

GENETIC SURVEY OF *PINUS RADIATA*. 5: BETWEEN-TRAIT AND AGE-AGE CORRELATIONS FOR GROWTH RATE, MORPHOLOGY, AND DISEASE RESISTANCE

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(Received for publication 8 May 1992; revision 5 May 1993)

ABSTRACT

Intercorrelations between traits and age-age correlations for some traits were studied to around age 10 years in a provenance-progeny trial of *Pinus radiata* D. Don on two test sites in Kaingaroa Forest in the central North Island of New Zealand, using seedlings and clones. The main seedling component of the experiment was supplemented by clones representing cuttings taken from c. 55 cm height on seedling ortets. All the natural populations, except for the Cedros Island population, plus two New Zealand controls were included in the clonal adjunct.

Estimates of genotypic correlations from the open-pollinated seedling progenies and the clones agreed well. Additionally, the clones afforded direct estimates of non-genetic correlations (among ramets within clones). These results, and the inherent precision of clonal experiments, indicate that juvenile or near-juvenile clones have major advantages for studying such correlations.

Between-trait genetic correlations appeared similar among populations, and results confirmed a pattern for volcanic plateau sites of generally favourable genetic correlations between growth rate, stem straightness, a wide-angled "multinodal" branching habit, and lack of stem malformation. Among these correlations those involving branch cluster frequency were stronger on the warmer, higher-index, test site, and so a strongly multinodal branching habit appears to be more advantageous there. Tree height at around 10 years was more favourably correlated genetically with tree-form traits than was current stem diameter.

Age-age environmental correlations between successive heights, and between stem diameters and successive heights, fitted a coherent and consistent pattern, but the pattern of the corresponding genetic correlations appeared to depend appreciably on both population and site. Early heights seem to be excellent predictors of subsequent stem diameters, and in the better-adapted material stem diameter tended to be more strongly correlated genetically with preceding heights than with current height. Analysis of covariance, adjusting 8-year diameter for 7-year diameter, appeared to give very sensitive detection of incipient changes in genotypic rankings for diameter, but it is not

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yet clear how best to use this feature for selection. Stem diameter increment was correlated with initial height and diameter as well as with foliage retention (*Cyclaneusma* resistance) score, but the specific contribution of resistance could not be closely evaluated. Age-age genetic correlations, between around 8 and 11.5 years, for subjectively scored tree-form traits appeared close to unity. Among juvenile morphological traits, retarded leader showed weak genetic correlation with subsequent tree form, and the onset of production of sealed buds almost zero correlation with growth rate.

Keywords: genetic correlation; age-age correlation; juvenile-mature correlation; inheritance; genetic architecture; growth rate; morphology; disease resistance; *Pinus radiata*.

INTRODUCTION

Associations or correlations between traits are of pervasive interest to the breeder, and to the developmental geneticist. While the phenotypic correlations are often the most evident, the genetic correlations tend to be the most crucial. Adverse genetic correlations impose severe constraints upon the gains that can be obtained simultaneously in the traits concerned, such that the breeder may need to produce different breeds for different situations, concentrating selection on traits that are crucial in each situation and possibly accepting deterioration in other traits that are not crucial.

An example in *Pinus radiata* is the adverse genetic correlation between “internode” length and branch size along with branch angle and various other traits, such that long internodes, while desirable in themselves, tend to be associated with heavy steep-angled branching, relatively high malformation rates, somewhat crooked stems, and slightly slower growth. As a consequence, breeding for increased internode length has in New Zealand been pursued in a specialised Long-Internode breed (Shelbourne *et al.* 1989).

Favourable genetic correlations, by contrast, make things much easier for the breeder, allowing rapid simultaneous gains to be made. They also allow the breeder to take advantage of indirect selection, so that a highly heritable trait that is favourably correlated with a poorly heritable but economically important trait can be used as a criterion for indirect selection to maximise economic gain. Indeed, the trait used for indirect selection does not need to be of any economic importance in itself. Thus the frequency of branch clusters (an inverse expression of internode length) in *P. radiata*, which is highly heritable, has been used as a criterion for indirect selection for smaller branches and other desirable features in the mainstream Growth and Form breed produced in the New Zealand breeding programme.

Where early selection needs to be made, as in almost all advanced-generation tree breeding, age-age genetic correlations for individual traits become very important, along with comparative heritabilities at different ages, for optimising the length of the breeding cycle (Burdon 1989; Magnussen 1991; Newman & Williams 1991). Typically, there is a strong trade-off between age of evaluation (with accelerated turnover of generations) and reliability of evaluation (which affects genetic gain per generation). Low reliability of early evaluation usually stems mainly from changes in time in the performance rankings of genotypes, these changes being reflected in imperfect age-age genetic correlations for performance. If, then, rank changes that are in progress can be detected and characterised the predictions of final rankings should be improved and genetic gains from early selection increased (cf. Burdon 1989).

For *P. radiata* various estimates have been made of genetic and phenotypic correlations among traits (e.g., Bannister 1980; Cotterill & Zed 1980; Shelbourne & Low 1980; *see also* Cotterill & Dean 1990; King & Burdon 1991; C.J.A. Shelbourne, A. Firth & Low unpubl.). Genetic correlations, however, tend to be estimated imprecisely unless sample populations are large, and while some of the studies involved large populations they often involved limited numbers of traits. Also, because they involved only cultivated stocks that are believed to be of similar Californian origin they possibly lacked generality. While some estimates of age-age genetic correlations have been made (Cotterill & Dean 1988; King & Burdon 1991), they also have limitations in scope.

This paper reports the results of studies of between-variable correlations based on data from the *P. radiata* Genetic Survey experiment (Burdon, Bannister, Madgwick & Low 1992). This experiment has served both as a gene-resource collection and as the material for a comprehensive investigation of the quantitative genetic architecture of the species. Compared with previous papers, it extends the scope of correlation estimates in several ways. As a large provenance-progeny trial, involving a total of 350 families from all native populations and two cultivated ones, it provided results for a comprehensive genetic sample of the species. The traits involved were many and varied, the correlations involving wood properties being covered in the next paper of the series (Burdon & Low 1992). The assessments at several ages, allowing estimates of age-age correlations both for individual traits and between different traits, offered new insights on the scope and possible methods for early selection. Finally, there was the clonal adjunct to the main seedling experiment. This afforded genotypic (clonal) correlation estimates, which have inherently good precision and, while not entirely comparable with the additive genetic correlation estimates from the seedlings, could be directly cross-referenced with the latter. It also afforded direct estimates of non-genetic correlations.

MATERIAL AND METHODS

The Experiment

Experimental details have been given by Burdon, Bannister, Madgwick & Low (1992). The main part of the experiment, involving seedlings, included samples from all five natural populations (Año Nuevo, Monterey, and Cambria from mainland California, and Guadalupe Island and Cedros Island) and two New Zealand populations (Kaingaroa and Nelson). Each population was represented (with minor exceptions) as 50 wind-pollinated progenies (families), which were replicated on two sites (A and B) in Kaingaroa Forest. Planting was spread over the years 1964, 1965, and 1967 (three stages), giving six site/stage blocks, with a sum total of around 40 seedlings per progeny. The clonal adjunct represented all populations except Cedros and contained 30 of the 50 families per population, which were replicated in the two Stage III blocks with two clones per family nested within each site and four ramets per clone, giving eight ramets per family per site. The clones represented comprised rooted cuttings taken from *c.* 55 cm height on their ortets, which had been grown in the nursery, and showed slight but definite maturation (“physiological aging”) (Burdon & Bannister 1985). Randomisation was virtually complete within each site/stage block.

Statistical Analysis

Between-variable correlations were studied using analyses of variance (ANOVAs) to estimate variance components for individual variables, and corresponding analyses of cross-

products to estimate the between-variable covariances by strictly analogous procedures. In this context a "variable" is the measured value of a trait at a specified age, and so pairwise between-variable correlations could represent between-trait correlations (for the same age or across two ages) or age-age correlations for the same trait.

Appropriate models for ANOVAs (and therefore for analyses of cross-products) have been set out by Burdon, Bannister, Madgwick & Low (1992) for the seedling material, for alternative samples or subsamples of the experiment. The appropriate models for the clonal adjunct have been indicated by Burdon, Bannister & Low (1992b). Two simplifications of models were deemed appropriate for this paper: the subpopulations classification was ignored for the Californian mainland and Cedros Island populations; and the families classification within populations was ignored for the clones.

Genotypic correlations

Genotypic correlations were estimated for all material. The estimates, involving measurements for both variables of any pair on the same set (or subset) of individuals, represent Type A genotypic correlation estimates (Burdon 1977).

A genotypic correlation (r_g), be it family or clonal, was estimated as:

$$r_g = c \hat{\text{cov}}_{g_{xy}} / (\hat{\sigma}_{g_x} \hat{\sigma}_{g_y}) \quad (1)$$

where $\text{cov}_{g_{xy}}$ is the genetic-group (seedling families or clones) covariance between variables x and y

and $\sigma_{g_x}^2, \sigma_{g_y}^2$ are the corresponding among-group variances for the respective variables.

Genotypic correlations in the seedlings, assuming that the families approximate to half-sibs and that epistasis is not major, represent essentially additive genetic correlations. The corresponding clonal correlations reflect the non-additive gene effects as well as the additive ones.

Two important and interrelated problems were deciding (1) where it was appropriate to combine estimates of genetic correlations over various subsets of the experimental material, and (2) what was the most practical way of achieving combined estimates at the time of data analysis with the existing limitations in computing capacity.

Estimates of genotypic correlations are subject to large sampling errors and these errors have distributions that are neither normal nor well understood, unless the sample population is very large. Such errors are particularly troublesome when heritabilities are low, and when the "signal-to-noise" ratio of the genetic group is low as with small half-sib family samples. Moreover, the 50 families in a population fell well short of the number that Brown (1969) recommended for reliable genetic correlation estimates from half-sib families. Thus the estimates for subsets of the experiment are very imprecise.

Deriving combined, or overall, estimates of genetic correlations (which should be far more precise) was eventually done using considerable approximations (*see below*). Cross-checks, however, were available by using alternative methods and by obtaining separate estimates for both seedling and clonal material.

The basic approach that was used throughout was as follows:

- (1) Estimate genotypic correlations (Eqn 1) for each population/block/propagule-type subclass, provided estimates of family or clonal differences were statistically significant ($p < 0.05$) for both variables of a pair;

- (2) Average, over all blocks, and separately for seedlings and clones, the estimates for each population of each such pairwise correlation between variables;
- (3) Inspect the correlations and, failing obvious disparities between populations or population groups, average the correlations arithmetically over the populations for each pair of variables. Standard errors could be calculated tentatively on the basis of variation among the estimates for individual population/block subclasses.

A cross-check of combined estimates obtained by this approach was available, for seedling material, from a subset of six variables that were assessed in all six blocks of the experiment. Rigorous estimates were made of all the 15 pairwise genetic correlations among these six variables, population by population (cf. Burdon, Bannister, Madgwick & Low 1992, Table 7). The estimates were then averaged over populations weighting each estimate by $h_x h_y$ (cf. Falconer 1981, Eqn 19.1), h^2_x and h^2_y being the estimated heritabilities for the respective traits in the population.

Environmental correlations

Estimates of between-variable environmental correlations (r_e) could be made only rather indirectly from seedling sib-family data (cf. Falconer 1981, Ch. 19), and are inherently biased by contamination from most of the non-additive genetic components. Such estimates were nevertheless attempted, but were so erratic and obviously imprecise that none are presented. Environmental correlations could be estimated more directly from clonal data as:

$$r_{e_{xy}} = c \hat{\sigma}_{e_{xy}} / (\hat{\sigma}_{e_x} \hat{\sigma}_{e_y}) \quad (2)$$

where $\text{cov}_{e_{xy}}$ = among-ramets-within-clones covariance between variables x and y

and $\sigma^2_{e_x}, \sigma^2_{e_y}$ are the corresponding among-ramets variances for the respective variables

Follow-up analyses

To detect changes in time of genotypic rankings for performance, analysis of covariance (ANCOVA) was used, adjusting sums of squares for one variable for within-class covariance on another which usually represented an earlier measure of the same trait. This was particularly appropriate with clonal data, where the within-class covariance was strictly non-genetic. The analysis could be used effectively as a test for departures from perfect genetic correlation, which was of interest in age-age correlation analysis. Also, heritability (h^2 for seedlings, H^2 for clones) could be estimated from the covariance-adjusted mean squares in the same way as it could be estimated from unadjusted mean squares (Burdon, Bannister & Low 1992a, b).

To help infer likely causal relationships, the estimates of simple correlations between selected pairs of variables were extended to partial correlation analysis (e.g., Steele & Torrie 1980, 14.6). This entailed calculating the correlation between a pair of variables when a third, intercorrelated variable is held constant. It serves to indicate whether, or to what extent, the correlation between the first two variables can be interpreted as being incidental to correlations between those two variables and the third one. Of special interest in this connection were the correlations involving periodic diameter increments.

RESULTS

Between-trait Correlations

Values around age 8

The estimates of genotypic correlations obtained for block/population subsets of data, while individually imprecise, tended to be very similar overall between populations and between sites. Accordingly, the correlation estimates presented (Table 1) are averages over both sites and populations.

TABLE 1—Estimated genotypic correlations, averaged over all populations, among growth-rate and tree-form traits at around 8 years from planting. Values above diagonal apply to seedling material, those in parentheses being weighted averages of pooled estimates over all blocks for each population. Values below diagonal apply to clonal material, and include a correlation array for leader dieback.

	HT	DIAM	BUTT	STR	BR QU	BR FR	BR ANG*	FORK*
HT	—	0.76 (0.69)	0.39 (0.09)	0.33 (0.45)	0.47 (0.29)	0.50	−0.26	−0.52 (−0.46)
DIAM	0.70	—	0.06 (−0.16)	0.36 (0.18)	0.21 (0.08)	0.52	−0.05	−0.36 (−0.15)
BUTT	0.06	0.03	—	0.80 (0.67)	0.13 (0.30)	−0.24	−0.07	−0.11 (−0.12)
STR	0.25	0.08	0.72	—	0.64 (0.61)	0.49	−0.12	−0.43 (−0.54)
BR QU	0.39	0.16	0.29	0.57	—	0.82†	−0.68	−0.33 (−0.49)
BR FR	0.44	0.32	0.05	0.36	0.57†	—	−0.53	−0.22
BR ANG*	−0.28	−0.22	−0.14	−0.16	−0.56	−0.49	—	0.11
FORK*	−0.38	0.00	−0.12	−0.38	−0.57	−0.40	0.43	—
DBK*‡	−0.21	−0.07	−0.01	−0.14	−0.22	−0.14	−0.07	0.24

* Inverse scale of desirability, small value desirable, large undesirable.

† Divergent values between sites, *see* text.

‡ Site A only.

HT = height; DIAM = dbhob; BUTT = butt straightness score; STR = stem straightness score; BR QU = branch habit quality score; BR FR = branch cluster frequency score; BR ANG = branch angle score; FORK = incidence of forking; DBK = incidence of dieback—*see* Burdon, Bannister, Madgwick & Low (1992) for fuller definition of traits.

Results for the two methods of obtaining combined estimates of the correlations, over all site/stage blocks, for seedlings were generally in close agreement. The main discrepancies between results using the respective methods involved the weakly heritable trait, butt straightness (BUTT), which gave very imprecise results, and in fact these discrepancies were clearly non-significant ($p > 0.05$). Otherwise, the agreement between estimates for seedling and clonal material respectively was generally very close; standard errors for the listed estimates, calculated on the basis of variation among point estimates from population/block subclasses, were generally between 0.05 and 0.1, the main exceptions involving BUTT as one variable.

Almost all the correlations were favourable, some strongly so. Height was very consistently involved in more favourable correlations with other traits than was diameter. Some of the

strongest genotypic correlations, apart from those between height and diameter, were among the branching traits, high-frequency (“short-internode” or “multinodal”) branching (reflected in BR FR) being strongly associated with relatively flat branch angles (reflected in BR ANG) and favourable scores for branch habit quality (BR QU). A strong association also appeared to exist between scores for freedom from butt sweep and those for stem straightness.

The one noteworthy exception to the close similarity, between sites, of the average genotypic correlation estimates, involved branch cluster frequency score (BR FR) and branch habit quality score (BR QU). These two traits were more positively correlated at Site A than at Site B, the genotypic correlations averaging around 0.6 greater at Site A than at Site B for both seedlings and clones.

The estimated within-clone correlations among the same group of traits (Table 2) were generally rather weaker than the between-clone correlations, and although the patterns were similar they were less pronounced. As with the genetic correlations, the estimates were generally consistent between the sites, the main exceptions being some less favourable correlations at Site B between branch cluster frequency and some other traits, notably branch habit quality.

TABLE 2—Estimated within-clone (ramet-to-ramet) correlations between 7- and 9-year variables (traits) averaged over Californian mainland and New Zealand populations, for Site A above diagonal, Site B below. See Table 1 for definition of traits.

	HT	DIAM	BUTT	STR	BR QU	BR FR	BR ANG*	FORK*	DBK*
HT	–	0.67	0.07	0.22	0.33	0.34	–0.04	–0.05	–0.27
DIAM	0.56	–	0.04	0.21	0.20	0.34	0.09	0.09	0.08
BUTT	–0.02	–0.11	–	0.30	0.07	0.04	–0.01	–0.01	0.02
STR	0.17	0.08	0.12	–	0.39	0.29	–0.16	0.07	–0.05
BR QU	0.16	0.04	0.06	0.34	–	0.53	–0.43	–0.15	–0.23
BR FR	0.17	0.28	–0.02	0.11	0.14	–	–0.24	–0.02	–0.14
BR ANG*	–0.04	0.02	–0.02	–0.00	–0.12	–0.18	–	0.04	–0.03
FORK*	–0.21	0.02	0.03	–0.14	–0.06	–0.03	–0.07	–	–0.09

* Inverse scale of desirability.

p = 0.05, r ~ 0.16

p = 0.01, r ~ 0.21

p = 0.001, r ~ 0.25

Juvenile morphological variables

Estimates of some genetic correlations involving juvenile morphological traits are summarised in Table 3. Clonal rankings for predisposition to retarded leader (RLDR) were evidently fairly consistent over the first 3 years, judging from the positive age-age correlations of around 0.4, and there were indications of a positive clonal association between retarded leader and forking (FORK). The association between early retarded leader and desirability of branching pattern appeared to be quite weak. Sealed bud scores (BUDS) showed virtually no clonal correlation with subsequent height or diameter. The branching-frequency traits—branch cluster counts (BR CLUS) and frequency scores (BR FREQ)—showed quite strong age-age correlations, except between ages 1 and 8.

Early height, at ages 1 or 2 from planting, showed consistently less-favourable genetic correlations with subsequent expressions of tree-form traits (Table 3) than did “8-year”

TABLE 3—Clonal correlations (average within-population values over both sites) of interest involving juvenile morphological traits.

Variables* (traits and ages)		Correlations
RLDR 1†	RLDR 2†	0.41
RLDR 1†	RLDR 3†	0.40
RLDR 2†‡	RLDR 3†	0.39
RLDR 2†‡	BR QU 8	-0.03
RLDR 3†	BR QU 8	-0.21
RLDR 1†	FORK†	0.46
RLDR 2†‡	FORK†	0.02
RLDR 3†	FORK†	0.29
BUDS	HT 8	0.06
BUDS	DIAM 8	-0.05
BR CLUS 1	BR CLUS 3	0.68
BR CLUS 1	BR FR 8	0.32
BR CLUS 3‡	BR FR 8	0.60

* RLDR = occurrence of retarded leader; BUDS = sealed buds score; BR CLUS = branch cluster count; other traits as defined in Table 1—for fuller definition of traits, see Burdon, Bannister, Madgwick & Low (1992).

† Inverse scale of desirability

‡ One site only represented.

height (Table 1). The overall differences, relative to the correlations between 8-year height and those tree-form traits shown in Table 1, were roughly 0.4, 0.3, 0.1, and 0.1 for branch habit quality score (BR QU), forking (FORK), butt straightness score (BUTT), and stem straightness score (STR), respectively. For environmental correlations (not tabulated) the corresponding differences were similar for butt and stem straightness, and about 0.15 to 0.2 for branch habit quality score and forking respectively.

Age-age Correlations

The age-age correlations for growth variables for the clonal material showed certain very clear patterns. The within-clone (among-ramets) correlations did not differ greatly between populations, and were generally similar between sites (Fig. 1). The correlations between diameters and successive heights showed a clear pattern of diameters being more strongly related to heights several years previously than to current heights.

The corresponding clonal (among-clone) correlations (Fig. 2) behaved in a more complex manner, the pattern differing between both population groups and sites. In the New Zealand and Californian mainland material at Site A the pattern was very similar to that for within-clone correlations, except that the early heights tended to show weaker clonal correlations with 8-year height. At Site B, however, the age-age correlations for height tended to be higher, and diameter, while still strongly correlated with earlier heights, was less imperfectly correlated with current height. In the Californian mainland material diameter was very strongly correlated with current height, more so than with any preceding height. For Guadalupe, diameter behaved in this way at both sites, although the correlations suggested more pronounced rank changes in this population at Site B.

Similar estimates of age-age genetic correlations were made for various subsets of the seedling data. The estimates were clearly very imprecise and generally did not yield coherent

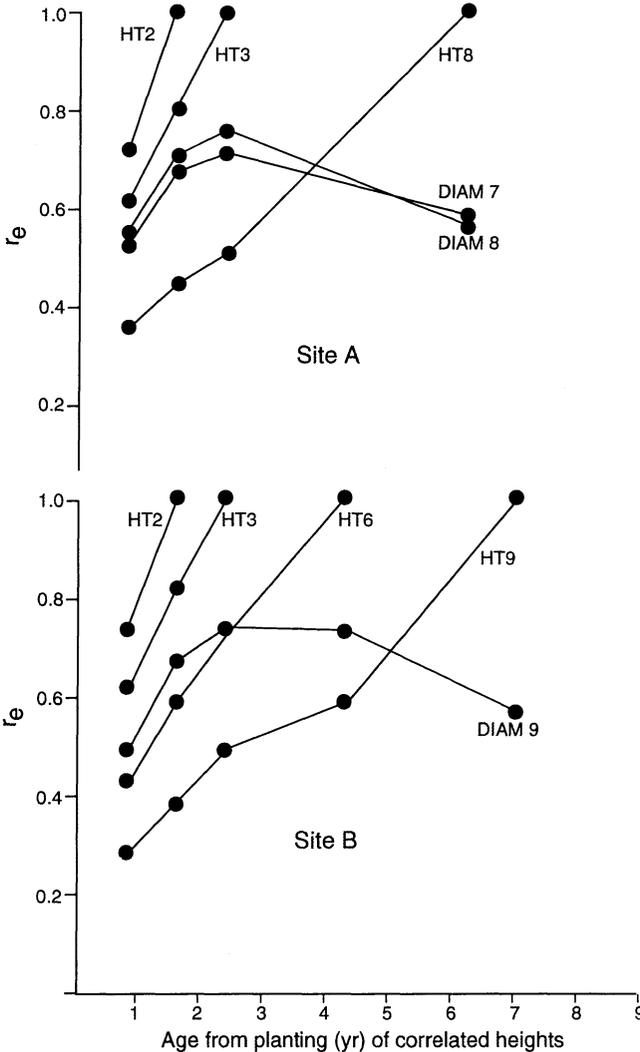


FIG. 1—Average within-clone (among-ramets) age-age correlations (Eqn 2) involving growth variables for Californian mainland and New Zealand material, at the respective sites. All correlations plotted are with heights (horizontal axis), lines joining plots of correlations of particular variables with successive heights.

patterns of the sorts shown in Fig. 2, although there was nothing to suggest that the situation was inherently different from that in the clones. The within-family correlations, since they would have confounded most of the genotypic covariances with the environmental covariances, were of less interest and as such were not pursued.

The age-age correlations were also studied in terms of their fit to the logarithmic equation of Lambeth (1980):

$$r_{\text{age.age}} = p + q \log_e [(\text{earlier age})/(\text{later age})] \tag{3}$$

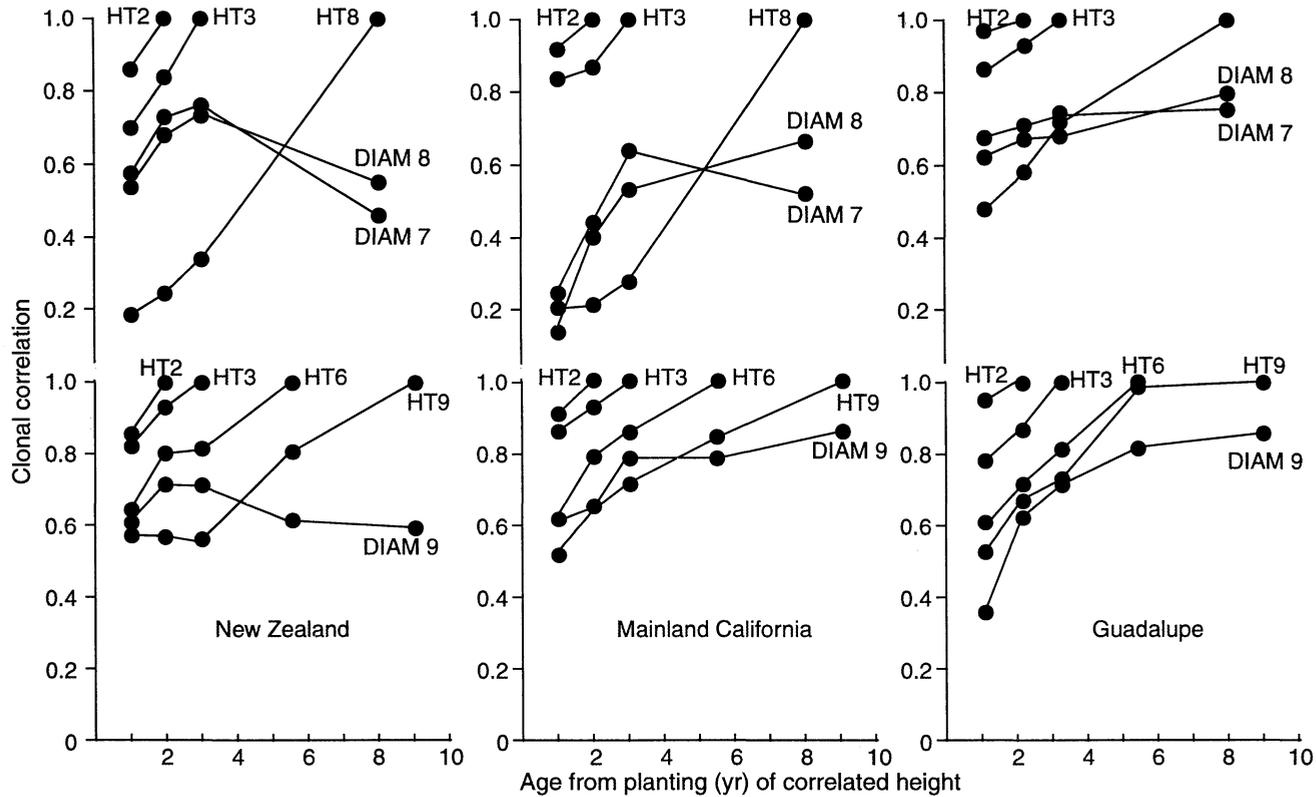


FIG. 2—Average between-clone age-age correlations (Eqn 1) between growth variables and successive heights, for the three population groups, results for Site A above, for Site B below. Plotting conventions are as for Fig. 1.

for both clonal and within-clone correlations. Fitted regressions are shown in Table 4. The regressions for within-clone correlations were similar in slopes and intercepts between both population groups and sites, intercepts averaging around 0.85 and slopes slightly less than 0.3. The corresponding regressions for the clonal correlations tended to show much poorer fit, and so while the estimated slopes appeared to differ widely the differences were clearly not statistically significant ($p > 0.05$), even accepting the nominal degrees of freedom. The low correlations (> 0.35) between early (1- to 3-year) heights and 8-year height in New Zealand and Californian mainland material at Site A (Fig. 2) clearly generated both steep regression slopes and poor fit. Intercepts, unlike those for regressions of within-clone correlations, were close to 1.0.

TABLE 4—Results of fitting Lambeth equation, $r = p + q \log_e$ (age ratio) to estimates of age-age correlations for height in clonal material.

Nature of age-age correlations	Population group	Site	Regression coefficient		df*	R ²
			Intercept \pm SE	Slope \pm SE		
Between ramets within clones (environmental)	New Zealand	A	0.85 \pm 0.046	0.27 \pm 0.038	4	0.93
		B	0.83 \pm 0.048	0.28 \pm 0.040	8	0.86
	Mainland	A	0.89 \pm 0.086	0.27 \pm 0.070	4	0.79
		B	0.86 \pm 0.053	0.26 \pm 0.044	8	0.81
	Guadalupe	A	0.83 \pm 0.090	0.35 \pm 0.074	4	0.85
		B	0.86 \pm 0.037	0.28 \pm 0.031	8	0.91
Clonal (total genotypic)	New Zealand	A	1.01 \pm 0.176	0.44 \pm 0.144	4	0.70
		B	0.95 \pm 0.042	0.18 \pm 0.035	8	0.76
	Mainland	A	1.04 \pm 0.260	0.43 \pm 0.211	4	0.51
		B	1.00 \pm 0.039	0.22 \pm 0.032	8	0.85
	Guadalupe	A	1.07 \pm 0.078	0.29 \pm 0.064	4	0.84
		B	1.00 \pm 0.050	0.23 \pm 0.042	8	0.79

* Defined as number of pairwise age combinations minus 2.

Results of ANCOVAs for clonal data at Site A, adjusting 8-year diameter sums of squares for individual covariance on 7-year diameter, are summarised in Table 5. Despite the extremely close within-clone correlations ($r^2 \geq 0.94$), and extremely high clonal correlations between 7-year and 8-year diameters ($r_g = 0.97, 0.99, 0.99$ for Californian mainland, New Zealand, and Guadalupe material respectively) individual broad-sense heritability estimates (H^2) for covariance-adjusted 8-year diameter were very highly significant ($p < 0.001$) and overall averaged very little lower than for unadjusted diameter. Moreover, the differences in adjusted values were attributable almost entirely to departures of means from their own regression (Snedecor 1956, p. 403) rather than to differences between the regressions of the means and the overall regressions, indicating that genuine changes in relative performance had been very clearly detected, even with only a year between measurements.

Many other such ANCOVAs were carried out (not reported in detail) which adjusted growth-trait (height and diameter) measurements for covariance on preceding height measurements. For almost all variables the estimates of heritability (H^2 , or h^2 for seedlings) were similar with and without the covariance adjustment.

TABLE 5—Summary of results of analysis of covariance for Site A clonal data, adjusting diameter in the clones at 8 years from planting for individual within-clone covariance on 7-year diameter, by population groups.

Population group	R^2_w *	H^2 †	
		Unadjusted	Adjusted
Californian mainland	0.96	0.28	0.34
New Zealand	0.94	0.38	0.21
Guadalupe	0.94	0.58	0.26

* Pooled within-clone (among-ramets) coefficient of determination.

† Clonal repeatability, or broad-sense heritability estimate based on Burdon, Bannister & Low (1992b, Eqn 2).

Age-age correlations were studied for the subjectively scored traits straightness, branch habit quality, and branch cluster frequency between around years 8 and 12 respectively, using data from the Stage I and Stage II blocks. Results are not tabulated, but phenotypic correlations within populations were around 0.5, 0.4, and 0.6 for scores for the respective traits; and estimates of genetic correlations clustered around +1.

Periodic Diameter Increments

Genetic correlation estimates (family and clonal) between periodic diameter increments (Δ DIAM) and associated variables are shown in Table 6. Interest centred around whether resistance to *Cyclaneusma* needle-cast, which is expressed in foliage retention and rated visually as the variable CROWN, had any marked influence on diameter increment. Strong correlations between CROWN and diameter increments were evident, but a high degree of autocorrelation existed among a number of variables including height (HT) and diameter (DIAM) at the start of the increment period, and branch cluster frequency (BR FR). Partial correlations between CROWN and increments, holding single "third" variables constant, were generally strong. There were, however, unexpected positive genetic correlations between CROWN scores and BR FR scores.

DISCUSSION

Basic Methodology

As had been hoped, the use of clonal material for this type of study appears to have two major advantages. Firstly, the inherently greater precision of clonal experiments, which was clearly manifested in this study, is particularly attractive for estimating the genetic parameters that are subject to large errors of estimation such as genetic correlations. Secondly, such experiments give direct estimates of strictly non-genetic correlations. The concerns, however, were two-fold: there was the question of whether the genetic parameters (including non-genetic variance) are sufficiently similar in vegetatively propagules and seedlings; there was also the fact that in clonal material, unlike the seedling material, genotypic effects include all the non-additive components. In this experiment, the genetic correlation estimates from the two classes of propagules appeared to be in excellent agreement, insofar as the seedling results were precise enough to judge. This, on top of the evidence that the variance structures were very similar between the classes and that genetic correlations between performance in the respective classes were very high (Burdon, Bannister & Low 1992b), indicates that the

TABLE 6—Average estimates of genotypic correlations (r_g) between periodic stem diameter increments (Δ DIAM) and associated variables. Variables designated by trait and age.

Y	X	X'*	$r_g \pm SE \dagger$	
			Seedlings	Clones
Stage II, both sites				
Δ DIAM (years 7–11 or 9–12)	"DIAM 8"‡	—	0.73 \pm 0.09	—
	"HT 8"‡	—	0.41 \pm 0.16	—
	"BR FR 11.5"‡	—	0.60 \pm 0.12	—
	CROWN 12	—	0.89 \pm 0.07	—
	CROWN 12	HT 8	0.88	—
	CROWN 12	DIAM 8	0.88	—
	CROWN 12	BR FR 11.5	0.84	—
CROWN	DIAM 8	—	0.51 \pm 0.15	—
	HT 8	—	0.31 \pm 0.16	—
	BR FR 11.5	—	0.52 \pm 0.12	—
Stage III, Site A				
Δ DIAM (years 7–8)	DIAM 7	—	0.80 \pm 0.07	0.67 \pm 0.07
	HT 8	—	0.71 \pm 0.14	0.82 \pm 0.04
	BR FR 8	—	0.82 \pm 0.15	0.50 \pm 0.09
	CROWN 7	—	0.46 \pm 0.14	0.56 \pm 0.05
	CROWN 7	HT 8	0.52	0.41
	CROWN 7	DIAM 8	0.56	0.56
	CROWN 7	BR FR 8	0.15	0.49
CROWN 7	DIAM 7	—	0.19 \pm 0.18	0.42 \pm 0.06
	HT 8	—	0.09 \pm 0.15	0.31 \pm 0.05
	BR FR 7	—	0.47 \pm 0.25	0.32 \pm 0.03

* Partial correlations of the form $Y/X.X'$, between Y and X for constant X' .

† Standard errors calculated from variance among point estimates for populations or population/site subclasses.

‡ Measured at slightly different ages in different stages.

CROWN = foliage retention (putatively *Cyclaneusma* resistance) score; other variables as defined in Table 1.

type of juvenile to early-adolescent material used gives information on between-trait correlations that is also valid for seedlings.

The visual ratings for various traits depended on observers being able to distinguish satisfactorily between the traits in question and other traits. Failure to do so can generate spurious correlations between such traits. Some concerns exist that the scores for stem straightness reflect butt sweep in some degree, although there could be a genuine correlation. There is also the question of whether scores for branch habit quality, branch angle, and straightness were causally influenced by the presence of dieback or actual malformation, although it is arguable whether the resulting correlations would be spurious. The most serious doubts arise from the apparently strong genetic correlation between foliage retention and branch cluster frequency, and it may be that a more open crown habit tended to bias downwards the scores awarded for foliage longevity.

Between-trait Correlations

The results have borne out other studies (Bannister 1980; Shelbourne & Low 1980; C.J.A. Shelbourne, A. Firth & Low unpubl.; see also Cotterill & Dean 1990) in the pattern of

genotypic correlations between traits, with growth rate, stem straightness, freedom from malformation, and branch angle being involved in favourable genetic correlations with the short-internode or multinodal characteristic. Detailed interpretation of different results must be made with caution because of varying bases on which branch habit quality was assessed, some authors (Shelbourne & co-workers) scoring it strictly in relation to a multinodal breeding goal. A further caveat attaches to the way in which the correlation between branch habit quality and other traits may be site-dependent. Indeed the weaker genetic correlation between branch habit quality score and branching frequency score at Site B corroborates the existing perception that a long-internode branching habit is associated with more acceptable tree form on cooler sites of moderate site index on the volcanic plateau of the central North Island. The less-favourable genetic correlation with tree-form traits shown by stem diameter than by tree height is a feature that has not been widely reported, probably because various of the earlier studies with *P. radiata* have not included height measurements, or if so, only on very young trees. This parallels the way in which height shows a weaker (if any) negative genetic correlation with wood density than stem diameter (Burdon & Low 1992). The strong favourable genetic correlations that forking (or lack of it) is involved in, together with the high heritability for some of the other selection criteria, notably branch cluster number traits (Burdon, Bannister & Low 1992a), probably account for the much-reduced malformation in genetically improved *P. radiata* (Carson 1987) despite the low heritability of malformation (Burdon, Bannister & Low 1992b). If so, this would represent effective indirect selection.

The between-trait genetic correlations appeared to be similar for all populations, although the evidence was limited and equivocal for the Cedros population which was not represented in the clonal adjunct.

The environmental correlations (between ramets within clones), while sometimes very much weaker than the estimated genetic correlations, tended to be of the same sign as the latter. It is likely that they are more specific to the experimental conditions. In this experiment, large experimental blocks (4 ha) were involved within which there was considerable microsite variation. If such microsite variation showed similar patterns for the various traits, the environmental correlations would tend to be inflated compared with those within smaller microsite units; conversely, if it showed different patterns among traits the environmental correlations would tend to be depressed. The errors in subjective assessment, unless correlated between traits, would tend to depress the apparent environmental correlations, and in fact the estimated environmental correlations were generally very weak for such traits.

Age-age Correlations

The patterns of age-age correlations for height growth appeared to vary according to population groups and sites, particularly for genetic correlations, although the imprecision of the various point estimates of genotypic correlations makes it difficult to draw firm conclusions. Genotypic rank changes appear to have been greater on Site A (Fig. 2), especially in the better-adapted New Zealand and Californian mainland material. These rapid rank changes are reflected in the steep (if imprecise) regression slopes for clonal age-age correlations *v.* \log_e (age ratio) in this material at Site A (Table 4); indeed, those slopes are markedly steeper than have normally been reported or implied for height (*see* King & Burdon 1991). The remaining slopes for clonal and within-clone correlations are more in line

with previous reports. The intercepts of less than unity for the regressions involving within-clone correlations are noteworthy, since they do not accord with previous reports. Random measurement errors could have contributed, since they would be expected to erode correlations between successive heights. The same effect could result from trees showing year-to-year oscillations about their inherent growth curves, which is plausible in view of the species' susceptibility to retarded leader. Contrary to Lambeth's results (1980), heights at year 1 did not seem to be involved in anomalous correlations relative to all subsequent heights. Even if the type of logarithmic relationship devised by Lambeth represents a valid framework for describing age-age genetic correlations for a trait, it seems inappropriate to generalise the parameter values from past studies unless very conservative assumptions are made.

The age-age correlations between stem diameter and height at various different ages, are particularly interesting. Even more clearly than the age-age correlations involving height they appeared to be markedly dependent on population(s) and site(s). The environmental correlations, which would have been estimated much more precisely, behaved similarly among populations and sites and showed an extremely coherent pattern. This is consistent with early height being a powerful predictor of subsequent diameter in a closed stand, to the extent that the information afforded by current diameter would have been largely available in earlier height. In the genotypic correlations this pattern was much less evident in the native-population material at Site B. It appears that in the native-population material, where a larger proportion of the trees were ill-adapted, early height growth reflected mainly a combination of inherent vigour and health. Conversely, in the well-adapted New Zealand material, in which genotypic variation in inherent vigour and health was presumably less, early heights are likely to have reflected in relatively greater degree inherent genetic differences in tree habit and/or long-term height growth curves. Moreover, the more dominant status of this New Zealand material may have reduced any tendency for early crown status to be reinforced by competition effects. The interpretation of the pattern observed in New Zealand material is supported by earlier observations (Burdon 1971) that the inherent vigour of genotypes may not be closely reflected in their comparative rates of height growth, even though height may greatly influence subsequent diameter growth in the competitive environment of a closed stand. At Site B the greater prevalence of *Dothistroma* needle blight may also have tended to create a stronger coupling between the rankings for height and diameter, since the disease tends to cause defoliation from the ground upwards which would favour the taller trees.

Overall, while height appears to be a good predictor of a genotype's future diameter growth, it may do so in respect of the genotype's competitive ability in a closed stand, rather than in respect of inherent per-hectare productivity of the genotype.

The way in which early height was less favourably correlated genetically than subsequent height with tree-form traits, notably branch habit quality and forking (Tables 1 and 3), accords with the better correlation of current tree form with height than with diameter, since early height is such a good predictor of diameter. It is not established whether there is a true adverse genetic association between rapid early growth and tree form, or early dominance has an adverse phenotypic effect on tree form through greater crown exposure; the latter, however, is suggested by our observation of similar if weaker within-clone (among-ramet) correlations.

The adjustment of 8-year diameters for covariance on 7-year diameters appears to have afforded a very powerful means of detecting incipient rank changes for stem diameter, and there was no reason to believe that it was invalidated by heterogeneity of within-group regressions. Less clear, however, is how to capitalise on this finding in selection. In principle, the sequential measurements could be used as separate terms in a selection index (Burdon 1989), but the high ratio between the ages is in the range where Lambeth's (1980) simple relationship (Eqn 3) often appears to break down (Burdon 1989), making problematic the wider extrapolation of age-age correlations that is always implicit in early selection. The sensitivity with which rank changes can apparently be detected, however, would seem to argue strongly for further methodological studies in this area.

Periodic diameter increments of genotypes evidently depend substantially on diameters and initial heights at the start of the increment period, which in this study were also positively correlated with branch cluster frequency. The influence of *Cyclaneusma* resistance appears to have been significant, but cannot be evaluated satisfactorily because of the high degree of autocorrelation among the possible explanatory variables and a suspicion that the scoring of crown retention contained an upward bias in genotypes of higher branch cluster frequency. A further influence on diameter increment is likely to be the genotypic value for wood density (Burdon & Harris 1973; Burdon & Low 1992).

For the tree-form traits that were subjectively assessed, the genetic correlations between assessment ages appear to be essentially perfect although the heritabilities tended to be higher at the later age (Burdon, Bannister & Low 1992a). Except, perhaps, for the branching traits, the later heritabilities did not appear to be sufficiently higher to justify such a delay in selection for those traits (cf. Burdon 1989).

Juvenile Morphological Traits

The positive age-age genetic correlations for retarded leader suggest that cumulative incidence of retarded leader would be far more heritable than single-year incidence, which did show low heritability (Burdon, Bannister & Low 1992a). Cumulative incidence may also be a better predictor of forking and branch habit quality than single-year incidence which did not appear to show strong genetic correlations with these tree-form traits. While retarded leader has caused past alarms in unimproved stands, it does not appear to be an important factor in genetically improved populations, which suggests that intensive selection for general tree form has acted effectively against severe retarded leaders.

The essentially zero genetic correlations between sealed bud scores and growth rate variables accord with the similar growth rates among Californian mainland populations that produce sealed buds at markedly different ages. Branching frequency showed the classical pattern of age-age genetic correlations that were positive but decreasing according to the ratio between assessment ages.

ACKNOWLEDGMENTS

The considerable contributions of others have been acknowledged in the first paper of this series. We also acknowledge receipt of Grant No. SR:14087 from the New Zealand Lottery Science Board, to support publication of this series of papers.

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