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The origin and genetic diversity of *Pinus radiata* in Australia

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Summary. Despite the fact that forest trees are in early stages of domestication there has been little direct evaluation of either the origin of, or genetic diversity within the breeding material in tree improvement programs. Allozyme variation was used to compare the total genetic diversity in the breeding programs of *P. radiata* within Australia and the five wild populations in North America.. The current breeding populations were very similar genetically and were essentially homogenous with only 1.8% of the variation among programs. The total genetic diversity in the species was 0.12, which is a low estimate compared to most conifers. Overall in the Australian material the genetic diversity was somewhat less. The comparison of allelic frequencies in the five native populations with the Australian material indicates that the Monterey and Año Nuevo populations were probably the major source of the original introductions and that a substantial portion of the genetic diversity in the two populations has been captured in current breeding programs. The three southern populations do not appear to be currently represented in the breeding programs. The implications for future breeding strategies are discussed.

Key words: Genetic diversity – *Pinus radiata* – Isozymes – Breeding programs – Domestication

Introduction

Worldwide, tree breeding programs involving about 50 forest tree species have been established. The vast majority of the species have only come under domestication this century and their domestication is still at an early stage (Libby 1973). With the possible exception of a few European species, most are still represented by areas of natural forest or stands produced by natural regeneration and plantations are the result of, at the most, two generations of artificial selection.

Therefore comparisons of the levels of genetic variation in the plantation areas with that in the natural populations should provide information on the origin of plantation material. Estimates can also be made of the proportion of the total genetic variation in the species that has been retained in the current breeding material through the domestication process. Isozyme analysis is currently the best method for estimating this genetic variation in the gene pools of species (Brown and Moran 1981). Despite some definite shortcomings, isozyme data allow a direct evaluation at the single gene level of the genetic diversity in forest trees, unlike the traditional quantitative characters.

Isozyme analysis of inbreeding crop plants such as barley show a loss in genetic variability during the domestication sequence from wild populations to land races to cultivars (Brown and Clegg 1983). Of interest is the extent to which this decline is largely a reflection of interaction between the high interpopulation genetic differentiation in inbreeders (Brown 1979) and the sampling of the gene pool of the species during the first stage of domestication. In marked contrast, outbreeding organisms like forest trees generally have high levels of allozyme variation within populations but little variation among populations (Brown and Moran 1981; Loveless and Hamrick 1984). This basic difference in the genetic structure of populations may be of critical importance in determining the ease and extent of capture of genetic variation during domestication.

Pinus radiata D. Don, the most widely planted exotic conifer worlwide, occupies about 3 million hectares in plantations. The great majority of these plantations are in the southern hemisphere (Table 1). The natural range of the species, however, is restricted to 5

Table 1. Details of the occurrence of *Pinus radiata* in 1982, (**A**) as approximate areas, worldwide (**B**) for Australian breeding populations

A Worldwide (ha × 10^3)

Natural stands	Exotic plantations				
North America	Chile	New Zealand	Australia	Other	Total
8.4	1,100	900	559	500	3,000

B Australian breeding populations[a]

	NSW[b]	VIC	SA	TAS	WA	ACT	Total
Plantation area (ha × 10^3)	187	177	76	59	42	13	559
No. of seed orchards	3	9	4	2	1	1	20
No. of clones in seed orchards	80	67	45	60	30	30	312
No. of clones sampled	30	31	29	22	20	30	162

[a] 19 New Zealand (NZ) clones that are in Australian breeding material were analyzed as a 7th "Australian breeding population" (see Text). This brings the total number of clones assayed to 181

[b] Abbreviations refer to the states of Australia. NSW = New South Wales; VIC = Victoria; SA = South Australia; TAS = Tasmania; WA = Western Australia; ACT = Australian Capital Territory

discrete populations encompassing a total of about 8400 ha in western North America. There are three small coastal Californian and two island populations off Mexico (Forde 1966; Libby et al. 1968). The wild populations are largely extant as before the occupation of western North America by European man. In Australia, *P. radiata* of unknown source was introduced into the Victorian and South Australian Botanic gardens around 1860 and the first forest plantings were in the 1870's. Since the turn of the century plantations have been established on a large scale (Table 1). Selections from these first generation plantations have subsequently been cloned into seed orchards to provide genetically improved stock for reforestation and to provide material for advanced generation breeding.

In this study, the genetic composition and diversity in the first generation selections of the breeding programs in Australia were evaluated using isozyme techniques. These breeding populations were also compared genetically to the 5 natural populations in an attempt to identify the source of the Australian material and to assess the extent to which the overall genetic diversity within the species is represented in the current breeding populations.

Materials and methods

Pinus radiata is grown primarily in the south-eastern part of Australia. Most of the plantations have been established by State forest services and breeding programs are largely confined within State boundaries. In this study genetic diversity in the first generation selections in the States was assessed. Seeds were supplied by co-operators from randomly chosen clones located in one or more seed orchards in each state (Table 1). These clones represented breeding material from private organisations as well as that of state breeding programs. A total of 180 clones, which is more than half those currently in Australian seed orchards, was sampled and assayed for their allozyme genotypes at 31 loci. The number of seed orchards within states and the number of clones sampled were approximately in proportion to state plantation areas (Table 1). Of the first series of clonal selections in New Zealand, before 1960, a small number of clones was introduced into Australian breeding programs and are currently represented in seed orchards. Nineteen of these clones were treated as a separate sample for analysis.

The allozyme genotypes of each clone at 31 loci were inferred from allelic arrays in haploid female megagametophytic tissue of 6 germinating open pollinated seeds. (The probability of failing to detect a heterozygote at any one locus was 3.1%). Estimates of allelic frequencies in the breeding material for each state were then derived from the appropriate clonal genotypes. Allelic frequency estimates for the same loci in each of the five natural populations of *P. radiata* were obtained as part of a separate study of population genetic structure of this species (Moran et al. 1987). For each natural population a minimum of 300 progeny were assayed (50 families × 6 progeny). The megagametophytes from the Australian clones and the germinated embryos from the natural poulations were crushed in two and one drops respectively of 0.1 M phosphate buffer (pH 7.0) containing 1 mg/ml of dithiothreitol, and the extracts absorbed onto paper chromatography wicks. The starch gel electrophoretic methods were as detailed previously (Moran et al. 1980; Moran and Bell 1983). The enzyme assays were essentially as in Conkle et al. (1982) and Vallejos (1983). The two enzymes not include in these references are mannose phosphate isomerase, which was assayed as in Buth and Murphy (1980) and glycerate dehydrogenase, which was stained by a slight modification of the procedure of Willis and Sallach (1962). All samples were assayed for 20 enzyme systems and scored for a total of 31 loci. The enzyme systems were: aconitase (AC), alcohol dehydrogenase (ADH), acid phosphatase (AP), alanine aminopeptidase (AAP), fumarase (FUM), glucose 6 phosphate dehydrogenase (G6PD), glutamate dehydrogenase (GDH),

glutamate oxaloacetate transaminase (GOT), glycerate dehydrogenase (GLY), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), 6 phosphogluconate dehydrogenase (6PGD), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI), peptidase (PEP), phosphoenol-pyruvate carboxylase (PC), malate dehydrogenase (MDH), menadione reductase (MR), mannose phosphate isomerase (MPI), and shikimate dehydrogenase (SDH).

Genetic control of the isozymes and the linkage relationships between loci were determined from band pattern arrays in megagametophytes from large samples of open pollinated seed from individual mother trees (Moran et al. 1983; Moran and Bell, unpublished).

Results

Of the 31 loci assayed in the Australian clones, seven (GOT-3, GOT-4, LAP-2, PGI-1, 6PG-2, MDH-5 and PC) were invariant in all 7 populations. A locus was considered variable if two or more alleles were detectable regardless of their frequency. At 18 of the 24 variable loci the most common allele in each state occurred at frequencies greater than 0.90 (Table 2). Overall, the rare alleles were present in the Australian breeding material at very low frequencies since at most of these loci the rare alleles were detected in only a few breeding populations. However, considerable variation was present at five loci (LAP-1, AP-2, ADH-2, AC and PGI-2). Levels of genetic variability in the breeding material were quite similar over the 6 Australian states and the NZ sample (Table 3). Thus the mean number of alleles per locus within breeding populations ranged from only 1.45 to 1.65 (mean = 1.58) and the percent polymorphic loci from 38.7 to 54.8 (mean = 48.4). There was close agreement between observed and expected heterozygosity values as has been quite commonly observed in conifers. The gene diversity analysis for subdivided populations (Nei 1973) was used to partition the total genetic diversity within the breeding populations. Even though just the 24 variable loci were included in the analysis the total genetic diversity was only 0.12% (Table 4). The great majority of this variation appears to reside within breeding populations with only 1.8% of the total genetic diversity due to differences among populations. Furthermore, contingency Chi-square analyses showed that there was significant heterogeneity between allelic frequencies among populations at only one of the loci (LAP-1, analyses not presented). Thus, at the allozyme level, the Australian breeding populations appear to be essentially homogenous.

With the state breeding populations genetically very similar the genotypic arrays for the 31 loci were combined across populations and gene frequencies calculated for the total Australian breeding material. Genetic distances (Nei 1978) were calculated between

Table 2. Allelic frequencies at 24 variable loci in the Australian breeding populations of *P. radiata*

Locus	Allele	NSW	VIC	SA	TAS	WA	ACT	NZ
GOT-2	1	–	0.02	–	0.02	0.03	0.02	–
	3	1.00	0.98	1.00	0.98	0.97	0.98	1.00
GOT-5	1	0.02	0.11	0.19	0.11	0.08	0.10	0.05
	2	0.98	0.89	0.81	0.89	0.92	0.90	0.95
GDH	1	0.97	1.00	0.98	0.98	1.00	0.95	0.92
	2	0.03	–	0.02	0.02	–	0.05	0.08
LAP-1	2	0.12	0.10	0.12	0.09	0.15	0.12	0.24
	3	0.88	0.74	0.88	0.84	0.82	0.78	0.74
	4	–	0.16	–	0.07	0.03	0.10	0.02
G6PD	1	1.00	0.98	1.00	0.98	1.00	1.00	1.00
	2	–	0.02	–	–	–	–	–
	3	–	–	–	0.02	–	–	–
AP-2	1	0.67	0.59	0.60	0.64	0.60	0.58	0.74
	2	0.31	0.41	0.40	0.36	0.40	0.42	0.26
	3	0.02	–	–	–	–	–	–
AP-3	1	1.00	1.00	0.98	0.98	1.00	1.00	0.97
	2	–	–	0.02	0.02	–	–	0.03
FUM	1	0.02	0.02	0.05	–	–	–	–
	2	0.98	0.98	0.95	1.00	1.00	1.00	1.00
ADH-2	2	0.18	0.27	0.17	0.21	0.28	0.23	0.21
	3	0.58	0.47	0.48	0.61	0.40	0.50	0.53
	4	0.27	0.27	0.35	0.18	0.32	0.27	0.26
AC	1	0.22	0.15	0.14	0.30	0.20	0.28	0.21
	2	0.77	0.85	0.86	0.68	0.80	0.72	0.79
	3	0.01	–	–	0.02	–	–	–
IDH	1	0.95	1.00	1.00	0.98	1.00	0.97	1.00
	2	0.05	–	–	0.02	–	0.03	–
SDH	1	–	–	0.02	–	0.08	–	0.03
	2	1.00	0.98	0.98	0.98	0.92	1.00	0.94
	3	–	0.02	–	0.02	–	–	0.03
PGI-2	2	0.85	0.77	0.83	0.77	0.72	0.85	0.79
	3	0.15	0.23	0.17	0.23	0.28	0.15	0.21
PGM	1	0.92	0.98	0.97	0.98	0.98	1.00	1.00
	2	0.05	0.02	–	0.02	–	–	–
	3	0.03	–	0.03	–	–	–	–
	4	–	–	–	–	0.02	–	–
6PG-1	1	0.02	–	–	0.02	0.02	0.02	–
	2	0.98	1.00	1.00	0.98	0.98	0.98	1.00
MDH-2	1	1.00	0.98	1.00	1.00	1.00	1.00	1.00
	2	–	0.02	–	–	–	–	–
MDH-3	1	0.03	0.05	0.05	0.05	–	–	0.03
	2	0.95	0.95	0.91	0.95	1.00	1.00	0.95
	3	–	–	0.04	–	–	–	0.02
	4	0.02	–	–	–	–	–	–
MR-3	1	0.02	0.03	0.03	–	0.08	0.02	0.03
	2	0.98	0.97	0.97	1.00	0.92	0.98	0.97
MR-5	1	1.00	0.98	0.98	1.00	1.00	1.00	1.00
	2	–	0.02	0.02	–	–	–	–
MPI	1	1.00	1.00	1.00	1.00	1.00	1.00	0.94
	2	–	–	–	–	–	–	0.06
PEP-1	1	–	0.02	–	–	–	–	0.03
	2	1.00	0.98	1.00	1.00	0.97	1.00	0.97
	3	–	–	–	–	0.03	–	–
PEP-2	1	0.96	0.98	1.00	0.97	1.00	0.97	0.97
	2	0.04	0.02	–	0.03	–	0.03	0.03
AAP-2	1	1.00	1.00	0.93	0.96	1.00	0.93	1.00
	2	–	–	0.05	0.04	–	0.07	–
	3	–	–	0.02	–	–	–	–
GLY	1	0.96	1.00	0.93	1.00	1.00	0.93	1.00
	2	0.04	–	0.07	–	–	0.07	–

Table 3. Genetic variation in Australian breeding populations for 31 loci

State	No. alleles/locus	% loci[a] polymorphic	Observed heterozygosity	Expected[b] heterozygosity
NSW	1.65	48.4	0.079	0.083
VIC	1.61	54.8	0.088	0.092
SA	1.61	51.6	0.097	0.097
TAS	1.65	54.8	0.088	0.095
WA	1.45	38.7	0.089	0.092
ACT	1.52	45.2	0.089	0.095
NZ	1.58	45.2	0.095	0.095
Average	1.58	48.4	0.089	0.091

[a] Loci considered polymorphic if more than one allele detected. If the criteria for a variable locus is changed so that the frequency of the most common allele ≤ 0.99 then A and P fall from 1.58 to 1.26 and 48.4 to 26.3, respectively

[b] Nei's (1978) unbiased estimate, calculated on the basis of allele frequencies

Table 4. Distribution of genetic diversity at the 24 variable loci among 7 breeding populations

Locus	H_T[a]	H_B	D_{BT}	G_{BT}
GOT-2	0.0229	0.0227	0.0002	0.0095
GOT-5	0.1713	0.1661	0.0051	0.0300
GDH	0.0560	0.0547	0.0014	0.0246
LAP-1	0.3194	0.3112	0.0082	0.0256
G6PD	0.0111	0.0109	0.0002	0.0160
AP-2	0.4675	0.4620	0.0055	0.0117
AP-3	0.0206	0.0203	0.0003	0.0147
FUM	0.0240	0.0234	0.0006	0.0264
ADH	0.6184	0.6101	0.0083	0.0135
AC	0.3436	0.3365	0.0072	0.0209
IDH	0.0298	0.0291	0.0007	0.0241
SDH	0.0515	0.0501	0.0014	0.0281
PGI-2	0.3219	0.3182	0.0037	0.0115
PGM	0.0508	0.0495	0.0013	0.0256
6PG-1	0.0231	0.0229	0.0002	0.0095
MDH-2	0.0066	0.0064	0.0001	0.0198
MDH-3	0.0788	0.0774	0.0015	0.0185
MR-3	0.0558	0.0548	0.0009	0.0168
MR-5	0.0094	0.0093	0.0001	0.0118
MPI	0.0176	0.0166	0.0010	0.0546
PEP-1	0.0229	0.0225	0.0005	0.0203
PEP-2	0.0406	0.0401	0.0042	0.0102
AAP-2	0.0521	0.0503	0.0019	0.0360
GLY	0.0493	0.0474	0.0019	0.0385
Mean	0.1194	0.1172	0.0022	0.0184

[a] H_T = overall diversity; H_B = diversity within populations; D_{BT} = diversity between populations; G_{BT} = proportion of total diversity (H_T) due to differences among breeding populations

the total Australian breeding material and the 5 native populations. These were used to construct a dendogram showing the genetic similarities between the Australian breeding material and the native populations (Fig. 1). Clearly the Australian material appears to be most similar to the Año Nuevo and Monterey populations, while the Cedros Island population is quite distinct. The large genetic differences between the breeding

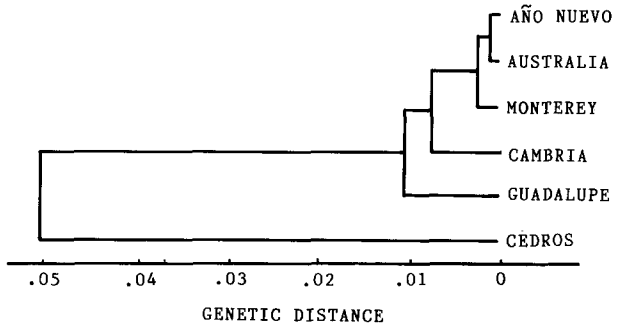

Fig. 1. Dendrogram showing similarities of Australian breeding material to natural populations using a weighted pair-group cluster analysis

materials and the Cedros Island populations is further verified by examining allelic frequencies at individual loci (Table 5). For instance, allele 1 at LAP-2 was not detected in Australia whereas the Cedros Island population is almost fixed for this allele. However most of the differences between the wild populations and the breeding material are in allelic frequencies rather than in the absolute presence or absence of alleles. Thus there are also marked allele frequency differences at PGI-2, ADH-2, LAP-1 and GOT-5 between Cedros and the breeding material. For instance, LAP-1 allele 1 is absent in Australia, but in relatively high frequency in Cedros. Similarly Guadalupe Island has alleles at LAP-1 and LAP-2 not present in the breeding material and there are large allelic frequency differences such as at AAP-2 and ADH-2. For the loci in Table 5 there was almost no differentiation between stands within each of the three mainland populations (Moran et al. 1987). The less common alleles at MDH-5, GLY and AAP-2 were present in all stands of the Cambria population but are either absent or in low frequency in Australia. These data suggest that the Cedros and Guadalupe populations have not been a component of the Australian introductions and that probably Cambria has not

Table 5. Allelic frequencies at loci that discriminate between the total Australian breeding material and one or more of the natural populations

Locus	Allele	Australia	Año Nuevo	Monterey	Cambria	Cedros	Guadalupe
GOT-1	1	0.10	0.26	0.05	0.04	0.32	0.12
	2	0.90	0.74	0.95	0.96	0.68	0.88
LAP-1	1		0.01		0.01	0.33	0.17
	2	0.13	0.10	0.16	0.22	0.02	
	3	0.81	0.82	0.73	0.72	0.65	0.79
	4	0.06	0.07	0.10	0.03		0.03
	5			0.01			0.01
	6				0.02		
LAP-2	1			0.01		0.96	0.12
	2	1.00	1.00	0.98	1.00	0.04	0.87
	3			0.01			0.01
ADH-2	1					0.03	
	2	0.22	0.22	0.21	0.16	0.29	0.50
	3	0.51	0.57	0.44	0.32	0.14	0.18
	4	0.27	0.21	0.35	0.52	0.54	0.32
PGI-2	2	0.80	0.81	0.76	0.80	0.26	0.88
	3	0.20	0.19	0.24	0.20	0.74	0.12
MDH-5	1				0.16		
	2	1.00	1.00	1.00	0.84	1.00	1.00
AAP-2	1	0.96	0.96	0.98	0.83	0.90	0.67
	2	0.04	0.04	0.02	0.17	0.10	0.33
GLY	1	0.97	1.00	1.00	0.72	1.00	1.00
	2	0.03			0.28		
SDH	1	0.02		0.02			
	2	0.97	1.00	0.96	1.00	0.94	0.95
	3	0.01		0.02		0.06	0.05

Table 6. Genetic diversity (H), alleles per locus (A) and percent loci polymorphic (P) in the 5 natural and 7 breeding populations. Estimates based on 31 loci

	Means within populations			Total		
	A	P	H	A	P	H_T
Breeding populations	1.58	48.4	0.091	2.16	77.4	0.092
Natural populations	1.79	56.8	0.098	2.39	87.1	0.117

been included either. Although the dendrogram indicated that the Australian breeding material was most similar to Año Nuevo seven rare alleles present in the breeding material (e.g. SDH alleles 1 and 3 in Table 5) were detected only in the Monterey population.

The total genetic diversity in the combined native populations appears to be somewhat greater than in the combined breeding populations (Table 6). In the first instance the data would indicate that there has been a substantial loss of genetic diversity during the first 100 years of domestication. However, there are two possible causes for genetic differences between gene pools of Australian breeding material and the wild populations. First there could be loss of genetic diversity during the selection of the first clones from the original plantations. Secondly, samples from all five natural populations may not have been introduced into the Australian gene pool and even those natural populations that are represented may not have been sampled thoroughly. Nevertheless, the genetic diversity within the total breeding material is quite similar to the mean levels of genetic diversity within each of the natural populations. This aparent lack of sampling of all the natural populations during the original introductions, coupled with the significant interpopulation diversity between the natural populations, could largely explain the absence of some of the total genetic diversity of the species in the Australian breeding material.

Discussion

The genetic homogeneity among the breeding material in the current breeding programs of *Pinus radiata* in Australia is evident from this study. The levels of genetic diversity in the Australian breeding material are

low compared to those reported in breeding programs of other gymnosperms such as Douglas-fir (Adams 1981) and Scots pine (Szmidt and Muona 1985). Not surprisingly these low estimates are a reflection of the low total genetic diversity in *P. radiata* compared to most other gymnosperms (Hamrick et al. 1981; Loveless and Hamrick 1984). Further, the genetic diversity in the Australian breeding material is less, but not substantially so, than in the likely sources of introductions, namely the Monterey and the Año Nuevo populations. This suggests that not only did the introductions contain a high proportion of the genetic diversity in these two populations but that a substantial amount of it has been maintained in the breeding programs.

The low genetic differentiation between stands within natural populations (Moran et al. 1987) makes it very difficult to determine whether the introductory seed material came from trees throughout the distribution of these two northern populations. Nevertheless, the presence of rare alleles at a number of loci in the Australian material at frequencies comparable to those in the Monterey population suggests that the original seed was from a substantial number of trees. It would be very useful to distinguish genetically more clearly between the Año Nuevo and Monterey populations. The current isozyme data set clearly does not do this satisfactorily. Preliminary data on seed proteins of *P. radiata* suggest that there could be more discrete differences between the two populations, and more extensive data may pinpoint more precisely the origins of Australian breeding material. The history of Australian introductions is further complicated since it is known that the seed source of some plantations in Australia between 1920 and 1940 was from stands in the Nelson area in New Zealand. However the New Zealand clones introduced directly into the Australian breeding programs in the 1950's, and which were analysed in this study, could not be distinguished genetically from the Australian breeding material. This study does not address the extent to which there has been genetic divergence between the original plantations and the selected breeding material – for instance there could have been a bias towards Monterey material in the first generation selection of plus trees from plantations.

Available data suggest that for gymnosperms the loss of genetic diversity during the domestication process has been relatively minor (Adams 1981; Szmidt and Muona 1985). Probably the major factor determining this is that domestication in these species is at a very early stage. Thus, the clones of *P. radiata,* which were sampled from the current breeding programs, were selected as plus trees in the first generation plantations. Perhaps nearly as important is the fact that a very high proportion of genetic diversity in conifers is found within populations and not distributed between them (Brown and Moran 1981). This distribution is no doubt due in part to the generally high outcrossing rate of trees (Hamrick et al. 1981; Brown et al. 1985) and indicates that a substantial fraction of the genetic resources of such species could be captured by sampling a limited a number of populations. However, it appears that for most conifers allozyme techniques will not discriminate unequivocally between populations. This suggests that in the future, at least with current techniques, it will most probably not be possible to discriminate between the different sources of a breeding population of a conifer when several natural populations are included.

The comparatively high interpopulation genetic differentiation in *P. radiata* indicates that the screening and selection of material from the three southern populations for utilization in breeding programs should be of high priority. Currently extensive field testing of growth and form of the five natural populations is being done in Australia and several other countries (Eldridge 1983). Strategies for incorporation of the new wild gene pools into existing breeding programs will be required. For instance, if such introductions were for the purpose of a general broadening of the genetic base then this could require a trade-off in economically important traits such as growth. In contrast, there are already indications that specific gains in resistance to western gall rust may be possible by incorporating material from the island populations (Old et al. 1986).

For agricultural crop plants, the differences in genetic diversity between cultivars and wild populations appears to be related, in general, to the nature of the mating system of the particular species. Thus in the case of radish, a naturally outcrossing species maintained in outcrossing open-pollinated breeding populations, there has been little loss of genetic diversity under domestication (Ellstrand and Marshall 1985). In marked contrast in inbreeders such as tomatoes (see Brown 1978 for details) and barley (Brown and Clegg 1983) there has been a significant loss in genetic diversity during the evolution from wild progenitors to modern cultivars. Apparently this loss is a reflection of the fact that up to 50% of the diversity is distributed among populations for inbreeding species (Brown 1979; Loveless and Hamrick 1984). In practice it would presumably be much more difficult to get a high proportion of the genetic resources of an inbreeder from the natural populations into a breeding program than for an outbreeder. In the case of *P. radiata* a high proportion of the total genetic diversity would be incorporated into a breeding program by the use of genetic material from all five populations. In particular, the results have demonstrated the potential importance of the Cambria and the two island populations as a source of new genetic material for incorporation into the Australian breeding populations.

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