some major theoretical advantages for quantitative genetic research (Burdon & Shelbourne 1974). Clonal differences reflect both non-additive and additive gene effects, and so clonal material should yield estimates of broad-sense heritability (H^2), which is the total genetic variance as a fraction of the phenotypic variance, while comparisons of between-clone variances with four times the half-sib family variances should yield estimates of non-additive gene effects. Such information is of special value for predicting the potential genetic gains from mass propagation of select clones, compared with those obtainable through propagation systems based on producing untested seedling genotypes from select parents. Moreover, the ramets of a clone do not have any of the genetic variation that exists among the seedlings of a family, even a pair-cross. Thus clonal experiments in principle offer far more precise genetic information and direct estimates of environmental variation.

With the above advantages in mind a clonal adjunct was included in the *Pinus radiata* Genetic Survey experiment (Burdon, Bannister, Madgwick & Low 1992). This experiment was a provenance-progeny trial, involving 50 wind-pollinated progenies of each of the natural populations (provenances) and two local naturalised ones. It was designed partly as a gene resource collection, in which an initial evaluation could be made of the material, and partly as the material for a comprehensive investigation of the quantitative genetic architecture of the species.

When the experiment was established it was anticipated that various non-genetic effects could arise in clonal material (cf. Libby 1962; Libby & Jund 1962). Such effects, as they were envisaged, included both those that are specific to individual clones and those that are specific to individual ramets, which might be termed C-effects and c-effects respectively. Those effects are at least in part analogous to general maternal effects (e.g., average seed-size effects) and specific material effects (e.g., individual seed-size effects) respectively in seedlings. It was believed, however, that the C-effects and c-effects, along with their counterparts in seedling material, would be essentially transient, affecting growth variables primarily during the earliest years after planting. Since the experiment was established, however, it has been realised that inheritance in clonal material is potentially much more complex than was originally thought. The sorts of complications that could arise were envisaged conceptually by Burdon & Shelbourne (1974). Maturation ("physiological aging") which is a well-known phenomenon in woody plants, had undoubtedly occurred to some degree in the clonal adjunct (Burdon & Bannister 1985). In principle, it could be addressed as a main effect that is superimposed straightforwardly upon effects of genotype. Differences between clones in maturation state, however, could cause obvious bias, being likely to inflate clonal differences. On the other hand, differences in maturation state could arise among ramets within a clone (Libby *et al.* 1972), which could inflate the variance

among ramets within a clone. Questions have also arisen, however, as to whether genotypic differences may not be expressed in the same ways in vegetative propagules as in seedlings (Burdon 1991a, c; King & Johnson 1991). In quantitative genetic terms such differences in expression of genotypic differences could be viewed as interactions between the effects of genotype and the effects of nominal maturation state (e.g., chronological age of an ortet) and/or mode of propagation (vegetative *v.* sexual) *per se* (Burdon & Shelbourne 1974). In practical terms all this amounts to whether genotypic effects are expressed similarly, in terms of rankings and variances, between clonal and seedling material (cf. Burdon 1989, 1991a, c). For instance, where advanced maturation is expressed in *P. radiata* it appears that the genetic variances, if not also the rankings, can differ substantially between clonal and seedling material (cf. Burdon 1991c; Shelbourne 1991). In the Genetic Survey experiment the degree of maturation in the clonal adjunct material was sufficient to improve tree form but not enough to impair growth (Burdon & Bannister 1985), and so the material was in the maturation stage when the expression of genetic variation is of especial interest.

For the breeder, the potential implications of differences between propagule classes in expression of genetic differences are two-fold: wrong genotypes can be selected, and genetic gain predictions can be misleading, particularly if the selections are erroneous. This can arise if selections are made and gains predicted either from seedling material when planting stock is produced by vegetative propagation, or vice versa.

Another complication stems from uncertainty concerning the exact mating pattern that produced the wind-pollinated progenies. It was provisionally assumed that half-sib mating (random interpollination within very large population/subpopulation units) had occurred, but there were undoubtedly some departures from this idealised pattern. While minor to moderate departures may cause very little bias in $\hat{H}^2$ from clonal material (Burdon, Bannister & Low 1992b, Eqn 3), and no major bias even in $\hat{h}^2$ (estimated narrow-sense heritability) in seedling material (Burdon, Bannister & Low 1992b, Eqn 1), the biases in statistics derived from direct cross-referencing seedling and clonal data (e.g., estimates of the ratio of non-additive to additive genetic variance obtained from differences between statistics from seedling and clonal material respectively) could be much more serious. Moreover, differences in mating patterns between native-population material and cultivated stocks can complicate comparative evaluation of these two types of population (Burdon, Bannister & Low 1992a). On the other hand, if genotypic effects are expressed very similarly between clonal and seedling material, the clonal data could be used to help infer the actual mating patterns.

This paper covers the estimation of variances and broad-sense heritabilities from the clonal material, and cross-references the results with those from the seedling material (Burdon, Bannister & Low 1992a) in order to infer as much as possible about the genetic control of growth-rate and tree-form traits, some other morphological traits, and disease resistances.

The major issues to be addressed were thus:

(1) **The consistency with which genotypic and environmental effects were expressed in seedling and clonal material respectively,** in terms of:
- phenotypic variances
- components of phenotypic variances

- genetic correlations between performance as seedling and clonal material.

This issue involves a major underpinning of the overall study, although it cannot be addressed in complete isolation from the others (*see below*)

(2) **The mating patterns in the respective populations.** Again, it relates to the underpinning of the study, and certainly cannot be addressed in isolation from the other issues. Fortunately, outside evidence is available for cross-checking.

(3) **Comparison of variance components and phenotypic variances, trait for trait, among populations,** which can be highly dependent on inferences concerning mating patterns.

(4) **Broad-sense heritability (H^2) for various traits.** Estimating these parameters is, of course, an immediate objective of the study and is pursued directly.

(5) **Ratios of non-additive to additive genetic variances.** This was another basic objective of the study, and was addressed largely by comparing estimates of genotypic variance between seedling and clonal material. Along with information on mating patterns, estimates of these ratios can be used to confirm or refine estimates of narrow-sense heritability (h^2) (Burdon, Bannister & Low 1992b).

In general it was not possible to address these issues individually, and so the approach was to consider what combinations of parameter values were most consistent with the observed set of genetic statistics.

MATERIAL AND METHODS

Experimental

The experiment has been described in detail by Burdon, Bannister, Madgwick & Low (1992). The clonal adjunct, which is the prime subject of the paper, contained samples from six populations: Año Nuevo, Monterey, and Cambria from the California mainland, Guadalupe Island, and the local New Zealand "land-race" populations Kaingaroa and Nelson. Each population sample comprised 30 progenies × 2 clones × 4 ramets per clone, on each of the two sites, giving a total of four clones per family. The 30 families were essentially random subsets of the 50 families per population used for the main seedling experiment but, unlike the families, the individual clones within families were each represented on only one site.

The clonal material comprised cuttings taken from seedling ortets that had been lined out in the nursery in late winter and lightly hedged, almost 2 years after germination. In May, in the third year after germination, the cuttings were harvested from the ortets at about 55 cm above the root collars, and showed minor but definite maturation (Burdon & Bannister 1985). They were planted as 1-year tubed stock, in random mixture with the seedling material at each site (A and B) in Stage III (1967) of the establishment programme. Thus, the clonal material was confined to only two of the six site/stage blocks used for the main seedling experiment.

Assessments continued till 8 years after planting on the warmer site (A) and 9 years on the cooler site (B). Data handling and preliminary analyses were as described by Burdon, Bannister, Madgwick & Low (1992).

Statistical Analysis

Analysis of variance models

Statistical analysis for the clonal material was focused on data sets within each of the two blocks (Stage III at the respective sites), since individual clones were not replicated between sites. The basic nested analysis of variance (ANOVA) model for a group of K populations (treating California mainland, New Zealand, and Guadalupe as the three groups with K = 3, 2, and 1 respectively), assuming the prescribed balanced classification, is shown in Table 1. With the slight imbalance encountered through occasional mortality or wind damage, there were minor departures from the above coefficients in the expected mean squares.

TABLE 1–Basic within-site analysis of variance for clonal material of a group of K populations

Item	Degrees of freedom	Expected mean square
A. Recognising the families classification		
Populations	K – 1	$\sigma^2_{w'} + 4\sigma^2_{c(f)} + 8\sigma^2_{f(p)} + 240\theta^2_p$
Families (populations)	(30 – 1)K	$\sigma^2_{w'} + 4\sigma^2_{c(f)} + 8\sigma^2_{f(p)}$
Clones (families)	(2 – 1)30K	$\sigma^2_{w'} + 4\sigma^2_{c(f)}$
Ramets (clones)	(4 – 1)60K	$\sigma^2_{w'}$
B. Dropping the families classification		
Populations	K – 1	$\sigma^2_{w'} + 4\sigma^2_{c(p)} + 240\theta^2_p$
Clones (populations)	(60 – 1)K	$\sigma^2_{w'} + 4\sigma^2_{c(p)}$
Ramets (clones)	(4 – 1)60K	$\sigma^2_{w'}$

where $\sigma^2_{w'}$, $\sigma^2_{c(f)}$, and $\sigma^2_{f(p)}$ are the variances among ramets within clones, among clones within families, and among families within populations respectively, and $\sigma^2_{c(p)}$ is the variance among clones within populations, while θ^2_p is the fixed-effect "variance" among populations, estimation of these variance components from mean squares being self-evident.

For K = 1, for a single population, $\sigma^2_{f(p)}$ and $\sigma^2_{c(p)}$ may be denoted σ^2_f and σ^2_c respectively.

The alternative ANOVAs for the seedling material have been covered by Burdon, Bannister & Low (1992b). For comparing genetic parameter estimates between clones and seedling material in this study the subpopulations classification is ignored, since the local differentiation of Californian material expressed on the tests sites was very minor. The seedling material yields estimates of σ^2_f (or $\sigma^2_{f(p)}$) that are strictly analogous to those for clones. The within-family variance for seedlings (σ^2_w), however, is not strictly analogous to the within-clone variance ($\sigma^2_{w'}$), since it includes genotypic variance.

After estimating variances for each population (or population group) separately for the respective sites, the estimates were combined for the two sites. This was usually done by arithmetically averaging the estimates, an approximation that worked well in practice.

Genetic Correlations between Seedling and Clonal Performance

Estimates of genetic correlations between seedling and clonal material (r_{gsc}), namely, family correlations between the two classes of material (stocktypes), were obtained using the method of Burdon (1977). An appropriate formula for estimating such correlations was:

$$r_{gsc} = \frac{\hat{cov}_{fcs}}{\hat{\sigma}_{fs} \cdot \hat{\sigma}_{fc}} \quad (1)$$

where cov_{fcs} = covariance between family means for seedling and clonal material respectively

and σ^2_{fs} and σ^2_{fc} are the among-families variances in seedling and clonal material respectively (Table 1,A; also Burdon, Bannister, Madgwick & Low 1992, ANOVA 1 or ANOVA 4).

The covariances could be estimated directly from mean cross-products between seedling and clonal family means for each trait. The within-population covariance estimates, and variance estimates (Burdon, Bannister & Low 1992b), were pooled for population groups across sites to obtain the requisite correlation estimates.

The assumptions entailed in this estimation procedure are limited. One is that C-effects, or their counterparts in seedlings, are unimportant—the C-effects could generate departures from perfect correlation (Eqn 1), even if the strictly genotypic effects were identical among the two stocktypes. The other obvious assumption is that non-additive gene effects show essentially the same seedling-clonal correlations as additive gene effects do, which appears very plausible (Burdon, Bannister & Low 1992c).

Interpretation of Variance Components

As a basis for interpreting the genetic statistics obtained in this study (Table 1), the expected composition of the variances thereby estimated is set out for a series of genetic models of increasing complexity: (i) an oversimplified model, (ii) the model elaborated to include additional effects, and (iii) the model elaborated further to accommodate departures from random (i.e., half-sib) mating.

Simplified genetic model

A simple genetic model assumes the following conditions:

(1) Genetic variance is purely additive, hence: $\sigma^2_A = \sigma^2_G$, σ^2_A and σ^2_G being additive genetic and total genetic variances respectively and $\sigma^2_{NA} = 0$, σ^2_{NA} being non-additive genetic variance.

(2) Parents are non-inbred, for which there is concrete evidence (*see* Burdon, Bannister & Low 1992b).

(3) Random mating occurs within (very large) populations, such as to produce 100% half-sib families, hence: $\sigma^2_f = {}^1/_4\sigma^2_A$, $\sigma^2_w = {}^3/_4\sigma^2_A - \sigma^2_e$, σ^2_e being within-block environmental variance.

(4) C-effects and c-effects in vegetative propagules are zero (or negligible), such that the corresponding variances, $\sigma^2_{M'}$ and $\sigma^2_{m'}$ also equal zero.

(5) Corresponding effects in seedlings, i.e., maternal effects, designated M-effects and m-effects respectively, in seedlings are also zero, hence $\sigma^2_M = \sigma^2_m = 0$.

(6) $\sigma^2_{w'} = \sigma^2_e$.

(7) Genotypic effects are expressed identically in the two stocktypes, such that:

(i) Variances are the same in seedlings and cuttings, e.g., σ^2_f the same in the two classes of propagule for a given population.

(ii) Perfect genetic correlations (cf. Eqn 1) exist between performance as seedlings and as cuttings respectively ($r_{gsc} = 1$).

Under these idealised conditions narrow-sense heritability (h^2) and broad-sense heritability (H^2) could be estimated without bias as:

$$\hat{h}^2 = 4\hat{\sigma}^2_f / (\hat{\sigma}^2_f + \hat{\sigma}^2_w) \quad (2)$$

$$\hat{H}^2 = \hat{\sigma}^2_c / (\hat{\sigma}^2_c + \hat{\sigma}^2_{w'}) \quad (3)$$

Also following from the above conditions are the expectations:

$$4\sigma^2_f = \sigma^2_c = \sigma^2_A = \sigma^2_G \quad (4)$$

$$h^2 = H^2 \quad (5)$$

$$3\sigma^2_f = \sigma^2_{c(f)} \quad (6)$$

$$\sigma^2_w - \hat{\sigma}^2_{w'} = {}^3/_4\sigma^2_c = 3\sigma^2_f \quad (7)$$

Extension to include non-additive genetic and epigenetic effects

Including in the model non-additive gene effects (dominance and epistasis), plus epigenetic effects (C-effects, c-effects, M-effects, and m-effects), we have the following expectations (cf. Kempthorne 1957; Mather 1974):

$$\sigma^2_c = \sigma^2_{M'} + \sigma^2_A + \sigma^2_D + \sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} \text{ etc.} \quad (8)$$

$$\hat{\sigma}^2_{w'} = \sigma^2_e + \sigma^2_{m'} \quad (9)$$

$$\sigma^2_f = \sigma^2_M + \tfrac{1}{4}\sigma^2_A + \tfrac{1}{16}\sigma^2_{AA} + \tfrac{1}{64}\sigma^2_{AAA} \text{ etc.} \quad (10)$$

$$\sigma^2_w = \sigma^2_e + \sigma^2_m + \tfrac{3}{4}\sigma^2_A + \sigma^2_D + \tfrac{15}{16}\sigma^2_{AA} + \sigma^2_{DD} + \tfrac{63}{64}\sigma^2_{AAA} \text{ etc.} \quad (11)$$

$$\sigma^2_{c(f)} = \sigma^2_{M'} + \tfrac{3}{4}\sigma^2_A + \sigma^2_D + \tfrac{15}{16}\sigma^2_{AA} \text{ etc.} \quad (12)$$

where σ^2_D = dominance genetic variance
σ^2_{AA} = additive × additive epistatic variance
σ^2_{AD} = additive × dominance epistatic variance
etc.,
the dominance and various epistatic variances being collectively designated non-additive genetic variance (σ^2_{NA}).

Various expectations follow from the above, e.g., $\sigma^2_c - 4\sigma^2_f = \sigma^2_D$ and $\sigma^2_D/\sigma^2_A = (H^2 - h^2)/h^2$, if σ^2_M, $\sigma^2_{M'}$, σ^2_m, $\sigma^2_{m'}$, and epistasis are zero.

Further extension to departures from random mating

This theory can be extended to non-random mating (Burdon, Bannister & Low 1992b), assuming a rate of selfing or equivalent inbreeding, z, and a rate of full-sibbing (the inverse of the effective number of pollinators per seed parent), y. Doing this, but simplifying the genetic model to additivity plus dominance (hence no epistasis) and not invoking inbreeding depression as such, we can adapt Eqn 1–4 from Burdon, Bannister & Low (1992b) to obtain the following:

$$\sigma^2_c = \sigma^2_{M'} + [1 + {}^1/_2z + (1 - {}^1/_4z)D]\sigma^2_A \quad (13)$$

$$= \sigma^2_f + \sigma^2_{c(f)} \text{ for a large population of clonal material}$$

$\sigma^2_{w'}$ unchanged

$$\sigma^2_f \text{ (seedlings)} = \sigma^2_M + [(1+z)^2 + y(1-z) + (y+z-yz)D]^1/_4\sigma^2_A \quad (14)$$

$$\sigma^2_f \text{ (clones)} = x\sigma^2_{M'} + [(1+z)^2 + y(1-z) + (y+z-yz)D]^1/_4\sigma^2_A \quad (15)$$

$$\sigma^2_w = \sigma^2_m + (^3/_4 + D - {}^1/_4y - {}^1/_4yD - {}^1/_2zD - {}^1/_4z^2 + {}^1/_4yz + {}^1/_4yzD)\sigma^2_A + \sigma^2_e \quad (16)$$

$$\sigma^2_{c(f)} = (1-x)\sigma^2_{M'} + (^3/_4 + D - {}^1/_4y - {}^1/_4yD - {}^1/_2zD - {}^1/_4z^2 + {}^1/_4yz + {}^1/_4yzD)\sigma^2_A + \sigma^2_e \quad (17)$$

where y = incidence of "full-sibbing", in terms of the reciprocal of the effective number of unrelated pollinators per seed parent.

z = level of inbreeding in terms of its equivalent rate of selfing in non-inbred parents ($0 < z < 1$), which equals 2F (F = fixation index).

$D = \sigma^2_D/\sigma^2_A$

x = proportion of $\sigma^2_{M'}$ occurring among families in clonal material, the balance occurring among clones within families.

The impacts, on certain expectations, of various departures from the simple genetic model leading to Eqn 2–7, are summarised in Table 2. Among the main biases would be the upward biases arising in $\hat{h}^2$ (and in $\hat{\sigma}^2_A$ and $4\hat{\sigma}^2_f$) from y, z, and D and from σ^2_M (Eqn 14, cf. Eqn 2). On the other hand, $\hat{h}^2$ and $\hat{H}^2$ would be depressed by σ^2_m and $\sigma^2_{m'}$ respectively. Estimates of H^2 and σ^2_c are by definition not biased by D, and are subject to relatively minor bias arising from y and z.

Further complications, which have been considered by Burdon, Bannister & Low (1992b), but which for want of sufficient indicative data are not considered formally in this paper, include variation between seed parents in their equivalent selfing rates, inbreeding depression (which is not satisfactorily handled by quantitative genetic models), and variations among seed parents in their levels of inbreeding depression per unit F.

TABLE 2–Summary of anticipated deviations from expected equalities arising from single complications of the basic genetic model reflected in Eqn 2–7.

Complication	Expectation					
	$4\sigma^2_f = \sigma^2_c$	$H^2 = h^2$	$\hat{H}^2 = H^2$	$\hat{h}^{2*} = h^2$	$\sigma^2_f = {}^1/_4(\sigma^2_f + \sigma^2_{c(f)})$	$\sigma^2_w - \sigma^2_{w'} = 3\sigma^2_f$
$\sigma^2_D > 0$	<	>	=	=	<	>
"Full-sibbing"	>	<	=	>	>	<
Inbreeding	>	<	>	>	>	<
$\sigma^2_{M'} > 0$	<	>	>	NA	<	=
$\sigma^2_{m'} > 0$	=	<	<	NA	=	<
$\sigma^2_M > 0$	>	<	≥	>	>	=
$\sigma^2_m > 0$	=	>	≥	<	=	>
Scalar effects ($\sigma \propto \bar{x}$)†	≤	~	~	~	~	<
Competitional effects†	≥	>	~	~	~	>

* Assuming random mating, such as to produce half-sib families

† Relating specifically to seedling material being smaller in this study than the clonal material and thus more susceptible to competitional influences.

RESULTS

Phenotypic Variances and Coefficients of Variation

Phenotypic variances for subjectively scored traits (details not tabulated) were mostly very similar between the two stocktypes. Phenotypic variances, however, could vary markedly between stocktypes if, in the population(s) concerned, the mean for one stocktype (e.g., sealed bud scores in cuttings) was close to one bound of the multi-point scoring scale (with consequent low variance) and that for the other class was near the mid-point. Such differences in estimated variances could be appropriately viewed as a statistical artifact. This type of statistical artifact also arose with binomial traits, e.g., presence or absence of retarded leader or of dieback; since the phenotypic variances (σ^2_P) are subject to the relationship $\sigma^2_P = x(1 - x)$, x being the overall proportion incidence which can range between 0 and 1 (Sohn & Goddard 1978), and could thus vary between stocktypes where the stocktypes differed markedly in $|x - 0.5|$ (*see* Burdon & Bannister 1985).

Comparisons of variances for cumulative variables, e.g., current total heights in contrast to periodic height increments, were potentially more complex; the prevalent scalar effects, with variances related to means (Burdon, Bannister & Low in MSb), argue for using coefficients of variation as a basis for comparison, yet the coefficients of variation show certain trends with size or age (Burdon, Bannister & Low 1992b), and so the interpretation is not straightforward. Phenotypic coefficients of variation are compared between stocktypes for cumulative variables in Table 3. The coefficients were, with two minor exceptions, lower for the cuttings than for the seedlings. Early branch cluster counts showed much higher coefficients of variation in the seedlings which had low average counts (around 1.5 and 1.2 on Sites A and B respectively, compared with 2.8 and 2.7 in the cuttings) at age 1.

The time trend for coefficients of variation for height is evident from Table 3. To make a critical comparison of variability in the respective stocktypes, the differences among stocktypes in height needed to be taken into account. It appeared appropriate to plot $\sigma_P^{0.5}$ *v.*

TABLE 3–Comparisons of within-population phenotypic coefficients of variation among individual trees (CV_P) (%), for seedlings (S) *v.* cuttings (C), pooled for population groups

Trait	Site(s)	Age from planting (years)	Population group					
			Californian mainland		New Zealand		Guadalupe	
			S	C	S	C	S	C
Height	Both	1	25	24	26	21	30	27
	Both	2	23	21	23	18	29	22
	Both	3	20	19	19	17	20	18
	B	5	16	15	17	13	15	15
	Both	~8	15	14	15	11	16	15
Diameter	Both	~8	24	20	21	17	27	23
Bark thickness	A	7	29	25	29	25	23	21
	B	9	47	42	47	37	49	40
No. of branch clusters	A	1	77	19	56	28	56	32
	B	1	94	34	65	28	53	30
	A	3	28	16	25	13	22	23

(mean height)$^{0.5}$ (Fig. 1), which gave convenient plotting intervals and very close to straight-line relationships. This shows that variances were almost always greater in relation to height in seedlings than in cuttings, the difference generally being most marked in New Zealand material and least in Guadalupe. At Site B the difference was marginal in the Guadalupe population but the criteria for acceptance for assessment caused significant truncation there at the lower end of the distributions for seedlings (Burdon, Bannister & Low 1992a). Overall, the absolute phenotypic variances were similar, within site/population categories, between the two propagule classes, and so it appeared that worthwhile, if tentative, comparisons could be made between actual variances.

Genotypic Variances

Estimates of genotypic coefficients of variation from clones and seedlings respectively (provisionally assuming half-sib families in the seedlings—cf. Eqn 4) are compared for height and diameter variables in Table 4. These coefficients were larger for diameter than for height at around 8 years, and were larger for clones than for seedlings in "8-year" diameter but generally similar between propagule types in "8-year" height. In "2.5-year" height the tabulated coefficients of variation were larger for clones and seedlings, except in the Californian mainland material. In all except 2.5-year height in Guadalupe, where the Stage III estimate for seedlings could be given very little weight, the differences in coefficients between clones and seedlings were greatest in New Zealand material.

Alternative estimates of genetic variance are shown for Californian mainland and New Zealand material in Table 5 (again, under the provisional assumption of a half-sib family structure); the results from the more limited Guadalupe sample, being erratic, are not presented. In most cases $\hat{\sigma}^2_c$ was greater than $4\,\hat{\sigma}^2_f$ but much more so in New Zealand than in Californian mainland material. The difference was very marked in early height and stem diameter, but not at all evident for "8-year" height. The third type of estimate of σ^2_A, $^4/_3(\hat{\sigma}^2_w - \hat{\sigma}^2_{w'})$, showed a less coherent pattern, usually falling either above or below the other two estimates.

TABLE 4–Estimates of genotypic coefficients of variation, averaged as root mean squares, between sites A and B (Stage III only), in clones ($\hat{\sigma}_c$/÷mean) and seedlings (2 $\hat{\sigma}_f$/÷mean, assuming half-sib families), for selected growth variables. Values in brackets represent results from seedlings similarly averaged over all six site/stage blocks of the experiment

Trait	Age from planting (years)		Population group		
			Californian mainland	New Zealand	Guadalupe
Height	~2.5	Clones	8.7	9.6	11.5
		Seedlings	8.8	6.5	0.8
			(9.1)	(7.8)	(9.1)
	~8	Clones	7.8	6.0	9.7
		Seedlings	8.5	6.9	9.6
			(7.3)	(5.6)	(11.7)
Diameter	~8	Clones	11.7	10.7	15.6
		Seedlings	10.9	6.8	14.8
			(10.0)	(7.7)	(16.7)

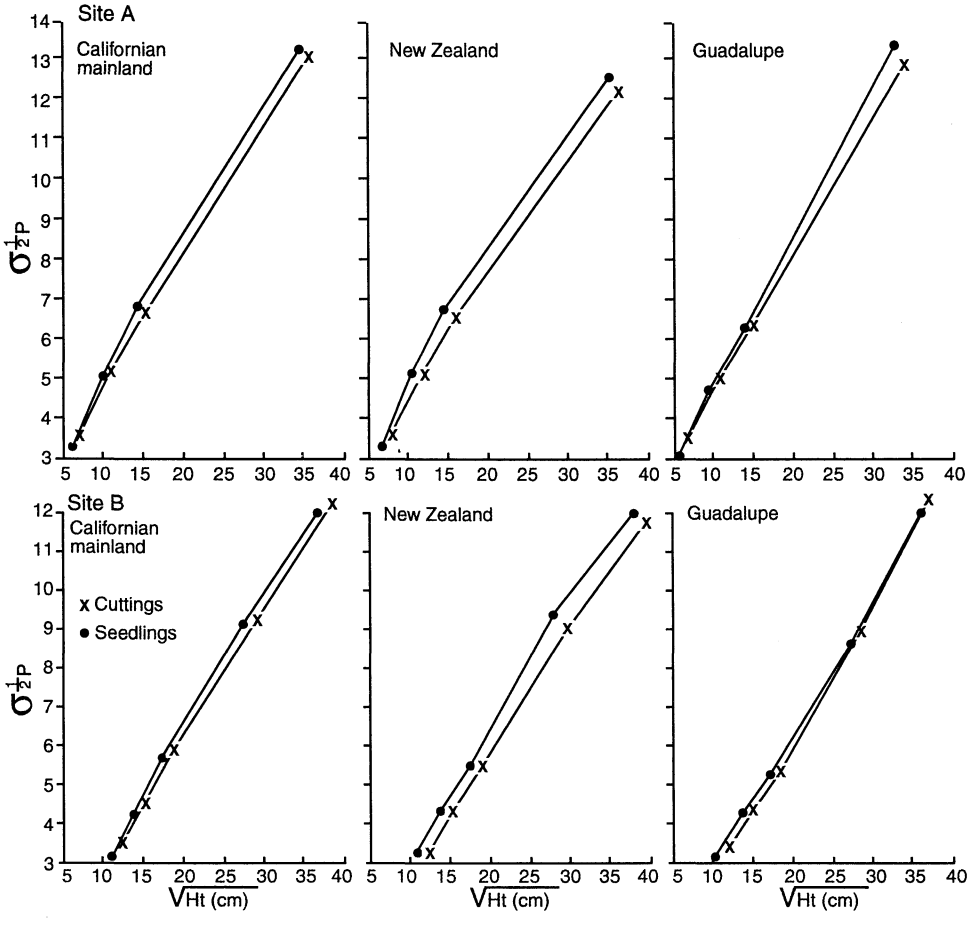

FIG. 1–Plots of the square roots of phenotypic individual-tree, within-population standard deviations ($\sqrt{\sigma_p}$) *v.* square roots of means for heights, for seedlings (x) and clonal material (•), by population groups, in Stage III blocks at sites A and B.

TABLE 5–Alternative estimates of genetic variance pooled for population groups and then averaged over the two sites, A and B (in Stage III): A = $\hat{\sigma}^2_c$ from cuttings; B = 4 $\hat{\sigma}^2_f$ from seedlings; C = $^4/_3(\hat{\sigma}^2_w - \hat{\sigma}^2_e)$, $\hat{\sigma}^2_w$ and $\hat{\sigma}^2_e (= \hat{\sigma}^2_{w'})$ from seedlings and cuttings respectively (cf. Table 2).

Trait	Age from planting (years)	Population group						D*
		Californian mainland			New Zealand			
		A	B	C	A	B	C	
HT	1	36	21	0	48	6	25	3
	2.5	228	110	12	248	5	248	> 4
	~8	8186	8822	9676	5885	5522	7281	0
DIAM	~8	479	313	598	492	113	794	2
BARK	~8	2.26	1.77	1.52	2.48	1.19	2.07	1
BR CLUS	1	0.19	0.27	0.15	0.17	0.19	0.42	0
BUTT	~8	0.145	0.10	0.21	0.16	0.06	0.31	≥1
STR	~8	1.27	1.00	1.09	1.32	0.80	1.40	0.75
BR QU	~8	1.02	0.92	0.81	1.06	0.30	0.96	≥1
BR FR	~8	0.44	0.30	0.23	0.35	0.25	0.27	0.75
BR ANG	~8	0.18	0.23	0.19	0.27	0.27	0.17	0
CROWN†	7	0.28	0.28	0.46	0.18	0.18	0.37	0

* Approximate ratios of σ^2_D/σ^2_A inferred from (A–B)/B assuming an additivity plus dominance genetic model, and after adjusting B as an estimate of σ^2_A iteratively, with respect to D and assumed mating pattern (Burdon, Bannister & Low 1992b, Eqn 1,3,4 and Table 3). (Tabulated values of B are unadjusted).

† One site only.

Approximate estimates of D (i.e., σ^2_D/σ^2_A) made by comparing $\hat{\sigma}^2_c$ with $\hat{\sigma}^2_f$ from seedling material (Table 5) differed erratically among the growth rate variables, but for none of the remaining variables did the values fall appreciably outside the range 0–1. The D values were not materially affected by reasonable alternative assumptions concerning mating patterns. Alternative estimates of D (details not shown) could be made assuming various reasonable values of the mating-pattern parameters y and z (cf. Burdon, Bannister & Low 1992b, Table 3) to satisfy Eqn 13 and 14 if σ^2_M and $\sigma^2_{M'}$ are assumed to be zero. In fact, the estimates of D were not very sensitive to the variations considered for y and z.

Heritability Estimates

Broad-sense heritability estimates showed no consistent pattern of differences among populations within groups (viz Californian mainland and New Zealand), and so are not shown for individual populations within these groups.

Accordingly, broad-sense and narrow-sense heritability estimates ($\hat{H}^2$ and $\hat{h}^2$ respectively) are listed for population groups in Table 6, $\hat{h}^2$ being obtained under the provisional assumption of random mating such as to produce half-sib families. (The alternative estimates of h^2, from seedlings, are presented because whereas one category was specific to the blocks that also contained the clones it was based on much more limited data than the other category.) The broad-sense estimates were almost all very highly significant statistically

TABLE 6–Comparisons of estimates of broad-sense heritability (H^2, from cuttings, Eqn 3) and narrow-sense heritability (h^2, from seedlings, provisionally assuming random mating, Eqn 2) averaged over blocks

Trait	Age from planting (years)	Population group									D*
		Mainland			New Zealand			Guadalupe			
		$\hat{H}^2$	$\hat{h}^2$ †		$\hat{H}^2$	$\hat{h}^2$ †		$\hat{H}^2$	$\hat{h}^2$ †		
			(1)	(2)		(1)	(2)		(1)	(2)	
HT	1	0.24	0.20	0.28	0.33	0.05	0.15	0.38	0.36	0.32	1
HT	2	0.18	0.12	0.20	0.30	0.12	0.14	0.34	0.08	0.25	1
HT	3	0.22	0.12	0.19	0.30	0.08	0.12	0.29	0.02	0.43	1
HT	~8	0.26	0.30	0.29	0.30	0.22	0.18	0.41	0.34	0.67	0.75
DIAM	~8.5	0.33	0.22	0.26	0.38	0.13	0.19	0.46	0.42	0.60	1
ΔDIAM‡	7–8	0.38	0.38	–	0.26	0.23	–	0.44	0.41	–	0.5
BARK	8	0.36	0.34	0.37	0.39	0.21	0.31	0.22	0.12	0.32	0.5
BUTT	~8	0.24	0.16	0.25	0.23	0.09	0.10	0.16	0.08	0.20	1
STR	~8	0.36	0.30	0.34	0.35	0.21	0.21	0.27	0.22	0.28	0.75
BR CLUS	1	0.24	0.34	0.33	0.26	0.21	0.20	0.20	0.30	0.25	0.25
BR CLUS	3‡	0.43	0.49	0.65	0.39	0.47	0.44	0.36	0.36	0.47	0
BR FR	~8	0.45	0.40	0.41	0.39	0.30	0.26	0.48	0.22	0.39	0.5
BR ANG	~8	0.25	0.31	0.27	0.34	0.34	0.23	0.34	0.16	0.32	0.5
BR QU	~8	0.29	0.28	0.23	0.31	0.09	0.12	0.40	0.11	0.25	≥1
FORK	~8	0.14	0.12	0.21	0.22	0.10	0.03	0.21	0.06	0.10	1
RLDR	1	0.16	0.10	~0	0.12	0.09	0.05	0.17	0.06	–	0.75
	2	0.16	0.03	0.13§	0.12	0.09	0.16§	0.21	0	0.12§	
	3	0.19	0.14		0.21	0.05		0.21	0.08		
CROWN‡	7	0.47	0.38	0.47	0.42	0.31	0.29	0.24	0.42	0.23	0.5
DBK‡	7	0.18	0.13	0.11	0.12	0.02	0	0.24	0.42	0.23	1
BUDS	2	0.60	0.62	0.59	0.50	0.54	0.56	0.16	0.66	0.75	0

* Approximate ratios of σ^2_D/σ^2_A, inferred from the expectation $D = (H^2 - h^2)/h^2$ with allowance made for likely bias in $\hat{h}^2$ arising from non-random mating and D (Burdon, Bannister & Low 1992b, Eqn 1, 2, 4 [cf. Eqn 14–16 of this paper] and Table 3).

† (1) Averaged over just the two blocks (Stage III, Site A and B) where the clonal and seedling material were intermixed.

(2) Averaged over all six site/stage blocks.

‡ One site only.

§ Estimate averaged over the two or three assessment-age variables

($p < 0.001$). Most important, they were, with some interesting exceptions, generally similar, variable for variable, among the population groups. Two of the main exceptions were in Guadalupe: one was a relatively high $\hat{H}^2$ value for dieback in Guadalupe in which the higher incidences are conducive to better resolution of clonal differences; and the other was a low $\hat{H}^2$ for bud scores, which for that population were clustered towards the upper bound of the rating scale, particularly in the cuttings. As in the seedling material (Burdon, Bannister & Low 1992b) adjusting bark thickness sums of squares for within-subclass covariance on stem diameter had little impact on estimated heritability, except for the Guadalupe population in which estimated heritabilities were thereby reduced to around zero.

Compared with corresponding $\hat{h}^2$ estimates, the $\hat{H}^2$ values differed according to certain general patterns (Table 6). In the New Zealand material $\hat{H}^2$ values tended to be markedly higher than $\hat{h}^2$ for the majority of the (trait/age) variables, the main exceptions being diameter increment, branching frequency variables, branch angle score, sealed bud score, and, to a lesser extent, crown retention score and bark thickness. In both the mainland and Guadalupe material the disparities between $\hat{H}^2$ and $\hat{h}^2$ were generally much smaller and usually well within likely estimation errors.

Relative Importance of Genetic Dominance Variance

The inferred values of D (i.e., σ^2_D/σ^2_A), assuming an additivity plus dominance genetic model (with no epistasis) and comparing $\hat{h}^2$ with $\hat{H}^2$, which have already been listed by Burdon, Bannister & Low (1992b), are also shown in Table 6. They tended to be high for growth-rate variables, particularly early height, and for those among the other traits that showed lower heritability. Only approximate figures are shown because there were two sets of estimates of h^2, neither being clearly more satisfactorily than the other, although they probably involved slightly different selective elimination of inbreds. In principle, iterative solutions could be made for $\hat{D}$ and $\hat{h}^2$ adjusted for non-random mating, but this would have been complicated by the presence of alternative estimates of h^2, while all indications were that the improvements in the estimates would have been very marginal.

Genetic Correlations between Seedling and Clonal Performance

Estimates of genetic correlations between clonal and seedling material (Table 7) were generally high, several exceeding 1.0, although there was one (small) negative value. The scatter of values doubtless reflects, in large measure, the inherently low precision of individual point estimates of genetic correlations based on sample populations of the sizes represented. Indeed, the estimates outside the range 0.5 to 1.0 were almost all among those that were inherently the least precise, through a limited database, the traits being recorded as binomial (0 or 1) data, or the traits being of genuinely low heritability.

Partitioning of Clonal Variance

The results of partitioning $\hat{\sigma}^2_c$ from just the clonal data into $\hat{\sigma}^2_f$ and $\hat{\sigma}^2_{(c)f}$ (Table 1) could be expressed in terms of several alternative ratios: $\hat{\sigma}^2_f/\hat{\sigma}^2_{(c)f}$ or $\hat{\sigma}^2_{(c)f}/\hat{\sigma}^2_f$, and $\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_{(c)f})$ or $\hat{\sigma}^2_{(c)f}/(\hat{\sigma}^2_f + \hat{\sigma}^2_{(c)f})$. Of these the latter two showed the better statistical properties, with closer to normal distributions, and results are expressed in terms of $\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_{(c)f})$. The values of $\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_{(c)f})$ (Table 8) behaved somewhat erratically from trait to trait, and were not closely related to inferred values of D for individual traits (Table 6). The salient pattern was a trend for the ratios to be substantially higher in the Californian mainland material than in the New Zealand samples, the respective averages over 14 variables being approximately 0.36 and 0.215 respectively, compared with an expected value of 0.25 for half-sib families with no epistasis. The values of $\hat{\sigma}^2_f$ for Californian mainland material could be revised downwards by partitioning off an allowance for variance among subpopulations within populations (Burdon, Bannister, Madgwick & Low 1992, Table 6, ANOVA 1) in the average proportions observed by Burdon, Bannister & Low (1992b). This, however, only reduced the average ratios (Table 8) from around 0.36 to around 0.32.

TABLE 7–Estimates of genetic (among-progeny) correlations between seedling- and clonal-family values for the Californian mainland and New Zealand population groups, derived by averaging estimates of variance/covariance components over population/site subclasses as input statistics for Eqn 1.

Trait	Years from planting	Population group	
		Californian mainland	New Zealand
Height	1	0.08	1.13
	~2.5	0.49	0.70
	~8.5	0.77	0.85
Dbhob	~8.5	0.70	≥0.75
Bark thickness	~8.5	0.82	0.52
Branch clusters	1	0.71	0.57
	3*	1.94	0.39
Branching frequency score	~8	0.92	0.58
Butt straightness score	~8	1.21	1.24
Stem straightness score	~8	0.85	≥0.51
Branch habit quality score	~8	0.78	≥0.51
Branch angle score	~8	1.10	0.82
Forking	~8†	1.36	-0.06
Retarded leader	1†	1.00	≥0.93
	2†	1.46	≥0.79
	3†	≥0.52	0.50
Sealed buds score	2	0.55	0.57
Dieback	7*†	1.49	0.73
Crown density score	7†	2.32	1.34

≥ Reflects revising some negative variance component estimates used in averages to lower theoretical bound of zero, generating some upwards bias in presented correlation estimates.

* Data available from one site only.

† Binomial (0 or 1) data, giving estimates of inherently low precision.

For comparison with the average ratios above, expected ratios are shown in Table 9 for varying ratios of D and for varying departures from random mating in the form of "full-sibbing" (y) and "equivalent selfing" (z), assuming z = 2F. To account exactly for the observed average ratio in New Zealand material, D must be lower than the apparent average of 0.7, or y must be markedly higher than the provisional assumed value of 0.1. Nevertheless the discrepancy, in relation to the average ratio of 0.216, is not statistically significant ($p > 0.05$) for any of the combinations of y and z considered. To account fully for the average observed ratio in the Californian mainland material, however, required combinations of D, y, and z that were well outside the likely range. Indeed, the expected ratios that fell within the 90% confidence interval, for the average observed ratio, with a lower limit of 0.31 (which may admittedly be too high because the calculated standard error took no account of intercorrelations among the variables considered), would all imply either values of D that were far below the apparent average of 0.7 or y values of around 0.3 or greater.

DISCUSSION

General Considerations

The genetic statistics based on data from seedlings and cuttings respectively are inevitably subject to estimation errors. Composite genetic statistics derived from genetic

TABLE 8–Ratios of $\hat{\sigma}^2_f/(\hat{\sigma}^2_f+\hat{\sigma}^2_{c(f)})$* (*see* Table 1,A) by population groups for clonal material (cuttings).

Trait	Years from planting	Population group	
		Californian mainland	New Zealand
Height	1	0.42	0.30
Height	~2.5	0.39	0.32
Height	~8	0.34	0.10
Dbhob	~8	0.27	0.26
Bark thickness	~8	0.36	0.40
Branch clusters	1	0.19	0.06
Branching frequency score	~8	0.43	0.25
Branch habit quality score	~8	0.54	0.17
Branch angle score	~8	0.26	0.22
Butt sweep score	~8	0.38	0.21
Stem straightness score	~8	0.37	0.16
Forking (0, 1)	~8	0.48	0.02
Retarded leader (0, 1)	1	0.30†	0.22†
Retarded leader	2		
Retarded leader	3		
Sealed bud score	2	0.33	0.33
Mean ± s.e.‡		0.362±0.025	0.215± 0.029

* Actually $\hat{\sigma}^2_{f(b)}/(\hat{\sigma}^2_{f(b)}+\hat{\sigma}^2_{c(f)(b)})$ as defined by Burdon, Bannister, Madgwick & Low (1992).

† Averaged over values for 3 years.

‡ Arithmetic average over the 14 trait/age variables, the standard error calculated disregarding interdependences.

TABLE 9–Expected ratios $\sigma^2_f/(\sigma^2_f+\sigma^2_{c(f)})$ assuming alternative rates of full sibbing (y), selfing equivalent (z), and D, with epistasis, σ^2_M, $\sigma^2_{M'}$, σ^2_m, $\sigma^2_{m'}$ all zero (*see* Eqn 13 and 14, for $\sigma^2_{M'}=0$).

z (=2F)	D	y			
		0.05	0.1	0.2	0.3
A. New Zealand material (observed average 0.216 ± 0.029)					
~0	0.25	0.21	0.23	0.25	•
	0.5	0.18	0.19	0.22	•
	0.75	0.16	0.17	0.19	•
B. Californian mainland material (observed average 0.362 ± 0.025)					
0.12	0.25	•	0.27	0.29	0.31
	0.5	•	0.23	0.26	0.28
	0.75	•	0.21	0.23	0.25
0.15	0.25	•	0.28	0.30	0.32
	0.5	•	0.24	0.27	0.29
	0.75	•	0.22	0.24	0.26
0.2	0.25	•	0.30	0.32	0.33
	0.5	•	0.26	0.28	0.30
	0.75	•	0.24	0.26	0.27

• Highly improbable combination of y and z for material concerned.

statistics from both stocktypes, such as $\sigma^2_w - \sigma^2_{w'}$ (*see* Table 1), are subject to the sum of the errors of the statistics from both stocktypes, and are thus less precise. Such composite statistics may also be subject to two-fold biases which could arise from disparities between the stocktypes in systematic errors. Even though the experiment was large the estimation errors were troublesome, particularly in cross-referencing variances between seedlings and cuttings for growth-rate variables, despite the similarities in variances between these propagules in relation to tree size (Fig. 1, Table 3). Pooling estimates across the designated population groups appeared inappropriate because of some marked disparities overall between the corresponding statistics for different population groups, but where pooled parameter estimates could be made satisfactorily for larger data sets the estimates clearly behaved much less erratically. Certain of the procedures used for pooling, e.g., taking arithmetic averages of genetic statistics across sites, which were occasioned primarily by limitations at the time in computing capacity, were inexact, but the approximations appear to have been minor in relation to the inherent estimation errors. For any one trait very large sample populations seem to be needed in order to obtain precise comparisons of the type in question. With the multiplicity of traits studied, however, certain trends emerged clearly.

Tackling the questions addressed in this study purely through statistics of traits that show either continuous variation or thresholds of expression (e.g., forking) tended to give highly ambiguous results, as will be discussed in more detail later. The ambiguities have arisen from the number of unknowns, which include: two aspects of mating patterns (inbreeding and full-sibbing) which in turn have undoubtedly varied among populations; the relative importance and nature of non-additive gene effects; the magnitude of epigenetic effects (viz C-effects and c-effects and the corresponding types of maternal effects in seedlings); and potential differences among populations in genetic parameters. The level of inbreeding (quantified by F, or $^1/_2$z) has a major influence on the interpretation of the statistics. The level is relatively well known, for the viable seeds produced, from availability of data on genetic markers such as isozymes and putative recessive chlorophyll deficiencies. Much less certain, though, is the level of inbreeding represented in the experimental trees, which would have reflected some selective elimination of inbred genotypes. Such selective elimination was probably greater, in relative terms, within the New Zealand material, in which the inbreeding presumably resulted almost entirely from selfing rather than the less closely related matings that were probably common in natural stands. Regarding the proportion of full-sibbing, there were no firm data for *P. radiata* on which to base expectations. The proportion undoubtedly varied among populations, and from family to family, although this family variation does not in itself represent such a significant complication as does family variation in level of inbreeding.

Equivalence of Gene Effects among Propagule Types

Overall, the phenotypic variances appeared to be similar between clonal and seedling material. As noted earlier, the few marked disparities generally appeared to be statistical artifacts, such as a stocktype showing a smaller variance when it averaged much closer than the other to a bound of the scoring scale. For the growth variables, the consistently larger coefficients of variation (CV) in seedlings at a given size was fortuitous, since this counteracted potential complications through the size differences (Burdon & Bannister 1985) between the two stocktypes. The smaller CVs in the cuttings, compared with

seedlings, may have in part reflected a standardisation of size of cuttings when they were set in the nursery (Burdon, Bannister, Madgwick & Low 1992).

The estimated genetic correlations between seedling and clonal performance appear overall to be in the range of 0.75 or better. While the correlations may differ among the variables studied, the individual estimates were not precise enough to allow any firm conclusions on this point. Suffice to say that family rankings as well as genotypic variances appear to have been closely similar between the two classes of propagules. This was despite a maturation difference that was greater than should be the norm for vegetative multiplication programmes, although possibly similar to what might be involved in a clonal forestry programme.

Mating Pattern

There is powerful biometric evidence that departures from random (i.e., half-sib) mating were indeed far greater in the native populations than in the New Zealand material. Comparison of ratios of $\hat{\sigma}_f^2/(\hat{\sigma}_f^2 + \hat{\sigma}_{c(f)}^2)$ between the native-population and New Zealand "land-race" cuttings (Table 8) points very strongly to this. Indeed the ratios indicate levels of full-sibbing of 30% or so in the native-population samples (Table 9) unless either the apparent D values (Tables 5 and 6) are considerably inflated or there had been almost complete selective elimination of inbreds. Such levels of full-sibbing seem implausible, particularly in the light of the results of Müller (1977) and Yazdani *et al.* (1989) for pines, although they are not out of line with some estimated for *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) (W.J. Libby pers. comm.).

In the New Zealand material, by contrast, these ratios gave no conclusive indication of non-random mating, even though the average ratio suggested nearly 30% full-sibbing (Table 9) unless the apparent D values are inflated. Moreover, the lower discrepancies between $\hat{H}^2$ and $\hat{h}^2$ (when h^2 is estimated assuming random mating) in native-population material than in New Zealand material (Table 6) also point to more full-sibbing and/or inbreeding in natural stands, since such matings cause a substantial upwards bias in $\hat{h}^2$ (Eqn 2, cf. Eqn 14) but very little in $\hat{H}^2$ (Eqn 3 and 13). The comparisons between $\hat{\sigma}_c^2$ and $4\,\hat{\sigma}_f^2$ (Table 5), although they are less consistent, point in the same direction.

To discriminate between full-sibbing and inbreeding, or ascertain their comparative importance, could be done to only a limited degree; however, both were important in the native populations (Table 9), while full-sibbing was almost certainly much the main non-random component of the mating pattern in the New Zealand material.

An upper limit to the likely level of inbreeding ($F \approx 0.1$, $z \approx 0.2$) in Californian mainland material is set by the results of Moran *et al.* (1988) plus those of Plessas & Strauss (1986). For the New Zealand material, the degree of concurrence between narrow-sense heritability estimates for wood density and turpentine composition from sib-analyses and offspring-parent regressions (Burdon & Low 1992; Burdon, Gaskin, Zabkiewicz & Low 1992) argues against over 10% full-sibbing.

It is very possible that a higher rate of full-sibbing in the native-population samples than in New Zealand land-race samples was in part an effect of cone collection procedures. In the New Zealand populations cones were deliberately taken from several years' crops and, where possible, from more than one crop per year, in order to minimise the full-sib relationships. In the natural stands, it was usually not practicable to take such precautions.

Comparisons of Variance among Populations

Phenotypic variances showed some differences among population groups in the cutting material (Table 3). The greater coefficients of variation (and, to a lesser extent, absolute variances) for growth rate variables in the native-population material than in the New Zealand land-race material are noteworthy. However, they probably reflect a combination of factors. Possibilities would include inflation of genotypic variances by inbreeding depression and even the increased expression of additive genetic variance through inbreeding—although the degree of selective elimination of inbreds was uncertain. They would also include: effects of smaller tree sizes *per se* (cf. Burdon, Bannister & Low 1992a), and therefore greater competition suffered by native-population material mixed with the faster-growing New Zealand material; and stronger resolution of genetic differences in material that was less well adapted.

Some of the other differences between populations in phenotypic variances reflect situations where variances are related to means, as with binomial (0 or 1) traits such as forking or dieback, or traits that were visually rated on "closed-ended" scales (e.g., sealed bud scores).

The estimates of components of variance in the cuttings (from Table 1,B) tended to reflect the same patterns as phenotypic variances, which might be expected in view of the way in which total clonal variances are expected to be far less influenced by departures from random mating than variances among open-pollinated families (Burdon, Bannister & Low 1992b, Eqn 2 and 3).

Broad-sense Heritabilities

Estimates of broad-sense heritabilities generally differed little among population groups, the main exception being sealed-bud scores in the Guadalupe cuttings in which the buds were almost entirely sealed thereby precluding the expression of much genetic variation. Given the expectation that $\hat{H}^2$ is relatively insensitive to non-randomness of mating patterns, and allowing for imprecision of point estimates, this strongly indicates that genotypic variance structures are generally similar among the population groups.

Broad-sense heritability appears to vary less among traits than narrow-sense heritability, which suggests that non-additive genetic variance tends to be more important than additive genetic variance in the less heritable traits. There are, however, indications (which are discussed later) that the disparities between $\hat{H}^2$ and $\hat{h}^2$ (Table 6) and the $\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_{c(f)})$ ratios (Table 8) have given inflated estimates of σ^2_D/σ^2_A.

Among other studies, that of Guinon *et al.* (1982) gave estimates of H^2 for corresponding traits in the material that were the most closely comparable to ours in terms of maturation state and populations represented, albeit on a markedly different site. Their estimates, however, were consistently lower than ours.

Non-additive Genetic and Epigenetic Variance

The estimates of D, namely σ^2_D/σ^2_A, (Tables 5 and 6) showed some patterns with respect to traits. Growth variables, particularly early heights and stem diameter, showed high apparent ratios of D, whereas later heights and stem-diameter increments tended to show

lower apparent values. This pattern accords with the results of Carson (1986), Carson (1991), Dean *et al.* (in press), Burdon (unpubl.), and Low (unpubl.), who observed a tendency for specific combining ability (SCA) to become relatively less important for growth variables with increasing age. Moreover, Dean *et al.* observed little SCA for periodic stem diameter increment. At the other extreme, some morphological traits, notably sealed bud scores and branch cluster counts, showed very low apparent D, which was expected, on the basis that in plants morphological traits generally show less specific combining ability, relative to general combining ability, than yield. Less expected, though, were the apparent D ratios of around 1 for stem straightness and butt straightness scores, and the ratios of 0.5 or greater for branch cluster frequency scores and branch angle scores. High ratios for branch habit quality scores, however, are understandable. This is because branch habit quality can be strongly non-linear in relation to the highly heritable trait branching frequency (its heritability being reflected best in that of branch cluster counts); the most desirable branching habits are at the two ends of the branching frequency scale (i.e., either "uninodal" or strongly "multinodal"). Since branch habit quality thus has a strongly non-linear relationship with "gene dosage" it can be expected to show strongly non-additive inheritance.

Overall, the apparent ratios of D tended to be higher than most of the ratios of SCA variance to general combining ability variance reported in other studies—noting that a very high ratio reported from a very small factorial cross by Wilcox *et al.* (1975) has been completely overturned by subsequent results (Low unpubl.) from the same trial.

Thus the estimates of D (Tables 5 and 6), while admittedly crude and imprecise, represent our most problematic results, because of apparent conflict with other results and an internal contradiction in the average ratios of $\hat{\sigma}^2_f / \hat{\sigma}^2_c$ for the cuttings. Apart from being higher than suggested by some other reports, the apparent values of D tend to be higher than are consistent with the average $\hat{\sigma}^2_f / (\hat{\sigma}^2_f + \hat{\sigma}^2_{c(f)})$ ratio under likely mating patterns in the Californian mainland and New Zealand material (we consider the most likely mating parameter values in the cuttings to be z = 0.12, 0–0.01, and 0.2, and y = 0.1–0.2, 0.05–0.1, and 0.2–0.25, for Californian mainland, New Zealand, and Guadalupe material respectively).

There are several possible reasons, which include contributions of epigenetic effects (C-effects, in this case), for these discrepancies:

(i) Variation between families in level of inbreeding. This would tend to inflate the between-families variance, particularly if seed parents varied in the amount of inbreeding depression per unit F. This is consistent with $\hat{\sigma}^2_f / (\hat{\sigma}^2_f + \hat{\sigma}^2_{c(f)})$ (Table 8) appearing to be anomalously high in the Californian mainland material, although the average ratio was still somewhat high, in relation to apparent D, for the New Zealand material, while the level of inbreeding represented in the mainland clones was uncertain. In any event, inbreeding depression can contribute to within-family variation (Burdon, Bannister & Low 1992b, Eqn A9) as well as to among-family variation.

(ii) Epistatic gene effects. In conjunction with inbreeding, the various orders of additive × additive gene effects could contribute strongly to σ^2_f, although the importance of inbreeding in the natural-population clones and of such epistasis are uncertain.

(iii) Between-clones variances being inflated by C-effects (i.e., $\sigma^2_{M'} > 0$). This is very possible, and could obviously have contributed to σ^2_c. It could also have contributed to both σ^2_f and $\sigma^2_{c(f)}$ in the cuttings. A larger contribution to σ^2_f than to $\sigma^2_{c(f)}$ might

conceivably have resulted from a lack of randomisation of the clonal ortets, although it seems unlikely to have been important.

(iv) Impacts of micro-environmental variation (σ^2_e) being greater in the seedlings than in the cuttings. This is plausible in view of (a) the standardisation of the size of the cuttings that were set, compared with variation in the sizes of individual seeds, and (b) the size difference between the cuttings and seedlings (Burdon & Bannister 1985), which would have made the latter more vulnerable to competitive influences. Greater micro-environmental variation in the seedlings would depress $\hat{h}^2$ but would hardly account for inflated values of $\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_{c(f)})$ in the cuttings. Nor is this possibility strongly supported by values of the statistic $\frac{4}{3}(\hat{\sigma}^2_w - \hat{\sigma}^2_e)$ (Table 5), except perhaps for the trait CROWN (foliage retention) for which the scores could be strongly affected by crown status.

(v) More subtle effects of localised genetic differentiation in natural stands. Such effects would have to reflect highly localised selective pressures, rather than consanguinity which would be reflected in H (heterozygosity) and F statistics derived from isozyme data. Such effects seem implausible, given the limited differentiation between evident subdivisions of natural populations (Burdon, Bannister & Low 1992a), but cannot be ruled out.

(vi) Effects of the cone collection procedure (*see earlier*) which, in the native populations, could have led to significant over-representation of full-sib relationships.

None of these possible effects resolves convincingly the apparent conflict, which is the main conundrum arising in this paper, between the relatively high apparent levels of D and yet the high ratios of $\hat{\sigma}^2_f/(\hat{\sigma}^2_f + \hat{\sigma}^2_{c(f)})$ in the cuttings. It seems likely that several of the effects have operated together, (i) and (vi) probably being important in the natural-population samples. This serves as a further caveat, however, against direct cross-referencing, of statistics from the two stocktypes, such as obtaining composite genetic parameter estimates as differences between statistics from the respective stocktypes.

CONCLUSIONS

Phenotypic variances were generally similar between the seedlings and the juvenile to early-adolescent cuttings.

Genetic (wind-pollinated family) correlations for performance between the seedlings and cuttings were evidently high, estimates averaging 0.75 or better.

Genetic differences appear to have been expressed similarly in manner and degree between the seedlings and the cuttings.

Broad-sense heritability (H^2) estimates generally differed little among populations, which accords with both the heritabilities being similar among populations (Cedros not being represented) and the estimates being theoretically insensitive to likely departures from random mating.

Comparisons between estimates of H^2 and h^2 (narrow-sense heritability) (the latter being estimated assuming random mating), and the apparent ratios of among-family to total clonal variances in cuttings, both indicated substantially greater departures from random mating in natural populations than in local (New Zealand) populations.

Allowing for differences in mating patterns, the variance structures and narrow-sense heritabilities appeared to be generally similar between the native and the local populations.

Broad-sense heritability estimates were generally higher than narrow-sense estimates, the greatest discrepancies tending to occur in traits that have been reported as showing relatively high ratios of specific combining ability : general combining ability (SCA:GCA) variance.

However, the apparent differences between H^2 and h^2, if attributed to genetic dominance effects, suggest levels of dominance variance that are higher than (1) those suggested by most reports of SCA:GCA variance and (2) those that could, under likely mating patterns, fully account for the apparent ratios of among-family : within-family clonal variance.

The above discrepancies could not be explained conclusively, although there were possible factors that could well suffice if several operated in conjunction.

Close cross-referencing of genetic parameter estimates between the two stocktypes, such as deriving parameter estimates as differences between estimates from the respective stocktypes, must be tentative if attempted at all.

Nevertheless, genetic gain predictions and selections made from seedling trials should be very largely valid for systems of mass vegetative propagation of juvenile to early-adolescent material.

By the same token, gain predictions and selections made from juvenile to early-adolescent cuttings should be largely valid for mass propagation by seed, albeit with some "slippage" which would result mainly from non-additive gene effects.

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