

GENETIC SURVEY OF *PINUS RADIATA*. 9: GENERAL DISCUSSION AND IMPLICATIONS FOR GENETIC MANAGEMENT

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ABSTRACT

Various issues arose from the results of the large *Pinus radiata* D. Don provenance-progeny trial in Kaingaroa Forest which included all five natural populations and two local "land-race" controls. Differences between the five natural populations are multi-dimensional, the apparent affinities between populations depending strongly on the traits considered. Assigning any given tree in the species unequivocally to its appropriate population by means other than pedigree information is difficult, and at present would require data sets that would be hard to obtain. The local land-race control populations, Kaingaroa and Nelson, appear to have obtained about two-thirds and slightly over half of their genes, respectively, from Año Nuevo and the rest from Monterey. The closer resemblance of Kaingaroa than Nelson to Año Nuevo was very consistent, yet the resemblances of the controls to their progenitor populations evidently varied markedly among traits; it is suspected that local "land-race" stocks, while otherwise quite broadly based genetically, may reflect relatively large genetic contributions from a small number of Monterey ancestors in the original introductions.

Interestingly, all five natural populations have shown very little local differentiation. Heritabilities seem similar trait for trait among the natural populations. Genetic correlation structures also appear similar among populations, suggesting that the correlations are essentially pleiotropic and thus constitute some important breeding opportunities, or constraints in the case of adverse correlations.

The scope for further research includes prospects for using molecular biology to complement the biometrical analyses covered in the preceding papers and to contribute to future genetic improvement.

Potential benefits of using native populations to bolster the breeding programme include: specific attributes that certain populations could contribute in the short term, new combinations of attributes in the medium term, and, in the long term, greater responses to directional selection. Among the specific attributes are the higher wood density and lower stem sinuosity of the Guadalupe population, and certain soil tolerances of the Monterey population. For the specific attributes to be worthwhile, their economic importance must in some situations outweigh the adverse features of native-population material, or the adverse features must be overcome either by heterotic effects in crossing with domesticated stocks or by genetic segregation in advanced-generation crosses. New seed orchard and vegetative propagation technologies facilitate incorporation of natural-population material in breeding lines and some production populations.

Natural-population gene resources should be managed, probably as both pure populations and hybrid combinations. A major unsolved problem for management is pollen contamination.

Keywords: provenance; genetic architecture; variation; gene conservation; gene resources; genetic management; breeding strategy; *Pinus radiata*.

INTRODUCTION

The preceding papers in the series (Burdon, Bannister, Madgwick & Low 1992; Burdon, Bannister & Low 1992a, b, c, d; Burdon & Low 1992; Burdon, Gaskin, Low & Zabkiewicz 1992; Burdon, Zabkiewicz & Andrew 1992) have covered various aspects of the quantitative genetic architecture of *Pinus radiata*. These aspects included population differences, local differentiation within native populations, variances, heritabilities, and intercorrelations among traits. Traits studied included: growth rate variables; numerous morphological traits; resistances to some environmental stresses, certain fungal diseases, and some other biotic factors; several wood properties; and monoterpene composition in oleoresin. Incidental to covering the genetic architecture, the papers also contain some findings that relate to the cross-referencing of genetic parameters between seedlings and cuttings (Burdon, Bannister & Low 1992c) and to methodology for early selection (Burdon, Bannister & Low 1992d; cf. Burdon 1989a).

Each paper in the series was aimed primarily at specific aspects of the genetic architecture, but some aspects, including certain of the broader issues, were inevitably addressed piecemeal in several papers. For the latter aspects the evidence and implications are discussed further and more broadly in this paper and conclusions drawn, under the following headings:

- Population differences (patterns of affinity among natural populations, identification of individual trees according to populations, and origins of New Zealand populations);
- Variation within populations (subpopulation differences, genetic parameters—heritabilities, coefficients of variation, and genetic correlations between traits);
- Pointers for future research (provenance trials, tests of provenance hybrids, physiological studies, within-population inheritance, applications of molecular biology);
- Use of native-population material (potential benefits, basic genetic considerations, prospective uses of specific populations);
- Management of native-population material.

It does not repeat the presentation already given (Burdon 1986, 1988) of the schema for managing native-population material and recruitment therefrom into the New Zealand breeding population, but instead focuses more closely on the genetic issues arising from this series of papers.

Not addressed in this paper are some important aspects that emerged incidentally to the main study and were covered in single papers, notably the comparative expressions of gene effects in seedlings and vegetative propagules (Burdon, Bannister & Low 1992c) and implications for early selection (Burdon, Bannister & Low 1992d).

POPULATION DIFFERENCES

Patterns of Affinity among Natural Populations

The pattern of differences among the natural populations (Burdon in press; Burdon, Bannister & Low 1992a, Tables 10 & 11; Burdon & Low 1992, Tables 1–3; Burdon, Gaskin,

Low & Zabkiewicz 1992, Tables 1 & 2; Burdon, Zabkiewicz & Andrew 1992) is doubtless highly multi-dimensional (cf. Libby & Critchfield 1987; Millar & Libby 1991), such that resemblances between particular populations depend greatly on the trait or group of traits considered. For example, the Cambria and Guadalupe populations differ relatively little in respect of cortical monoterpene composition, but contrast strongly in cone size and shape and in persistence of juvenile characteristics. Among the mainland populations, Monterey is intermediate between Año Nuevo and Cambria in persistence of juvenile characteristics and, to a lesser extent, in cortical monoterpene composition, yet Año Nuevo is intermediate in various cone characteristics (Forde 1964; Burdon unpubl.). In resistance to the needle-cast diseases and *Diplodia*-associated dieback, Año Nuevo and Monterey were very similar, yet Butcher & Stukely (1986) observed intermediate resistance to *Phytophthora cinnamomi* Rands in Monterey compared with Año Nuevo and Cambria.

The distinctiveness of the two island populations was confirmed for various traits. Less clear, though, is how distinct these populations are from each other. For characteristics of post-emergent seedlings and palatability to browsing animals these two populations stand largely at opposing ends of the scale (Burdon, Bannister & Low 1992a). That contrast might be readily explained in terms of responses to the selective pressures imposed by the very different biotic environments in which the populations have existed since colonising the islands. These populations also contrast strongly in cortical oleoresin composition (Burdon, Zabkiewicz & Andrew 1992) and isozyme composition (Moran & Bell 1987; Moran *et al.* 1988). On the other hand, the immunochemical results of Murphy (1981) did not suggest a great difference between the two island populations. In growth rate as a pure population, Cedros stands much further apart from the mainland populations than does Guadalupe, yet hybrids between Cedros and New Zealand material have shown vigour similar to that of the New Zealand parents (C.J.A. Shelbourne unpubl.), as have Guadalupe/New Zealand hybrids (P.J. Simmons unpubl.; Low & G.T. Stovold unpubl.).

As stated by Burdon, Bannister & Low (1992a), the population differences presumably reflect a combination of founder effects and local selective pressures, plus interactions between these two main factors. The founder effects, in turn, are likely to reflect both the characteristics of the populations from which colonisation or recolonisation occurred and sampling effects within those populations.

Origins of New Zealand Populations

The two New Zealand populations certainly appear to have derived entirely from Año Nuevo and Monterey, leaving the question of the proportions of genes contributed by these two native populations. Estimates of proportions, on the basis of "distances" between New Zealand populations and the two progenitors, are shown for various traits in Table 1.

The estimates vary widely from trait to trait. Between the estimates based on cortical and bole monoterpenes respectively, for which the standard errors could be estimated fairly satisfactorily, the discrepancies fell within normally accepted sampling errors. In other traits the sampling errors were not readily definable, but they appear most unlikely to explain all the discrepancies observed. For example, the estimates of percentage of Año Nuevo genes based on bud scores were very consistent among data sets, all within-set figures exceeding 100 for Kaingaroa (Kaingaroa means falling outside the intervals between Año Nuevo and Monterey means). For bark thickness, the figures were more variable from set to set, which

TABLE 1—Estimates of percentage of Año Nuevo genes in New Zealand populations, on the basis of resemblances (relative distances* ± standard errors where applicable) for different variables.

Source	Variable	Covariate if any	Basis for calculation	No. of data sets	NZ population†	
					Kaingaroa	Nelson
Burdon, Banister & Low (1992)	Sealed bud score	Current height	Weighted mean performance rating over data sets	8	130–	70–
	Bark thickness, (reverse transformed mean of $\sqrt{\text{values}}$)	Current dbhob	Weighted mean performance rating over data sets	11	80+	53+
Burdon, Zabkiewicz & Andrew (1992)	Cortical monoterpenes	–	Canonical variate distances	1	66 ± 12	52 ± 14
Burdon, Gaskin, Zabkiewicz & Low (1992)	Bole monoterpenes	–	Pinene ratio	1	50 ± 13	25 ± 12
Blight <i>et al.</i> (1964)	Bole monoterpenes	–	Pinene ratio	1	[84‡	64]
Burdon & Low (1992)	Grain spirality	Ring width	Mean of within-set distances	2	49–	38–
Burdon & Bannister (1973, and unpubl.)	Flowering onset—trees with strobili (%)	–	Mean of within-set distances	3	≥80	≥80
Burdon & Bannister (unpubl.)	Seed weight	–	Simple means	1	[80	78]

* Relative distance = $|(\text{NZ} - \text{M})/(\text{A} - \text{M})|$ where NZ, A, and M are the means for the New Zealand population in question, Año Nuevo, and Monterey respectively—figure of >100 results from NZ falling outside the range between A and M.

† Plus or minus signs suffixing figures allow for presumed bias through covariance adjustments tending to under-correct.

‡ Square brackets denote figures based on *in situ* (in the respective habitats of the various populations) rather than common-garden phenotypes.

could be attributed largely to variable resolution of the difference between Monterey and Año Nuevo, among data sets from the various site/stage blocks (Burdon, Bannister & Low 1992a).

The comparisons were subject to biases, of which some were potentially significant. Exact percentages would depend on the method of calculation, several alternatives being available for most traits, but choice of method was clearly a minor factor relative to the differences observed. For several variables that showed appreciable within-population correlations with growth-rate variables, covariance adjustments were clearly appropriate in order to correct for the faster growth of the New Zealand populations. Such variables, especially sealed bud score and bark thickness, are subject to measurement error (plus additional biological “noise” variation) which would bias the regressions downwards and thus make the covariance adjustments conservative. Results based on the expression of traits within the respective habitats of the various populations are subject to obvious bias from local environmental effects, but they did not generate obvious outliers in Table 1, although the figures obtained thus for bole monoterpenes differed strongly from those for the common-garden experiments.

The Nelson population sample consistently showed a closer resemblance to Monterey than did that from Kaingaroa, among variables including individual cortical monoterpenes (Burdon, Zabkiewicz & Andrew 1992) and among different data sets for each variable, despite the apparently marked differences according to variable in the affinities of the New Zealand populations with the two progenitor populations. The only minor exceptions were some data sets for onset of flowering.

Two possible causes remain for trait-to-trait differences in the affinities to progenitor populations shown by New Zealand populations, apart from sampling errors and biases in determination. These are responses to selective pressures and founder effects. Some tree-form traits, notably branch cluster frequency, do differ appreciably between Monterey and Año Nuevo but have clearly shifted in response to natural and/or silvicultural selection pressures since the species was introduced to New Zealand (Burdon, Bannister & Low 1992a), and so they are not considered here. Reproductive precocity, for which Nelson compared anomalously with Kaingaroa in resembling Año Nuevo slightly more than Monterey (Burdon & Bannister 1973), could well have responded appreciably to selective pressures, given the variation within the species in age of onset of reproduction (Bannister 1965), the heritability of early cone production (C.J.A. Shelbourne, I.J. Thulin & R.M.H.C. Scott unpubl.), and some past seed collection practices (Bannister 1959).

For the traits included in Table 1, there is no direct evidence of any responses to selective pressures in New Zealand. While early results (Burdon & Bannister 1973) indicated that a high level of carene in cortical oleoresin is associated with resistance to *Diplodia*-associated shoot dieback, more recent results (Burdon unpubl.) suggest that the association noted was fortuitous. Responses to selective pressures in other traits, however, cannot be ruled out, and must be suspected in the scores for sealed buds in the Kaingaroa population. Strong *a priori* reasons for expecting such responses are lacking; however, thinner bark may confer some selective advantage in dense plantations in New Zealand—the lesser diversion of biomass into bark is likely to be advantageous in such conditions—and this may have contributed to the apparently close resemblance between Kaingaroa and the relatively thin-barked Año Nuevo population.

There is little doubt that Año Nuevo has predominated in the ancestry of the Kaingaroa population, probably to the extent of having provided two-thirds or more of the genes. The contribution of Año Nuevo to Nelson was evidently less than to Kaingaroa, although differences between Kaingaroa and Nelson are statistically non-significant ($p > 0.05$) for most of the traits, but it is still likely to have been 50% or so. More recent results (Burdon *et al.* in prep.), using large, broadly based, regional seedlots from Kaingaroa, Golden Downs (Nelson), and Southland-Otago, suggest around 60% Año Nuevo ancestry in New Zealand stocks, and less regional differentiation among those New Zealand stocks in respect of their Californian origins.

If there are genuine large trait-to-trait differences in the resemblances of New Zealand populations to the native Californian progenitors (Año Nuevo and Monterey), yet a consistently closer resemblance of Nelson than Kaingaroa to Monterey, a possible explanation emerges. This situation could arise through the two New Zealand populations having derived, in differing proportions, from two elements:

- (i) A narrowly based sample from one progenitor which would be subject to founder effects that would differ from trait to trait;
- (ii) A more broadly based sample from the other progenitor population which would be essentially free of founder effects.

Circumstantially, this is plausible. The earliest importations of *P. radiata*, from 1859 to the late 1860s, were evidently on a small scale, mainly for specimen-tree planting (*see* Shepherd & Cook 1988; Shepherd 1990), and at least some evidently came via Britain, possibly even from seed produced in Britain by trees from the original collection by Douglas at Monterey. In any event Monterey would have been a logical site for seed collection before it was superseded by San Francisco as the main seaport in central California. Larger seed importations, totalling at least 24 kg in at least nine significant consignments, began in the late 1860s, evidently finishing around 1880, and those that have been traced are known to have come via San Francisco (Shepherd & Cook 1988; *see also* Shepherd 1990). It is likely that Año Nuevo figured prominently in these collections, since it was close to San Francisco and produces good crops of cones, and the cones there are reputed to remain closed longer than those at Monterey (W.B.Critchfield, pers. comm.).

A few trees involved in the first importations could have contributed substantially to local stocks, because of their “head start” in cone production which would have been helped by their growing in virtual isolation. If the two New Zealand populations represent a fusion, in different proportions, of a narrowly based Monterey element and a more broadly based Año Nuevo element, then the Monterey component could have been subject to a common founder effect in both local populations. One cannot exclude the possibility that natural selective pressures in Nelson had increased the proportion of Monterey genes since introduction to New Zealand, particularly as the Monterey population has shown good tolerance of infertile clay soils (Burdon in press) and infertile heavy-textured soils are prevalent in Nelson.

Some reservations, however, exist concerning the hypothesis of New Zealand material deriving from a narrowly based element from Monterey and a broadly based one from Año Nuevo. The height-adjusted sealed bud scores of Kaingaroa would suggest a founder effect from within Año Nuevo, unless they reflect a statistical bias and/or a response to local selective pressures. Moreover, Moran & Bell (1987) found that out of 13 rare (frequency

~0.01) isozyme electromorphs that were detected in Monterey but not in Año Nuevo seven were detected in 181 plus-trees from Australia and New Zealand. The New Zealand selections were only a small minority (19) of those considered, but no differences were detected among the groups of Australasian selections which overall showed a marginally closer resemblance to Año Nuevo than to Monterey, while significant seed transfers from New Zealand to Australia (at least Victoria and Tasmania) are known to have occurred (Burdon in press). Whether the intensive selection of plus-trees would have boosted the representation of Monterey genes relative to the base populations is unproven, although it is suggested by the poorer tree form of Año Nuevo (Burdon, Bannister & Low 1992a).

The recovery rate of rare alleles needs to be considered in the light of the following expectation (cf. Burley & Namkoong 1980; Krusche & Geburek 1991).

$$PR = 1 - (1 - p)^{2N} - (1 - p)^{2n}$$

where PR = probability of recovery of an allele which empirically was around 50%, i.e., seven out of 13

p = initial frequency of allele at Monterey (≈ 0.01)

N = (unknown) effective number of parents originally represented from Monterey

p' = allele frequency in domesticated stock which, unless zero, will tend to exceed $1 - (1 - p)^{2N}$

n = No. of parents sampled in the domesticated stocks (= 181).

The second and third terms of the expectation relate to probabilities of allele loss in original seed importations and in sampling for isozyme study respectively.

The roughly 50% recovery rate suggests an effective representation (N) of at least 35 original parents, the likely allele "loss" represented in the final term being very minor for n = 181. Such an estimate, however, takes no account of: possible departures from [Castle-] Hardy-Weinberg equilibria (probably unimportant overall); sampling deviations from expected recovery rates for the rare alleles (potentially important); variations about the assumed $p \approx 0.01$ (estimates of p for individual alleles would be imprecise); a small but non-zero probability of Australian material including alleles (not found) that were present but not detected in Moran *et al.*'s (1988) Monterey sample; and possible selection against the rare alleles (cf. Strauss & Libby 1987; Bush & Smouse 1991).

If the genetic bottleneck involved, in the extreme case, a single seed parent, that would suggest an effective representation of at least 70 pollen parents. Moreover, the probability of one or more such allele being represented in the seed parent, and thus showing a sharp increase in frequency, is not high (c. 0.1). However, 70 pollen parents per seed parent seems implausibly high (Burdon, Bannister & Low 1992b, c). The recovery of roughly half the rare alleles that are apparently unique to Monterey does not seem inconsistent with a genetic bottleneck of seed parents so long as numerous pollen parents were represented, but it seems inconsistent with such a bottleneck extending over more than a single generation as might have since happened in England. Not precluded, however, is the possibility that the Monterey component itself contained both a broadly based element and a narrowly based one; if any one parent contributes a substantial proportion of the genes, founder effects can be expected with respect to genetically variable quantitative traits.

The genetic base of the New Zealand populations is restricted in that it represents only two of the five natural populations, although those populations are the best adapted overall to

New Zealand conditions and numerous parents must have originally been involved (given that a total of at least 24 kg of seed was imported in at least nine significant shipments—Shepherd & Cook 1988; *see also* Shepherd 1990). It is uncertain how restricted the genetic base is in terms of the geographic representation within those two populations; it could well be restricted, particularly in respect of Monterey, but although such a situation may be less than ideal the evidence suggests that the importance of this factor has not been great. While the total number of parents represented in the ancestry of the New Zealand populations has probably been considerable, a small number of Monterey ancestors could well have contributed a disproportionate number of the genes.

A difficulty does exist in that the postulated founder effects might be expected to be accompanied by inbreeding effects, and yet signs of inbreeding were notably absent in the New Zealand populations (Burdon & Bannister 1973; Burdon, Bannister & Low 1992a, b; Burdon & Low 1992; Burdon, Gaskin, Zabkiewicz & Low 1992). The quantitative relationships between founder effects and effects of associated inbreeding are not clear, and derivation of expectations would be complicated by ignorance of: number of generations since initial hybridisation; numbers of genetic loci involved for the traits concerned; and gene frequencies at those loci. Concerning the magnitude of within-population genetic variances, any effects of disproportionate contributions from a few ancestors could have been offset by release of new genetic variation after hybridisation.

Conclusions

The pattern of differences among natural populations is highly multi-dimensional, patterns of resemblance varying widely among traits.

For most traits there is strongly overlapping variation among populations.

Exceptions to this pattern of overlap are the consistently binate fascicles and much thinner bark of the island populations, Guadalupe and Cedros, which are separate taxonomic varieties.

The two local “land-race” populations have derived entirely from Año Nuevo and Monterey, Kaingaroa differing from Nelson in apparently having an appreciable preponderance of the Año Nuevo ancestry.

The local populations, however, probably have quite a broad genetic base, although it is suspected that a few Monterey ancestors may have made a relatively large genetic contribution.

VARIATION WITHIN POPULATIONS

Subpopulation Differences

Almost all studies, involving a wide range of attributes, have pointed to very weak local differentiation within the various natural populations. The clearest exception was the paradoxical pattern of salinity tolerance in the Monterey populations (Cromer *et al.* 1982) with the coastal dune material in particular showing the lowest tolerance. Other exceptions (Falkenhagen 1991; Burdon, Bannister & Low 1992a) have been the relatively poor growth of collections from the Swanton locality at Año Nuevo, and the poor growth of the progeny of five isolated high-altitude relicts from Guadalupe. It seems no coincidence that the results

of Moran *et al.* (1988) suggested the greatest inbreeding, as evidenced by $\hat{H}_e - \hat{H}_o$, among mainland seedlots, in those from Swanton and the Monterey coastal dunes. On the other hand, Moran *et al.* (1988) did not observe a greater $H_e - H_o$ in the high-altitude outliers of Guadalupe compared with the main stand, but Burdon, Bannister & Low (1992a) found chlorophyll defectives to be particularly common among seedlings of the five high-altitude progenies.

Given the range of sites in some of the natural populations and, in particular, the geochemical diversity of Monterey sites (Lindsay 1932; Forde 1966), the weak local differentiation within populations is noteworthy. It suggests that the effects of gene flow, presumably mainly through pollen, have tended to outweigh any selective pressures that are specific to localities. This in turn suggests that broad geographic representation within a population, while desirable for gene conservation if it can be conveniently achieved, is not crucial.

Genetic Parameters

Genetic parameters (viz variances and heritabilities of given traits, and correlations between given pairs of traits, especially genetic correlations) appear to be generally similar among the various populations, when allowance is made for certain scalar effects and some differences between the parental populations in mating patterns (Burdon, Bannister & Low 1992b). However, the evidence concerning the Cedros population, and to some extent Guadalupe, is much more limited because of losses of trees in the common-garden plantings, mainly through suppression (Burdon, Bannister, Madgwick & Low 1992). Nevertheless, both island populations clearly show the large and heritable tree-to-tree variation in branching pattern that is such a feature of the species, and the equally distinctive tree-to-tree variation in cone sizes and shapes (Bannister 1958, and unpubl.; Axelrod 1980) which appears to be highly heritable at least in the broad sense (Burdon & Low 1973). For wood density (Burdon & Low 1992) all populations were variable, although Año Nuevo appeared to show inherently less genetic variation than the others, while the especially high phenotypic variance in Guadalupe may largely have reflected the degree of inbreeding.

Accepted heritabilities, coefficients of variation (where meaningful), and economic importance of a wide range of traits are summarised in Table 2 (cf. Burdon, Bannister & Low 1992b; Burdon & Low 1992). These are not discussed, beyond recapitulating the following points:

- A trait must be economically important to be worth pursuing, as a breeding goal in itself or as one of a group of traits that define a composite breeding goal.
- Several traits of substantial economic importance have low heritabilities (< 0.2).
- Weakly heritable traits should be selected for largely on the basis of family (e.g., progeny) information, whereas highly heritable traits can be selected for efficiently on individual phenotypes alone.
- Traits of no direct economic importance may still be very worthwhile selection criteria if they are both strongly heritable and in close genetic correlation with economically important traits (which make up the actual breeding goals).

Inferred values of genetic correlations are summarised in Table 3 (cf. Burdon, Bannister & Low 1992d; Burdon & Low 1992). That the genetic correlations appear to be similar in

TABLE 2—Estimated heritabilities for various traits under typical New Zealand conditions. Figures drawn primarily from results of this Genetic Survey experiment, but also from results of other trials. (*see* Burdon, Bannister & Low 1992b).

Traits	Heritability	Coefficient of variation (%)*	Economic importance†
Turpentine composition	>0.9	—	Negligible
Grain spirality	>0.8	45	Possibly major (-ve)
Wood density (cores)	0.7	7	Sometimes major
Cone characters:‡			
volume, seed weight	>0.5	20–35	Minimal
length, shape, scale No.	>0.5	12–18	
Branch clusters on bole (cf. internode length)	>0.5	20–30	Often high, but indirect
Stem sinuosity§	0.4	—	Not major (-ve)
Wood density (penetrometer/ torsionmeter) measurements	0.3–0.4	—	As for wood density
Branching habit overall§	0.3	—	Generally high
Height to first cone	0.3	20–30	Little direct importance
Dothistroma attack (where present)§	0.3	—	Locally major (-ve)
Cyclaneusma needle cast§	0.1–0.35	—	Considerable (-ve)
Branch angle (steepness)§	≥0.2	—	Considerable (-ve)
Height	0.2	12	Limited in itself
Stem diameter (and volume)	0.1–0.3	15	Consistently v. major
General stem straightness§ (sweep + lean + sinuosity)	0.1–0.3	—	Generally major
Branch diameter	0.2	—	Major (-ve)
Frost resistance (controlled environment)	<0.2	—	Minor overall
Butt sweep§	0.1–0.2	—	Often major (-ve)
Forking etc.	0.05–0.1	—	Major (-ve)
Wind damage	0.05	—	Locally major (-ve)
Leader dieback	0.05	—	Sometimes important (-ve)

* Within populations (where measurement scale allows valid estimates).

† In relation to potential for tree breeding.

‡ Estimates for broad-sense heritability (H^2) but should apply closely to narrow-sense heritability (h^2).

§ Visual scores, with individual observer error depressing the heritability values.

|| Within-stand variation in stem volume being dominated by stem diameter.

all populations (subject to reservations relating to sketchy evidence from the island populations, especially Cedros) supports the presumption that the genetic correlations mainly reflect pleiotropy rather than chromosomal linkage. As such, the adverse genetic correlations are likely to represent long-term constraints upon the genetic gains that are simultaneously obtainable in certain pairs of traits. Nevertheless, the performance of F1 hybrids between New Zealand and island populations, which appear to have combined the faster growth of the New Zealand parents with an intermediate wood density (Burdon unpubl.; P. Simmons unpubl.; Low & G.T. Stovold unpubl.), seems to have largely overcome an adverse genetic correlation through heterosis for growth rate. Whether this effect holds for whole-crop performance, or extends to other combinations of traits, remains to be established. In the longer term, however, trade-offs such as that between wood density and stem volume production are likely to remain significant, and the trade-off between internode

TABLE 3—Approximate genetic correlations between different traits in *Pinus radiata* in New Zealand. Figures drawn primarily from results of this Genetic Survey experiment, (Burdon, Bannister & Low 1992d; Burdon & Low 1992) but also from results of other trials.

A. General								
	Height	Wood density	Stem straightness	Branch frequency	Forks etc.	Cycla.	Doth.	Flowering* (precocity and/or abundance)
Diameter	0.7†	-0.2 to -0.4‡	0.1	0.15-0.45	-0.1	Varying widely with disease levels	~0	~0?
Height		0.15	0.2	0.2-0.45	-0.35			
Wood density			0	-0.05	0	~0	~0	~0?
Stem straightness				0.4	-0.5	~0	~0	~0?
Branch cluster frequency i.e., ("internode length") ⁻¹					-0.4§	~0	~0	~0?
Forks, etc. (0=good, >1=bad) ("malformation")						~0	~0	~0?
Cyclaneusma needle cast							0.25-0.8	~0?
Dothistroma infection								~0?
B. Branch characteristics and forking								
				Branch diam.	Branch angle			Forking (incidence)
Branch cluster frequency				-0.75	-0.6			-0.4
Branch diameter					-0.65			-0.3
Branch angle (low = flat, high = steep)								0.4

* J.N.King (unpubl.)

† Results mainly from stands before competition became extreme

‡ tending to increase with age

§ tending to vary with site.

length and desirable branching characteristics, for instance, will surely remain so. This, along with the phenotypic plasticity of *P. radiata* (which can make tree form and wood density problems on some sites but not others) and the range of characteristics desired by different processors or end users, argues for producing a range of specialised breeds.

Conclusions

Local genetic differentiation within native populations appears to be generally minor, despite some considerable site variation within populations.

Heritabilities, while varying widely according to traits, tend to be very similar among populations, most of the apparent exceptions being readily explainable.

Likewise, genetic correlations between traits tend to be similar among the various populations, suggesting pleiotropic effects.

The main adverse genetic correlations are between wood density (if high is desirable) and stem diameter growth, and between "internode" length, on the one hand, and growth rate and several tree-form traits, on the other.

Interpopulation heterosis for growth rate, however, may largely overcome the negative genetic correlation between wood density and stem diameter growth.

POINTERS FOR FURTHER RESEARCH

Provenance Testing

Further empirical field-trial data on the performance of the various natural populations from the 1978 seed collection (Eldridge 1978) would be very welcome. The resulting New Zealand-wide series of provenance trials, planted in 1980, has already given much information on adaptive profiles of the mainland populations (Burdon unpubl.), but further information may come available as the trees get older. Further comparisons of wood properties are desirable, and can readily be made from existing trials. Testing in other countries is patchy. Australia has also a considerable network of trials from the 1978 collection, and various comparisons have been made in California (e.g., Hood & Libby 1980; Guinon *et al.* 1982; Old *et al.* 1986) based mainly on an earlier independent collection of material. The coverage in other countries with an interest in *P. radiata*, however, has been much more limited.

Tests of native populations in known hybrid combinations with other populations have been limited. Hybrids between island populations and “land-race” stocks appear to have been studied most, and have performed very promisingly, but information is not available from a large sample of test sites. Other known hybrid combinations have tended to be based on very limited parental population samples, and tested on only a very few sites.

Progeny Trials

While the quantitative inheritance of within-population variation in *P. radiata* is reasonably well known for a number of traits, much remains to be learnt. To date the inheritance studies have covered relatively few wood properties. Not only are there certain wood properties (e.g., micellar angle) of which the inheritance has yet to be studied, but also there appear to be certain basic wood properties of major technical importance which have yet to be defined as a prerequisite for studying inheritance. An example of the latter would be the basic properties (which are now largely elucidated) that determine some particularly favourable characteristics for mechanical pulping (Donaldson 1993). Knowledge of the inheritance of resistance to certain diseases and pests is limited, or often applicable to limited sets of environmental conditions. Nothing is known, for instance, about genetic variations in susceptibility to the European pine shoot moth (*Rhyacionia buoliana* Denis et Schiff) which has become a troublesome pest of *P. radiata* since its recent appearance in Chile.

Information on genetic correlations between traits always tends to be less reliable than that on variances and heritabilities for single traits. A particularly important gap is the relatively weak information on the strength of the trade-off between precocity of flowering and fecundity, on the one hand, and rotation-age wood production, on the other.

In any event, field plantings of material of known pedigree will form an essential basis for certain applications of molecular biology (*see below*).

Physiological Studies

Physiological studies of the comparative tolerance of different populations of *P. radiata* (e.g., Cromer *et al.* 1982) have been limited in number, but further studies should provide a valuable complement to field-trial information on site tolerances. Should physiological studies elucidate the detailed bases of field tolerances and inherent differences in productivity, more powerful tools should be available for early selection.

Scope for Molecular Biology Techniques

Much future work will undoubtedly concern variation within and between the populations in the DNA features that can be addressed by convenient techniques of molecular biology. This will certainly add to our understanding of the population differences, but in an iterative process whereby existing knowledge is initially used to help calibrate certain DNA features for their informativeness within the species. The average heterozygosity in *P. radiata* for the "standard" isozymes has proved to be relatively low (Plessas & Strauss 1986; Moran *et al.* 1988), considering the heterozygosity shown by various other conifers. On the other hand, there is a high level of tree-to-tree genetic variation in *P. radiata* for various morphological traits, wood properties, disease resistances, and even monoterpene composition, just to mention traits for which actual data have been collected. Similarly, the genus *Sorghum* shows notably little isozyme variability, despite having a great degree of heritable variation in economic traits (M.M. Goodman, pers. comm.). In *Populus deltoides* Marsh. geographic patterns of isozyme variation have recently been found to be unrelated to geographic patterns of morphological variation (Rajora *et al.* 1991). Also, it has recently emerged that cultivated maize has a high level of detectable DNA polymorphisms in material with little genetic variability in economic traits, while the opposite holds for melons (Shattuck-Eidens *et al.* 1990). Very recently it was found in the Californian closed-cone pines (*P. attenuata* Lemm., *P. muricata* D. Don, and *P. radiata*) that the "molecular clock" in the chloroplast genome is apparently running at extremely different rates even among populations within a species, apparently "racing" in the northernmost populations of *P. muricata* (Strauss, Bousquet, Hipkins & Hong 1992).

The occurrence of *P. radiata* in only five discrete natural populations offers exceptional prospects of identifying genetic markers that are unique to individual populations. While fixation of different alleles in different populations may be uncommon, new DNA technology can identify so many marker sites that it may still be possible to locate a good number of markers that are diagnostic of individual populations. That could have several benefits. It could allow individuals to be placed unequivocally according to natural populations. At present that often cannot readily be done, even without hybridisation between populations, because of the amount of between-populations overlap in individual quantitative traits; while, in principle, individuals might be reliably assigned to populations by multiple discriminant analysis it may be difficult to obtain information on all of the requisite traits for one individual. For identifying the ancestry of a hybrid, in terms of the proportions and the parts of its genome contributed by different natural populations, the potential advantages of genetic markers are even greater.

Genetic markers may prove valuable for detecting quantitative trait loci (cf. Strauss, Lande & Namkoong 1992) with allele differences of large effect both within and between populations, such loci being extremely difficult to detect only from quantitative phenotypic data. While detecting consistent quantitative differences between populations at individual loci is speculative it could be a particularly powerful tool for selecting individuals containing desirable alleles from two or more natural populations in advanced-generation hybrids. All such work, however, will depend on having adequate genetic experiments planted out in the field.

In the longer term, molecular biology, by using cDNA libraries should contribute to the developmental analysis required for identifying genes that contribute to traits that are

important in breeding goals. They could help both in selecting genotypes produced by normal sexual reproduction and in identifying the genes that should be incorporated by genetic transformation.

Conclusions

Provenance trial evaluation should continue in order to extend knowledge of the characteristics of different natural populations.

Further evaluation is also needed of the attributes of various interpopulation hybrid combinations.

Knowledge of variances, heritabilities, and genetic intercorrelations needs to be extended to additional traits, notably resistance to certain diseases and pests and various wood properties.

Physiological studies should provide a valuable complement to information from field genetic experiments.

Major scope exists for the use of molecular biology, to define better the affinities among natural populations, to identify markers that are diagnostic of natural populations, and to identify quantitative trait loci.

Such work on genetic markers, however, will require good field plantings of pedigreed genetic material.

In the longer term, molecular biology may serve to identify the appropriate genes required for use in genetic transformation, but this requires better definition of breeding goals.

USE OF NATIVE POPULATION MATERIAL

Potential Benefits

The potential benefits of using native-population material to bolster the breeding programme fall into several overlapping categories:

- (1) Capturing predictable benefits from known attributes of particular natural populations, the significance of which will depend largely on the relative importance of different breeding goals in the particular situation;
- (2) Capturing heterotic effects (at least with respect to mid-parent values) which may be needed to make Category (1) worthwhile in the short term;
- (3) Combining desirable attributes of different populations by genetic recombination;
- (4) Extending the future responses to selection by contributing favourable alleles not represented in the existing breeding population.

Category (2) is immediately realisable through producing F1 hybrids. Such benefits may be necessary to make Category (1) immediately worthwhile, otherwise the Category (1) benefits are liable to be outweighed by the additive inheritance of the less desirable features of the native population. With new propagation technology, in the forms of control-pollinated seed orchards and/or mass vegetative multiplication, these two categories are now readily accessible in *P. radiata*. Category (3) is likely to require longer-term breeding—unless sophisticated genetic transformations can be targeted, achieved, and proven safe. Category (4) clearly represents benefits from longer-term breeding.

Basic Genetic Considerations

The value of any native population for future breeding work will ultimately depend on differences in allele frequencies between that population and existing cultivated stocks. At the most superficial level, allele frequency differences are the basis of population differences. Such allele frequency differences may represent, in the extreme, fixation of different alleles in the respective stocks, or markedly different frequencies of alleles that are common to the populations concerned. The mode of gene action, viz dominance or epistasis *v.* straightforward additivity, is also relevant.

Fixation of favourable alleles at different loci in different populations can have two major implications. If such alleles are fully dominant, with no complications from epistasis, both-parent heterosis (with offspring excelling both parents) can be expected. In fact, island/mainland hybrids, which are between parental populations that are not closely related, show considerable mid-parent heterosis (with offspring excelling only mid-parent values) for growth rate, which may translate into both-parent heterosis for stemwood dry weight in view of the strongly additive inheritance of wood density. In segregating generations (F₂, etc., or backcrosses) some homozygotes for less desirable alleles would appear, which are likely to depress average performance in addition to producing a highly variable hybrid swarm. High variability has been observed by the author in F₂ *P. elliotii* Engelm./*P. caribaea* Morelet hybrids in Queensland.

Even without allelic dominance the fixation of different favourable alleles at different loci can have important implications. In the medium term it is likely to be manifested in transgressive segregation, whereby genotypes in segregating generations fall outside the ranges of variation shown by parental populations. This transgressive segregation will extend the limits of responses to selection. It will, however, often be undesirable within commercial crops, particularly with certain non-linear economic worth functions in combination with high heritabilities (Burdon 1990). Capitalising on the additional additive genetic variation released by hybridisation will not be rapid, because of the slow approach towards gene fixation. Non-additive gene effects, however, may be effectively captured in early segregating generations by clonal forestry (Burdon 1989b).

The opportunities to study transgressive segregation in *P. radiata* are still limited. Firstly, the only advanced-generation hybrids available to study in quantity are the spontaneously occurring Año Nuevo/Monterey hybrid swarms represented by New Zealand land-race stocks. No obvious signs of transgressive segregation were evident from this experiment—unless one includes the superior growth of many of the land-race trees, which could well be interpreted as a different type of phenomenon (Burdon, Bannister & Low 1992a). Secondly, the one trait in which the parental populations differed markedly, namely, sealed bud scores, appeared to be no more variable in the New Zealand populations than in either of the progenitors, let alone show clear transgressive segregation. There are several possible reasons for this lack of obvious transgressive segregation, which may not negate the expectation that hybrid swarms will be capable of greater long-term responses to selection than any pure population. They include:

- (1) The expression of genetic variation tending to be exaggerated within natural populations, in respect of both additive and non-additive gene effects (Burdon, Bannister & Low 1992b), by the significant inbreeding that occurs in natural populations;

- (2) Closely related to (1), phenotypic stability being reduced by the inbreeding such that phenotypic variance is inflated;
- (3) Scalar effects, which are particularly liable to arise with subjectively scored traits, preventing reliable cross-comparisons of variances among populations.

It should be noted that it is still only a presumption that the New Zealand populations are indeed advanced-generation hybrid swarms, although the presence of 90% or so identifiable hybrids in seed collected from pure Guadalupe material abutting on to local stock (Burdon unpubl.) makes the presumption extremely strong.

Overall, while there is still no hard evidence for fixation within populations of alleles controlling quantitative economic traits in *P. radiata*, it seems prudent to allow for it in genetic management. Fixation of different alleles, if it has occurred, or nearly so, in different populations, would mean that even though improved domesticated stocks are currently superior to any natural population for certain traits, the infusion of germplasm from natural populations could improve the longer-term response to selection in such traits.

Very little is known about epistasis in *P. radiata*, other than the finding of Wilcox (1983) that an additivity-plus-dominance genetic model could not adequately account for the behaviour of self progenies relative to outcross progenies of the same parents—which was intuitively plausible. Epistasis could contribute importantly to between-population heterosis as well as inbreeding depression, and delay the decay of heterosis after the F1 hybrid generation. Significantly, it could mask the expression of unfavourable additive gene effects in native-population material when it is crossed with improved New Zealand stock.

Although not directly relating to the Genetic Survey experiment it is noteworthy that Monterey material has substantially outperformed local land-race stock on phosphorus-deficient “gumland” clays (Burdon, M.A. Miller, Low & A. Firth unpubl.). Thus, the land-race stock was only intermediate between Monterey and Año Nuevo in its growth performance on such sites. This was despite the evident “neighbourhood inbreeding” in natural stands and apparently about 40% Monterey genes in the local stock. Such a result suggests a high degree of additivity in the genetic control of this tolerance, or else several generations since initial hybridisation which could have largely dissipated any initial heterosis—assuming that the populations have indeed hybridised.

Prospective Uses of Specific Populations

Obvious scope for drawing on natural populations exists where one or more such populations have a substantial advantage over local stock. (The advantages and disadvantages of the various natural populations, relative to each other, are summarised in Table 4.) The inheritance of the various traits will generally be important, because any one natural population will usually have significant disadvantages for several traits compared with improved breeds.

To be useful in the short term, a natural population must not only have some clear advantage, but that advantage must also be crucial in certain situations—unless there is significant both-parent heterosis (which has not yet been observed) among populations for any simple trait in *P. radiata*. The condition of different traits being critical in different situations can certainly be met in *P. radiata* (Burdon in press). To exploit this feature, however, requires that it be both feasible and economic to produce specialised seedlots or

TABLE 4—Summary of pattern of known advantages and disadvantages of individual natural populations (after Burdon in press). Pluses denote superiority, minuses inferiority, zeros essentially average, dots no data located; (a) denotes a large body of solid experimental evidence (many sites), (b) good experimental evidence but from limited number of sites/pot trials, (c) slender evidence, two letters denoting intermediate weight of evidence. Information from Genetic Survey experiment unless otherwise indicated.

Attribute	Weight of evidence	Population				
		Año Nuevo	Monterey	Cambria	Guadalupe	Cedros
Growth rate	a	+	+	+	-	--
Ease of transplanting *	bc	+	0	-	+(+)	--
Resistance to/tolerance of:						
Frost	b	++	+	-	0?	--
Snow damage†	c	+	0	-	•	•
Boron deficiency	b	+	+	+	--	--
Phosphorus deficiency (i.e., "gumland" clays)†	b	-	++	++	-?	--
<i>Dothistroma pini</i>	ab	++	++	--	0	--
<i>Cyclaneusma minus</i>	a	+	++	--	-	--?
<i>Diplodia pinea</i>	b	++	++	--	--	-
<i>Phytophthora cinnamomi</i> ‡	b	--	+	++	•	•
<i>Endocronartium harknessii</i> §	b	+	-	--	++	+
<i>Pineus pini</i>	c	+	+	-	--	+
Damage by mammals:						
deer/rabbit browse	bc	0	0	0	-	+
deer browse	b	-	0	+	•	•
porcupines	b	+	+	--	•	•
Soil salinity ¶	bc	0	+	++	--	-
Tree form:						
Overall	a	--	0	+	+	--
Stem straightness	a	--	0	+	++	+
Forking (lack): early	a	--	0	0	++	+
later		-	+	+	-	-
Branch habit: early	a	--	0	0	++	+
later		-	+	+	-	-
Butt straightness	a	--	--	+	++	++
Wood properties:						
Basic density	a	-	0	--	++	++
Compression wood (lack)	c	-	0	+	0?	?
Grain spirality (lack)	c	-	+	+	-	?

* Shelbourne *et al.* (1979)

† Burdon, M.A. Miller, Low & A. Firth (unpubl.)

‡ Butcher & Stukely (1986)

§ Old *et al.* (1986)

|| Hood & Libby (1980)

¶ Cromer *et al.* (1982)

even breeds, for particular situations, which is now possible through new seed orchard technology and/or vegetative multiplication (Shelbourne *et al.* 1989).

Unless one trait is paramount in a breeding goal it will almost certainly be necessary to hybridise natural-population material with improved breeds based on local land-race stock.

The hybrids are likely to be intermediate between the parents (or better) with respect to various economic traits.

An obvious example of a trait where native-population material may contribute important short-term gains is wood density, which within the corewood zone is 10% higher in the island populations but, although very heritable, has a low within-population coefficient of variation (c. 7%). Using island-population trees to produce F1 hybrids with local stock will give a 5% gain in corewood density without any selection for that trait. Selection within local stock to achieve the same gain, assuming narrow-sense heritability (h^2) = 0.7, with increment-core determinations, would require a selection differential of 7.14% of the mean which represents 1.07 standard deviations, which in turn requires a culling rate of 63% (Lindgren & Nilsson 1985). With less-precise determinations, say, by penetrometer ($h^2 \approx 0.35$) the requisite culling rate would become 95%. The implications of using Guadalupe selections, in terms of trees screened per trees saved, to meet increasing “target” levels of wood density are illustrated in Table 5. The higher the target, the more necessary it becomes to use island parents in order to avoid having to cull for wood density at a rate that is prohibitively intensive in terms of both work content and the rejection of genetic material.

While there is potentially a “genetic opportunity cost” in using island parents through their being largely unimproved, New Zealand/Guadalupe hybrids have, as mentioned earlier, shown strong mid-parent heterosis for growth rate and superior straightness compared with New Zealand material despite the New Zealand parents being highly select for straightness. This would theoretically translate into both-parent heterosis for stem dry matter production, although that remains to be demonstrated at the level of the whole stand.

Another feature of the Guadalupe population, which could be of major value in the Northern Hemisphere, is its apparently superior tolerance of continental-type frost (W.J.Libby unpubl. data).

Other traits for which native-population material may be able to make significant short-term contributions to genetic gain in New Zealand include: western gall rust resistance from Guadalupe (cf. Old *et al.* 1986); tolerance of certain infertile clay soils from Monterey and/or Cambria (Burdon, M.A.Miller, Low & A.Firth unpubl.); tolerance of soil salinity (Cromer *et al.* 1982); and resistance to *Phytophthora cinnamomi* (Butcher & Stukely 1986) from Cambria. More speculative contributions, which might be expected from the nature of the island habitats rather than evidence from provenance trials, are resistance to exposure and snow damage from Guadalupe, and resistance to heat and drought from Cedros. (It is assumed that the desirable features of Año Nuevo are already well represented in New Zealand land-race stocks.) Some desirable attributes of native populations are accompanied by characteristics that are highly adverse in many of the environments where the species is cultivated. For instance, Cedros, along with its prospective heat and drought tolerance, shows very strong taproot development which makes it difficult to transplant, particularly under droughty conditions; and it is prone to boron deficiency which is a problem on many droughty sites unless corrected. In such cases it remains to be seen whether F1 hybrids combine the favourable features of the respective parental populations.

Conclusions

Despite the generally good performances of local “land-race” stocks, native-population material is of interest for future breeding.

TABLE 5—Expected numbers of trees to be screened per parent tree saved in order to meet corewood density targets under alternative breeding options, in relation to using Guadalupe parents.

Breeding options	Target density (kg/m ³)								
	340	350	360	370	380	390	400	410	420
A. Selecting (solely for density) within New Zealand to produce pure New Zealand	1.9	4.8	17	82	625	6775	10 ⁵	→∞	
B. Producing F1 Guadalupe/New Zealand hybrids, but selecting parents for density only within New Zealand	1*	1.9	17	625	10 ⁵	→∞			
C. Producing F1 hybrids, equal culling rate in New Zealand and Guadalupe	1*	1.2	2.4	6.7	24	125	850	8300	>10 ⁵
D. Selecting within Guadalupe to produce pure Guadalupe	1*	1*	1*	1.5	3.2	8.9	33	167	1140

* Target density met, or exceeded, without any within-population selection.

Conditions: (i) Expectations exclusive of culling for any other trait.

(ii) Base population means of New Zealand and Guadalupe 328 and 360 kg/m³ respectively.

(iii) Normal distributions and selection from within large undifferentiated populations.

(iv) $h^2 = 0.7$, and phenotypic coefficient of variation 0.07 in each population.

(v) Hybrids intermediate between mean genotypic values of the selections from the respective parental populations.

Note: (1) Number of trees represents inverse of culling rate (truncation selection) required to give selection intensity, i (selection differential in standard deviations) (Lindgren & Nilsson 1985) that reaches target density in offspring.

(2) Density = $p_{NZ} \{328 + i_{NZ} \times 0.7 \times (328 \times 0.07)\} + p_{Gua} \{360 + i_{Gua} \times 0.07 \times (360 \times 0.07)\}$

where

p_{NZ} = proportion of New Zealand parents used = 1, 0.5, 0.5, and 0 for options A, B, C, and D respectively

p_{Gua} = proportion of Guadalupe parents used = $1 - p_{NZ}$

i_{NZ} and i_{Gua} are the selection intensities in New Zealand and Guadalupe material respectively, which are subject to the constraints

$i_{Gua} = 0$ in options A and B,

$i_{NZ} = i_{Gua}$ in option C, and

$i_{NZ} = 0$ in option D.

Increased representation from Monterey in the breeding population is of obvious interest, mainly for extending edaphic tolerances, but also for helping to improve needle-cast resistance.

The Guadalupe population is of considerable interest for producing F1 hybrids with local stock, to give superior stem straightness and wood density combined with high vigour and possibly some other desirable features.

The Año Nuevo population, although well adapted to New Zealand conditions, is of lesser interest because of its predominant historical contribution to existing land-race stocks.

Conservation and incorporation of the other two populations, Cambria and Cedros, may nevertheless still be of real value because of unpredictable benefits of completely new gene combinations and to help meet unforeseen selection criteria that might emerge in the future.

MANAGEMENT OF NATIVE-POPULATION MATERIAL

Between these various potential benefits of using natural populations for the breeding programme, two separate approaches to the use of native-population material are indicated: (i) maintaining pure-population lines, and (ii) early hybridisation leading on to segregating generations. The first approach would be combined with progressive genetic improvement of the native populations for the basic, widely agreed, selection criteria (general health, growth rate, and quality of tree form). With Guadalupe, it would also serve to perpetuate, albeit at a reduced effective size, a population that has recently become almost extinct in the wild. Selection within a pure population may well operate more effectively against the generally undesirable genes that it contains, because the phenotypic expression of such genes may be clearer against the unimproved genetic background—which is consistent with a genetic model of epistatic gene effects in F1 hybrids masking certain additive gene effects within parental populations. The second approach would logically also involve selecting the more desirable segregants.

Decisions in managing pure native-population material are largely driven by what the populations are hoped to contribute (Burdon 1988). The decisions involve: the deployment of the material, in terms of sites; the pressures of selection to be maintained, beyond those imposed directly by the sites; the sizes of the population samples to be maintained; and the mating system(s) employed.

It seems appropriate to locate material, as far as logistics permit, on sites where the selective pressures will reinforce the adaptational advantages of the respective native populations. Some additional selection for general tree form seems imperative, and while mild to moderate selection for silvicultural traits seems unlikely to reduce the genetic base significantly, intensive selection is likely to cause a major run-down of effective population size.

The most problematic issues are the requisite sizes of such gene resources and the mating system. How many individuals of each population are appropriate for gene conservation will depend on the number of loci involved and the frequencies of various unrecognised low-frequency alleles that could eventually prove desirable. Even if many individual traits prove to be controlled mainly at limited numbers of loci, the sheer numbers of traits of potential interest mean that numerous loci are likely to be involved. The actual frequencies of low-

frequency alleles that are of potential importance are conjectural. With the general lack of definite information, a conservative course, retaining generous numbers of unrelated individuals, seems prudent.

In another respect, exact frequencies of such alleles are unimportant. If native-population selections are to be incorporated into the breeding population they will need to be acceptable for the range of traits that represent the basic selection criteria, at least for some subset of the breeding population. If such selections are to be used in seed orchards they will need to be of even higher genetic merit. That is likely to require favourable alleles at numerous loci (even though some genes of large effect may prove to exist for some economic traits). Achieving high frequencies of such genes at the various important loci is likely to require appreciable selection which will need to be repeated over generations. Such selection inevitably requires large numbers of individuals to give worthwhile selection intensities, particularly if effective population size is to be maintained.

The selection is admittedly contentious, because it conflicts with purist notions of gene conservation. Any selection theoretically incurs the risk of shifting the population mean further away from future breeding goals that may emerge—but this has happened dramatically with carcass fat content in animal breeding—but there seems little doubt that we can safely choose a set of basic selection criteria for certain forest gene resource plantings. In any event, selective forces are unavoidable where material is maintained as closed-canopy plantations. Allele loss is always a concern, but it is considered that any losses resulting purely from mild to moderate selection are likely to be outweighed by the benefits of being able to maintain larger population sizes, which is likely to be acceptable if moderate genetic improvement reduces the opportunity costs of maintaining a given area of gene-resource planting. Moreover, latest moves towards more stringent conservation of the Californian mainland populations of *P. radiata* (Anon. 1993), with emphasis on preventing genetic contamination, should help retain gene resources of last resort.

The repeated (i.e., recurrent) selection demands sexual propagation and active management of gene resources. The need for sexual propagation, however, raises the need to avoid pollen contamination, which poses a serious problem. Very large areas of intensively improved stands will produce enormous pollen clouds which are likely to cause significant pollen contamination in relatively small areas of gene resource planting. The intensively improved status of the contaminant pollen is likely to give the resulting offspring a major selective advantage in an ensuing generation of gene-resource plantings, with the consequence that the contribution of unpedigreed gene resources to an expanded genetic base would be gravely compromised. The planting of large gene-resource blocks would mitigate pollen contamination but not eliminate it. Indeed, the pollen contamination problem provides a powerful argument, in addition to the diversion of resources from producing wood to reproduction (cf. Burdon 1989b), for developing commercial crops that are sterile.

An alternative, or complementary, proposal for managing native-population material (Burdon 1986, 1988; cf. Bannister 1963) is to perpetuate the unpedigreed hybrid swarm that the Genetic Survey experiment could be expected to produce. A systematic interpopulation diallel cross, representing worthwhile samples of each population was proposed but not adopted because of the effort entailed (Burdon 1986, and unpubl.). Collections of open-pollinated seed that are segregated on the basis of maternal population lineage could be used for testing on a variety of sites to probe the environmental tolerances of various populations

in hybrid combination, on the premise that the native populations are likely to be used only in hybrid combination with improved local stock. The longer-term maintenance of a complex hybrid swarm, however, is also beset by the problem of pollen contamination from intensively improved stands.

Along with these problems of pollen contamination in managed gene resources are the physical difficulties of collecting material from the Genetic Survey experiment in which many of the trees are over 40 m tall. It is potentially a very valuable source of genetic material, because of the broad geographic representation, the seed-parent pedigree, quality of the sites as screening environments, and the appreciable selection that can be practised. Some genetic material has been collected, but that still represents a limited sample of what is potentially valuable. Collection costs have been a deterrent, particularly with the recent beleaguering of forest research in New Zealand, but deferral makes collection more difficult and costly, and sacrifices some genetic advance through extending generation time. There is thus no cause for complacency.

Conclusions

To be useful for purposes of short- to medium-term breeding, native-population material will need to be managed as living collections growing in the field, under some selection to improve silvicultural acceptability.

Desirably, a sizeable sample of each native population should be maintained as a pure strain, from which selections could be drawn at any time in the future.

Maintaining pure strains, however, will be very difficult because of a major problem of pollen contamination under open pollination.

The Guadalupe Island population is the top priority for maintaining as a pure strain by controlled crossing.

Nevertheless, it is also desirable to have intercrossing among populations in order to proceed to segregating hybrid generations in which some future selection can be done.

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