in relation to the breeding of low mimosine lines. Crop Sci. 7: 140—143 (1976). — Gottlieb, L. D.: Electrophoretic evidence and plant systematics. Ann. Missouri Bot. Gard. 64: 161— 180 (1977). — Hamrick, J. L. and Loveless, M. D.: Association between the breeding system and the genetic structure of tropical tree populations. In: J. Bock and Y. B. Linhart (Ed.). Evolutionary ecology of plants. Westview Press, Boulder, Colorado. (1989). — Harris, S. A., Chamberlain, J. R. and Hughes, C. E.: New insights into the evolution of *Leucaena* Benth. In: R. M. Polhill and B. Pickersgill (Ed.). Advances in Legume Systematics. Royal Botanic Gardens, Kew (in press). — Harris, S. A. and Ingram, R.: Chloroplast DNA and biosystematics: The effects of intraspecific diversity and plastid transmission. Taxon 40: 393—412 (1991). — Harris, S. A. and Ingram, R.: Molecular systematics of the genus *Senecio* L. I. Hybridisation in a British polyploid complex. Heredity 69: 1—10 (1992). — Hughes, C. E.: *Leucaena* genetic resources: The OFI *Leucaena* seed collections and a synopsis of species characteristics. Oxford Forestry Institute, Oxford. (1993). — Hughes, C. E. and Harris, S. A.: The characterisation and identification of a naturally occurring hybrid in the genus *Leucaena* (Leguminosae: Mimosoideae). Plant Syst. Evol. (in press). — Hughes, C. E. and Styles, B. T.: The benefits and risks of woody legume introductions. In: C. H. Stirton and J. L. Zurucchi (Ed). Second International Legume Conference, Missouri Botanical Gardens (1989). — Hutton, E. M.: Natural crossing and acid tolerance in some *Leucaena* species. Leucaena Res. Rep. 2: 2—4 (1981). — King, L. M. and Schaal, B. A.: Ribosomal DNA variation and distribution in *Rudbeckia missouriensis*. Evol. 43: 1117—1119 (1989). — Lavin, M., Mathews, S. and Hughes, C.: Chloroplast DNA variation in *Gliricidia sepium* (Leguminosae): Intraspecific phylogeny and tokogeny. Am. J. Bot. 78: 1576—1585 (1991). — Lewontin, R.: The apportionment of human diversity. Evol. Biol. 6: 381—398 (1972). — Maniatis, T., Fritsch, E. F. and Sambrook, J.: Molecular cloning: a laboratory manual. Cold Spring Harbor Laboratory (1982). — Namkoong, G.: Genetics and the forests of the future. Unasylva 152: 2—18 (1986.). — National Academy of Sciences: *Leucaena:* promising forage and tree crop for the tropics. Washington, DC (1984). — Nei, M., Maruyama, T. and Chakraborty, R.: The bottleneck effect and genetic variability in populations. Evolution 29: 1—10 (1975). — Palmer, J. D.: Isolation and structural analysis of chloroplast DNA. Meth. Enzym. 118: 167—186 (1986). — Palmer, J. D., Jansen, R. K., Michaels, H. J., Chase, M. W. and Manhart, J. R.: Chloroplast DNA variation and plant phylogeny. Ann. MO. Bot. Gard. 75: 1180—1218 (1988). — Palmer, J. D. and Thompson, W. F.: Rearrangements in the chloroplast genomes of mung bean and pea. Proc. Natl. Acad. Sci. U. S. A. 78: 5533—5537 (1981). — Peet, R: The measurement of species diversity. Ann. Rev. Ecol. Syst. 5: 285—307 (1974). — Pielou, E. C.: An introduction to mathematical ecology. Wiley-Interscience, New York (1969). — Pound, B. and Martínez, C.: *Leucaena:* its cultivation and use. Overseas Development Administration, London (1983). — Rafalski, J. A., Wiewiorowski, M. and Soll, D.: Organisation of ribosomal DNA in yellow lupin (*Lupinus luteus*) and sequence of the 5.8S RNA gene. F.E.B.S. Lett. 152: 241—246 (1983). — Rogers, S. O., Honda, S. and Bendich, A. J.: Variation in the ribosomal RNA genes among individuals of *Vicia faba*. Pl. Mol. Biol. 6: 339—345 (1986). — Saghai-Maroof, M. A., Soliman, K. M., Jorgensen, R. A. and Allard, R. W.: Ribosomal DNA spacer-length polymorphism in barley: Mendelian inheritance, chromosomal location and population dynamics. Proc. Natl. Acad. Sci. U. S. A. 81: 8014—8018 (1984). — Schaal, B. A. and Learn, G. H.: Ribosomal DNA variation within and among plant populations. Ann. MO. Bot. Gard. 75: 1207—1216 (1988). — Schaal, B. A., Leverich, W. J. and Nicoto-Sotelo, Ribosomal DNA variation in the native plant *Phlox divaricata*. Mol. Biol. Evol. 4: 611—621 (1987). — Schifino-Wittmann, M. T. and Schlegel, M.: Isozyme patterns of *Leucaena leucocephala, Leucaena diversifolia* and their hybrids selected for acid soil tolerance. Leucaena Research Reports 11: 47—49 (1990). — Schnabel, A. and Hamrick, J. L.: Organisation of genetic diversity within and among populations of *Gleditsia triacanthos* (Leguminosae). Am. J. Bot. 77: 1060—1069 (1990). — Shibata, K.: Estudios citologicos de plantas colombianas silvestris y cultivadas. J. Agr. Sci. 8: 49—62 (1962). — Simons, A. J.: Genetic improvement of non-industrial trees. Agroforest. Syst. 18: 197—212 (1991). — Soltis, D. E. and Soltis, P. S.: Isozymes in plant biology. Chapman and Hall, London. (1990). — Soltis, D. E., Soltis, P. S. and Milligan, B. G.: Intraspecific chloroplast DNA variation: Systematic and phylogenetic implications. In: P. S. Soltis, D. E. Soltis and J. J. Doyle (Ed.). Molecular Systematics of Plants. Chapman and Hall, London. pp. 117—150 (1992). — Soltis, P. S. and Soltis, D. E.: Multiple origins of the allotetraploid *Tragopogon minus* (Compositae): rDNA evidence. Syst. Bot. 16: 407—413 (1991). — Sorensson, C. T. and Brewbaker, J. L.: Interspecific compatibility among fifteen *Leucaena* species (Mimosoideae) via artificial hybridisations. Am. J. Bot. (in press). — Sorensson, C. T., Pan, F. J., Booman, J. L. and Brewbaker, J. L.: Interspecific hybridisation in the genus *Leucaena*. Leucaena Research Reports 5: 94—95 (1984).— Surles, S. E., Arnold, J., Schnabel, A., Hamrick, J. L. and Bongarten, B. C.: Genetic relatedness in open-pollinated families of two leguminous tree species, *Robinia pseudoacacia L.* and *Gleditsia triacanthos L.* Theor. Appl. Genet. 80: 49—56 (1990). — Sytsma, K. J. and Schaal, B. A.: Genetic variation, differentiation and evolution in a species complex of tropical shrubs based on isozymic data. Evol. 39: 582—593 (1985). — Tijo, J. H.: The somatic chromosomes of some tropical plants. Hereditas 34: 135—146 (1948). — Torres, A. M.: Isozyme analysis of fruit trees. In: D. E. Soltis and P. S. Soltis (Ed). Isozymes in plant biology. Chapman and Hall, London. (pp. 192—205) (1990). — Turner, B. L. and Fearing, O. S.: Chromosome numbers of the Leguminosae. III. Species of the Southwestern United States and Mexico. Am. J. Bot. 47: 603—608 (1960). — Weeden, N. F. and Wendel, J. F.: Genetics of isozymes. In: D. E. Soltis and P. S. Soltis (Ed.). Isozymes in plant biology. Chapman and Hall, London. (pp. 46—72). (1990). — Welsh, J., Honeycutt, R. J., McClelland, M. and Sobral, B. W. S.: Parentage determination in maize hybrids using the arbitrarily primed polymerase chain reaction (AP-PCR). Theor. Appl. Genet. 82: 473—476 (1991). — Welsh, J. and McClelland, M.: Fingerprinting genomes using PCR with arbitrary primers. Nucleic Acids Res. 18: 7213—7218 (1990). — Wendel, J. F. and Weeden, N. F.: Visualisation and interpretation of plant isozymes. In: D. E. Soltis and P. S. Soltis (Ed.). Isozymes in plant biology. Chapman and Hall, London. pp. 5—45 (1990). — Wheeler, R. A., Brewbaker, J. L. and Pecson, R. C.: New arboreal *Leucaena leucocephala* accessions. Leucaena Research Reports 8: 77—78 (1987). — Wilson, M. A., Gaut, B. and Clegg, M. T.: Chloroplast DNA evolves slowly in the palm family (Arecaceae). Mol. Biol. Evol. 7: 303—314 (1990). — Zarate, S. P.: Taxonomic identity of *Leucaena leucocephala* (Lam.) de Wit. with a new combination. Phytologia 63: 304—306 (1987).

Isozyme Variation and Mating System in Eucalyptus urophylla S. T. Blake

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Summary

The natural distribution of *Eucalyptus urophylla* is a series of disjunct population areas on a number of islands in eastern Indonesia. Thirteen loci in 8 enzyme systems were used to estimate genetic diversity and outcrossing rates, using seed collections from the full range of the species. Levels of genetic diversity were similar to other *Eucalyptus* species that have widespread distributions. Most diversity is located within populations (G_{ST} = 11.75

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%). Genetic distances between populations were small, and a cluster analysis revealed no striking patterns that could be related to geography: only those populations from the island of Wetar clustered together on the basis of their isozyme genotypes. This lack of isozyme differentiation between populations is in contrast to the high degree of differentiation in morphological characters in the species. Outcrossing rates measured in two populations were high (>90%), with little between-tree variation. The possible origins of the species are discussed.

Key words: Population genetics, isozymes, mating system, outcrossing rates, *Eucalyptus*.

FDC: 165.3; 165.42; 165.5; 176.1 *Eucalyptus urophylla*.

Introduction

Knowledge of the distribution of genetic variation within and between populations is of substantial benefit in tree breeding and in the conservation of plant genetic resources (Brown et al., 1990; Adams et al., 1992). A number of studies have been published of isozyme variation in the genus *Eucalyptus*, focussing mainly on (1) conservation genetics of rare or restricted species (Fripp, 1982; Hopper and Moran, 1981; Moran and Hopper, 1983, 1987, 1989; Peters, Lonie and Moran, 1990; Prober et al., 1990; Sampson, Hopper and James, 1988) and (2) commercially important species (Brown, Matheson and Eldridge, 1975; Burgess and Bell, 1983; Burgess, Bell and Van Wyk, 1985; Cook, 1989; Coates and Sokolowski, 1989; Moran and Brown, 1980; Moran, Bell and Griffin, 1989; Yeh et al., 1983).

Eucalyptus urophylla S. T. Blake is extensively planted for pulp production in Brazil and is becoming increasingly important for wood production in China, South Africa and southeast Asia (Eldridge et al., 1993). It is one of the best eucalypt species for plantation forestry in lowland tropical sites with prolonged wet and humid seasons (Jacobs, 1981) displaying rapid growth and good disease resistance under these conditions.

The species is 1 of only 2 in the genus *Eucalyptus* that do not occur in Australia, the other being *E. deglupta* Bl. Its natural distribution is as a series of disjunct occurrences on 7 islands of the Sumba archipelago in eastern Indonesia (*Figure 1*). It occupies both valleys and mountain slopes on a variety of soil types (but not limestone-derived soils) in open-forest and tall open-forest formations, often associated with rainforest on especially good sites (e.g. basalt-derived soils) (Gunn and McDonald, 1991; Pinyopusarerk et al., 1993). It has the widest altitudinal range of any *Eucalyptus* species, growing from about 90 m on Wetar to nearly 3000 m on Timor (Gunn and McDonald, 1991), and there is a commensurate variation in form and morphological characters. On high mountain sites (e. g. at 3000 m on Mt Tatamailau, Timor) it occurs as a stunted bush 2 m tall, but on more favourable sites it is a tall to very tall forest tree, reaching 55 m in height and 2 m diameter (Turnbull and Brooker, 1978). On wet and high altitude sites (> 2200 m) most trees have thinly flakey greyish bark to at least half way up the bole (Pryor et al., submitted), and small-fruits, whereas at lower elevations in drier conditions trees are mainly smooth-barked with only a short rough stocking at the base of the trunk, and with much larger fruits (Martin and Cossalter, 1975 to 1976; Gunn and McDonald, 1991).

E. urophylla is placed in the subgenus *Symphyomyrtus*, section *Transversaria*, series *Salignae* subseries *Resinferinae* by Pryor and Johnson (1971). According to this classification, its closest relatives are *E. pellita* F. Muell. from northern Australia and New Guinea, and *E. notabilis* Maiden, *E. scias* Johnson and Hill and *E. resinifera* Smith from eastern coastal Australia (Chippendale, 1988; Boland et al., 1984; Johnson and Hill, 1990). A new classification of *E. urophylla* is proposed by Pryor et al. (submitted) in which 2 further species are described.

Provenance trials of *E. urophylla* in many tropical countries have shown that low to mid-altitude seed sources perform considerably better (in height growth) than those from high altitudes (Eldridge et al., 1993), although seed has not been generally available from the full range of the species until recently. Between and within provenance variation in seedling morphology (Pinyopusarerk et al., 1993) and essential leaf oils (Doran et al., submitted) has also been demonstrated. This paper examines genetic variation in the species using isozyme markers. It is the first population-wide study of genetic variation in an exclusively tropical species of *Eucalyptus*.

Materials and Methods

Sampling strategy

Seed collections from almost the full range of the species were used for this study. Sampling of populations was based on obtaining representative samples from each island and, where available, from a range of altitudes

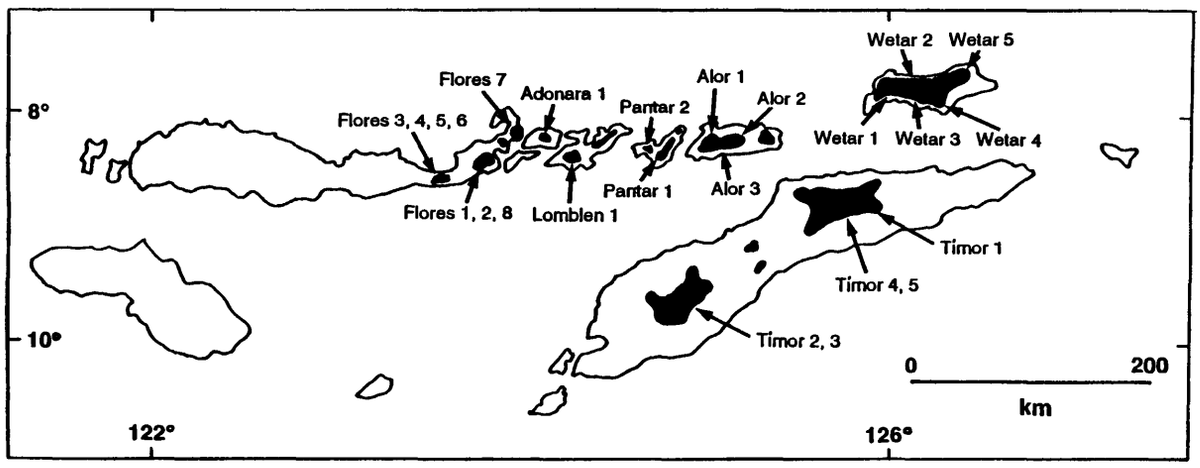

Figure 1. — Natural distribution of *Eucalyptus urophylla*, showing locations of seed collections used in this study.

within each island. Also, where field information suggested between-population differences in tree morphology (mainly bark and fruit characters) populations were sampled to take this into account. For most populations, a minimum of 50 seedlings were assayed for isozyme variation. Five progeny from each of 10 mothers per population were sampled where individual tree collections were available, or a minimum of 50 seedlings in total from bulked seed collections. Details of the 25 populations sampled are given in *table 1*.

Two populations (Wetar 5 and Alor 1) were chosen to estimate mating system parameters. For these, 20 progeny from each of 10 mother trees were assayed for their isozyme genotypes at 6 and 5 variable loci respectively.

Isozyme analysis

Seeds were germinated on moist filter paper in incubators set at 30 °C with 14 h day and 10 h night. Seven to 9-day old seedlings were crushed in 50 μl of 0.05 M, pH 9.0 borate grinding buffer to which 1 mg ml^{-1} dithiothreitol and 20 mg ml^{-1} polyvinylpyrrolidone (MW = 40 000) were added. Isozyme assays were made by starch gel electrophoresis following the general procedures described in Moran and Bell (1983). Gel slices were stained for 8 enzyme systems: malate dehydrogenase (MDH, EC 1.1.1.37); isocitrate dehydrogenase (IDH, EC 1.1.1.42); phosphogluconate dehydrogenase (PGD, EC 1.1.1.44); uridine diphosphogluconic pyrophosphatase (UGP, EC 2.7.7.9); glucosephosphateisomerase (GPI, EC 5.3.1.9); glycerate dehydrogenase (GLY, EC 1·1.1.29); esterase (EST, EC 3.1.1.-); and aspartate aminotransferase (AAT, EC 2.6.1.1).

Genetic interpretation of electrophoretic variants was based on progeny arrays from open-pollinated families. Banding patterns that did not conform to Mendelian segregation were excluded. For loci within an enzyme system the fastest migrating was designated 1, the next fastest 2 and so on. Similarly, within each locus the most anodally migrating allele was designated 1 and successive slower alleles 2, 3 etc. The distance each allele had migrated from the origin was measured to the nearest millimetre in order to establish allelic identity across populations.

Genotype arrays were analysed using the BIOSYS-1 package (Swofford and Selander, 1989), and multi-locus estimates of outcrossing rates were made using the procedures of Ritland and Jain (1981).

The private allele method of Slatkin (1985) was used to estimate gene migration between populations per generation. The number of migrants (N_m) is calculated as

$$\ln(p(1)) = -0.505(\ln(N_m)) - 2.44$$

and corrected for sample size by the method of Slatkin (1985).

Results

Seedling genotypes were scored for a total of 13 loci in 8 enzyme systems, all of which were variable in at least one population. Some loci were apparently invariant but also consistently difficult to score and thus excluded from the analysis (AP-1, AP-2, LAP-1). Others were variable but not scored because of overstaining of one locus on top of another, e·g. PGM-1, or because of very faint ban-

Table 1. — Details of *E. urophylla* populations sampled. CSIRO seedlot number, location, latitude, longitude, altitude and number of individual mother trees in sampled populations (N).

Pop. no.		CSIRO seedlot no.	Locality	Lat. (°N)	Long. (°E)	Alt. (m)	N
1.	Flores 1	13011	Mt Lewotobi	8°32'	122°47'	500	10
2.	Flores 2	17565	Mt Lewotobi	8°32'	122°48'	375	10
3.	Flores 3	17567	Mt Egon	8°38'	122°27'	450	10
4.	Flores 4	14531	Mt Egon	8°38'	122°27'	515	10
5.	Flores 5	17572	Mt Egon	8°37'	122°27'	600	4
6.	Flores 6	17573	Mt Egon	8°36'	122°28'	725	2
7.	Flores 7	17564	Mandiri	8°15'	122°58'	410	10
8.	Flores 8	15638	Wukoh	8°31'	122°45'	750	5*
9.	Adonara 1	12898	Gunung Boleng	8°21'	123°15'	890	6
10.	Lomblen 1	18096	Labala	8°23'	123°32'	500	53*
11.	Pantar 1	17842	Mt Dalaki	8°31'	124°05'	440	6
12.	Pantar 2	17843	Baubillatung	8°20'	124°02'	285	9
13.	Alor 1	17841	Piritumas	8°19'	124°31'	355	10
14.	Alor 2	17840	Wai Kui	8°14'	124°44'	540	10
15.	Alor 3	17839	Apui	8°17'	124°40'	1115	10
16.	Timor 1	8238		8°41'	125°33'	910	5*
17.	Timor 2	13828	Mt Mutis	9°34'	124°17'	1200	6*
18.	Timor 3	12960	Soe	9°51'	124°16'	1250	2
19.	Timor 4	10140	Hato Bulico	8°53'	125°32'	2100	6*
20.	Timor 5	10138	Mt Tatamailau	8°55'	125°30'	2790	6*
21.	Wetar 1	17835	Carbubu	7°56'	125°53'	175	10
22.	Wetar 2	17838	Lalikki	7°42'	126°21'	220	10
23.	Wetar 3	17832	Arnau	7°49'	126°10'	315	10
24.	Wetar 4	17831	Ilwaki	7°52'	126°27'	515	10
25.	Wetar 5	17836	Uhak	7°39'	126°29'	500	10

*) bulk seedlots, number = number of mothers.

Table 2. — Allele frequencies at variable loci in *E. urophylla*.

	Population (see Table 1 for codes)*																								
	F1	F2	F3	F4	F5	F6	F7	F8	AD1	L1	P1	P2	AL1	AL2	AL3	T1	T2	T3	T4	T5	W1	W2	W3	W4	W5
Locus																									
MDH-1																									
(n)	90	81	76	90	96	50	74	70	90	61	75	68	70	60	81	65	61	65	66	64	69	50	50	62	60
1											0.11		0.01				0.05	0.03				0.02	0.01		
2	0.98	0.96	0.99	0.98	0.99	1.00	1.00	1.00	0.99	0.99	0.87	1.00	0.97	0.99	0.99	0.99	0.93	0.96	0.98	1.00	0.70	0.84	0.72	0.51	0.81
3	0.02	0.04	0.01	0.02	0.01					0.01	0.02		0.01	0.01	0.01	0.02	0.02		0.01		0.28	0.14	0.27	0.49	0.19
4									0.01				0.01				0.01	0.01	0.01		0.02				
MDH-2																									
(n)	90	81	76	90	96	50	74	70	90	61	75	68	70	60	81	65	61	65	66	64	71	50	50	62	60
1				0.01					0.03							0.01				0.01	0.01	0.06	0.02	0.04	0.12
2									0.01						0.01						0.01			0.07	0.02
3	1.00	1.00	1.00	0.99	1.00	1.00	0.99	1.00	0.96	1.00	1.00	1.00	1.00	0.99	0.99	0.99	0.98	1.00	1.00	0.98	0.97	0.93	0.98	0.90	0.85
4							0.01							0.01			0.02			0.01		0.01			0.01
IDH-1																									
(n)	90	81	76	90	96	50	74	70	90	61	75	68	69	59	81	65	61	65	66	64	71	50	50	62	59
1	0.17	0.05	0.09	0.09	0.31	0.02	0.21	0.34	0.07	0.05	0.12	0.17	0.06	0.07	0.06	0.02		0.01			0.04		0.03	0.16	
2														0.01											
3	0.73	0.85	0.81	0.80	0.65	0.97	0.68	0.64	0.93	0.76	0.83	0.75	0.93	0.86	0.90	0.92	0.96	0.98	0.97	0.89	0.96	0.98	0.97	0.82	0.82
4	0.11	0.11	0.11	0.11	0.04	0.01	0.12	0.03		0.19	0.05	0.08	0.01	0.07	0.04	0.06	0.04	0.02	0.03	0.11		0.02		0.02	0.18
PGD-1																									
(n)	90	81	76	90	96	50	74	70	90	61	75	68	70	60	81	65	61	65	66	64	70	50	50	62	60
1		0.01	0.03		0.01	0.03	0.03							0.02						0.01	0.01				
2	0.81	0.88	0.85	0.88	0.87	0.89	0.78	0.74	0.89	0.88	0.66	0.87	0.82	0.62	0.78	0.88	0.42	0.66	0.92	0.99	0.91	0.91	0.92	0.77	0.87
3	0.09	0.02	0.04	0.04	0.12	0.07	0.17	0.23		0.02	0.05	0.10	0.03	0.13	0.18	0.10		0.30	0.08		0.08	0.01	0.03	0.07	
4	0.11	0.09	0.09	0.08	0.01	0.01	0.01	0.03	0.11	0.11	0.29	0.03	0.15	0.23	0.04	0.02	0.58	0.04			0.01	0.08	0.05	0.16	0.13
PGD-2																									
(n)	90	81	76	90	96	50	74	70	90	60	75	68	70	60	81	65	61	65	66	64	71	50	50	62	60
1	0.09	0.01	0.01	0.01				0.11		0.00			0.01	0.02			0.07			0.02	0.10	0.02	0.01		
2	0.90	0.99	0.98	0.98	0.99	1.00	0.94	0.87	0.98	0.97	0.95	1.00	0.99	0.97	1.00	0.98	0.89	0.94	0.78	0.76	0.86	0.96	0.97	1.00	0.98
3							0.02			0.01	0.04		0.01			0.01	0.01	0.01	0.02			0.01			
4	0.01		0.01	0.01	0.01		0.04	0.01	0.02	0.02	0.01			0.01		0.01	0.03	0.05	0.20	0.22	0.04	0.01	0.02		0.02
UGP-2																									
(n)	70	81	76	80	96	50	74	70	80	61	75	58	60	50	81	60	61	55	66	64	61	50	50	62	50
1	0.01	0.01		0.05	0.01			0.07	0.01	0.14		0.04	0.01	0.02			0.05	0.01			0.19		0.03	0.01	0.08
2	0.99	0.99	0.99	0.94	0.98	1.00	0.99	0.93	0.95	0.85	1.00	0.88	0.92	0.95	1.00	1.00	0.61	0.95	0.99	0.95	0.77	1.00	0.96	0.99	0.92
3	0.01	0.01			0.01				0.03	0.00			0.02				0.09	0.01	0.01		0.03				
4							0.01			0.01				0.01			0.02								
5			0.01	0.01	0.01				0.01			0.08	0.06	0.02			0.21	0.03		0.05	0.02		0.01		
6																	0.03								

	F1	F2	F3	F4	F5	F6	F7	F8	AD1	L1	P1	P2	AL1	AL2	AL3	T1	T2	T3	T4	T5	W1	W2	W3	W4	W5
GPI-2																									
(n)	80	81	76	80	96	50	74	70	80	61	75	68	70	60	81	60	61	55	65	64	71	50	50	62	60
1										0.02															
2	0.13	0.01		0.09	0.01		0.01	0.04	0.09	0.01			0.09	0.01		0.01	0.01	0.11	0.05	0.03	0.01	0.01	0.03		0.02
3	0.62	0.64	0.67	0.68	0.55	0.74	0.73	0.56	0.42	0.43	0.95	0.82	0.35	0.58	0.70	0.57	0.21	0.74	0.60	0.21	0.34	0.32	0.37	0.26	0.19
4	0.15	0.14	0.18	0.09	0.15	0.15	0.09	0.21	0.18	0.26	0.01	0.15	0.37	0.14	0.09	0.03	0.24		0.13	0.10	0.20	0.18	0.26	0.22	0.21
5	0.01			0.01									0.01	0.02	0.05	0.01	0.07			0.02	0.01	0.01	0.02		0.01
6	0.10	0.21	0.15	0.12	0.29	0.11	0.18	0.18	0.31	0.28	0.03	0.03	0.16	0.25	0.17	0.39	0.47	0.15	0.22	0.64	0.43	0.48	0.32	0.52	0.57
7		0.01		0.01									0.01												
GLY-1																									
(n)	59	81	76	70	96	50	74	70	79	61	75	68	70	60	81	65	61	65	66	62	71	50	50	62	60
1									0.01				0.01							0.09					
2	0.95	0.77	0.88	0.83	0.82	0.85	0.98	0.99	0.94	0.86	0.91	1.00	0.96	0.97	0.99	0.95	0.99	0.98	0.92	0.62	0.92	0.97	0.95	0.96	0.90
3	0.05	0.14	0.02	0.16	0.12	0.15	0.02	0.01	0.04	0.14	0.09		0.01	0.02		0.03		0.02	0.05	0.33	0.04	0.03	0.05	0.04	0.1
4		0.09	0.1	0.01	0.06				0.01				0.01	0.01	0.01	0.02	0.01		0.03	0.04	0.04				
EST-1																									
(n)	47	57	50	39	49	49	53	50	48	60	71	53	59	51	74	50	50	45	50	50	66	50	50	50	59
1	0.10	0.05	0.28	0.18	0.01	0.15	0.17		0.31	0.16	0.01	0.19	0.08	0.15	0.26	0.37	0.02	0.01	0.07	0.10	0.26	0.26	0.25	0.27	0.17
2	0.21	0.34	0.42	0.32	0.08	0.03	0.17	0.20	0.05	0.14	0.32	0.18	0.56	0.21	0.37	0.18	0.45	0.53	0.42	0.54	0.52	0.62	0.51	0.43	0.63
3	0.69	0.61	0.30	0.50	0.91	0.82	0.66	0.80	0.64	0.70	0.66	0.63	0.36	0.65	0.37	0.45	0.53	0.46	0.51	0.36	0.22	0.12	0.24	0.30	0.20
EST-2																									
(n)	50	50	76	50	70	50	64	65	56	61	72	60	70	55	51	50	56	55	51	50	71	50	50	52	60
1	1.00	1.00	0.99	1.00	0.94	1.00	1.00	1.00	1.00	0.97	0.97	0.93	1.00	1.00	0.98	1.00	0.97	0.98	1.00	0.99	0.99	1.00	1.00	1.00	1.00
2			0.01		0.06					0.03	0.03	0.07			0.02		0.03	0.02		0.01	0.01				
AAT-1																									
(n)	50	60	76	50	96	50	74	65	60	61	53	42	60	50	81	50	56	55	51	50	49	50	50	62	50
1										0.02	0.09		0.07									0.04		0.02	
2	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.98	0.91	1.00	0.93	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	0.96	1.00	0.94	0.99
3								0.01									0.01							0.03	0.01
AAT-2																									
(n)	50	60	76	50	95	50	74	65	60	61	55	42	60	50	81	50	56	55	51	50	49	50	50	62	50
1								0.05						0.02					0.02			0.13		0.08	
2	1.00	0.95	1.00	0.99	0.46	1.00	0.99	0.95	0.98	0.99	0.97	0.96	0.97	0.88	0.96	1.00	0.95	0.97	0.98	1.00	0.99	0.87	1.00	0.92	1.00
3		0.05		0.01	0.54		0.01	0.01	0.02	0.01	0.03	0.04	0.03	0.10	0.04		0.05	0.03			0.01				
AAT-3																									
(n)	50	60	76	50	96	50	74	65	60	61	55	42	60	50	81	50	56	55	51	50	49	50	50	62	50
1								0.01		0.01				0.03		0.01	0.01	0.03			0.02				
2	0.98	0.97	1.00	0.97	1.00	0.99	0.98	0.99	1.00	0.99	1.00	0.93	0.99	0.96	1.00	0.98	0.99	0.97	0.99	0.99	0.97	0.98	1.00	0.99	1.00
3	0.02	0.03		0.03		0.01	0.02					0.07	0.01	0.01		0.01			0.01	0.01	0.01	0.02		0.01	

*) F = Flores; AD = Adonara; L = Lomblen; P = Pantar; AL = Alor; T = Timor; W = Wetar.

Table 3. — Estimates of genetic diversity (with standard errors) for populations of *E. urophylla*. A = mean no. of alleles per locus; P = percentage of loci polymorphic (0.99 criterion).

Population		A	P	Mean heterozygosity: Direct-count H_o	Mean heterozygosity: Hdy-Wbg expected H_e*
1	FLORES 1	2.31 ± 0.33	69.2	0.099 ± 0.034	0.170 ± 0.058
2	FLORES 2	2.46 ± 0.33	69.2	0.104 ± 0.033	0.168 ± 0.055
3	FLORES 3	2.23 ± 0.28	46.2	0.070 ± 0.027	0.158 ± 0.062
4	FLORES 4	2.62 ± 0.35	76.9	0.112 ± 0.033	0.174 ± 0.058
5	FLORES 5	2.46 ± 0.31	61.5	0.103 ± 0.046	0.190 ± 0.060
6	FLORES 6	1.85 ± 0.30	46.2	0.074 ± 0.032	0.098 ± 0.041
7	FLORES 7	2.31 ± 0.29	53.9	0.094 ± 0.033	0.156 ± 0.058
8	FLORES 8	2.23 ± 0.26	61.5	0.109 ± 0.050	0.180 ± 0.058
9	ADONARA 1	2.38 ± 0.31	76.9	0.091 ± 0.041	0.145 ± 0.059
10	LOMBLEN 1	2.54 ± 0.27	69.2	0.125 ± 0.039	0.186 ± 0.059
11	PANTAR 1	2.23 ± 0.23	76.9	0.133 ± 0.045	0.161 ± 0.046
12	PANTAR 2	2.00 ± 0.25	61.5	0.115 ± 0.043	0.155 ± 0.049
13	ALOR 1	2.92 ± 0.38	76.9	0.122 ± 0.046	0.170 ± 0.062
14	ALOR 2	2.92 ± 0.33	69.2	0.141 ± 0.048	0.187 ± 0.061
15	ALOR 3	2.15 ± 0.30	46.2	0.092 ± 0.036	0.143 ± 0.062
16	TIMOR 1	2.46 ± 0.35	69.2	0.127 ± 0.056	0.140 ± 0.060
17	TIMOR 2	3.00 ± 0.39	76.9	0.156 ± 0.056	0.234 ± 0.072
18	TIMOR 3	2.46 ± 0.24	84.6	0.093 ± 0.034	0.148 ± 0.052
19	TIMOR 4	2.31 ± 0.29	61.5	0.116 ± 0.050	0.155 ± 0.060
20	TIMOR 5	2.31 ± 0.31	69.2	0.136 ± 0.053	0.182 ± 0.064
21	WETAR 1	2.92 ± 0.29	84.6	0.178 ± 0.049	0.223 ± 0.064
22	WETAR 2	2.54 ± 0.31	84.6	0.112 ± 0.037	0.174 ± 0.056
23	WETAR 3	2.31 ± 0.33	69.2	0.114 ± 0.049	0.171 ± 0.068
24	WETAR 4	2.31 ± 0.21	69.2	0.148 ± 0.054	0.233 ± 0.066
25	WETAR 5	2.23 ± 0.32	76.9	0.138 ± 0.046	0.202 ± 0.056
Mean		2.42	68.3	0.116	0.172

*) Unbiased estimate (see NEI, 1978).

ding patterns that could not be properly interpreted e.g. AC-1, AC-2, LAP-2, GPT-2, GDH-1, ME-1, GPI-1.

Allelic frequencies for all scorable loci in each population are shown in *table 2*. At most loci (MDH-1, MDH-2, IDH-1, PGD-2, UGP-2, GLY-1, EST-2, AAT-1, AAT-3) the commonest allele is the same in all populations. There is considerable within island variation in allele frequencies at several loci, with some populations having commonest alleles that differ from those in other populations from the same island (e.g. population Timor 2 at PGD-1; Alor 1 and Timor 2 at GPI-2; Flores 3, Alor 1, Timor 3 and Timor 5 at EST-1; Flores 5 at AAT-2). Wetar populations are distinguished by having a different commonest allele at EST-1 compared to most other populations, and lower frequencies of the commonest allele at MDH-1.

Measures of genetic diversity

The overall level of genetic diversity within the species (*Table 3*) is within the range for other eucalypts with similar extents of distribution (MORAN, 1992). The mean number of alleles per locus (A) and the percentage of polymorphic loci (P) across all populations are high compared with other species of the genus. There is some variation in mean A between islands, from 2.1 on Pantar to 2.6 on Alor. Within islands, A ranges from a high of 2.9 (in Timor 2, Wetar 1, Alor 1 and Alor 2) to a low of 1.8 (Flores 6). In all populations the proportion of polymorphic loci is high. Despite the high levels of P, the mean frequency of the commonest allele was less than 0.8 at only 2 loci (GPI-2 and EST-1). The mean estimates of genetic variability are all lower than those for a single Flores provenance of *E. urophylla* grown in Hawaii des-

Table 4. — Measures of total genetic diversity in natural populations of *E. urophylla* and 5 other widespread eucalypts. Note that A_S and P_S are based on any level of variation in any of the loci assayed in any population sampled.

species	H_T	H_S	G_{ST} (%)	A_S	P_S
E.urophylla	0.195	0.172	11.8	4.00	100.0
E. grandis[1]	0.190	0.167	12.0	2.93	92.9
E. saligna[1]	0.260	0.239	8.0	2.86	92.9
E. delegatensis[2]	0.272	0.238	12.5	4.10	100.0
E. nitens[2]	0.202	0.140	30.2	3.35	96.6
E. cloeziana[3]	0.230	0.205	11.0	2.71	85.7

H_T = total genetic diversity; H_S = genetic diversity within populations; G_{ST} = genetic diversity between populations: A_S = mean number of alleles per locus at species level; P_S = percentage of polymorphic loci at species level.
[1]) Bell (unpublished); [2]) Moran (unpublished); [3]) Turnbull (1980).

cribed by Aradhya and Phillips (1993), in which A = 3.7, P = 85.7, H_o = 0.429, and H_e = 0.495. This discrepancy may be the result of gene exchange between species, as the Hawaiian material came from multi-species trials (Aradhya and Phillips, 1993).

Most of the measures of total genetic diversity fall within the range for other species of *Eucalyptus* with similar distributions (*Table 4*). The level of genetic diversity between populations, G_{ST}, was estimated at 11.75%, indicating that most of the total genetic diversity in the species is found within populations rather than between. This, and the estimate for total genetic diversity H_T (0.195), is comparable but slightly lower to those found for other widely distributed eucalypts.

A cluster analysis based on Nei's (1978) unbiased genetic distance (D) and using the UPGMA algorithm reveals low levels of genetic separation between the populations (*Figure 2*). Errors for the higher orders of the dendrogram are large, signifying that little confidence can be placed on the distinctness of the clusters formed. Of the 7 islands, only the populations from Wetar group together. The population from Flores (Flores 5), which is separated from the rest of the populations at the first clustering level, is anomalous in that there is no clear environmental explanation as to why it should be different. Isozymically it differs from all other populations in having a higher proportion (0.537) of the slowest allele at the AAT-2 locus — none of the other populations have this allele at >0.05. This population occurs at moderate altitude (600 m) on a large mountain (Mt Egon) from which other samples were taken at both higher (Flores 6) and lower (Flores 4, Flores 3) elevations. There is no suggestion from the field data collected that trees sampled were of hybrid origin, or that

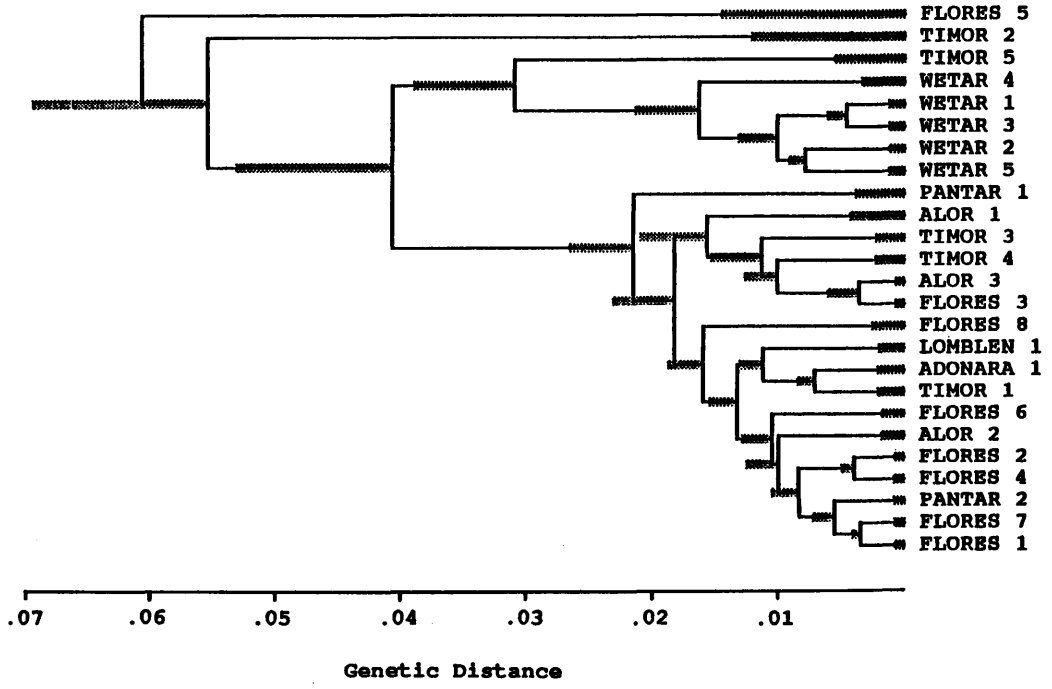

Figure 2. — Cluster diagram of *E. urophylla* populations based on the UPGMA algorithm and Nei's (1978) genetic distance, and using the GD program (Ritland, 1989) to fit error bars. Clusters are significant where the error bar is less than half the branch length.

Table 5. — Estimates of gene flow between populations of *E. urophylla* on each of the islands from which more than one population was sampled and between islands (populations grouped together). N_m estimated using the private allele method, corrected for sample size (SLATKIN, 1985).

Island	$N_{p(1)}$	p(1)	$(N_m)_{est}$	mean no. progeny assayed
Flores	7	0.0170	8.97	71
Timor	5	0.0172	10.54	59
Alor	17	0.0165	10.55	64
Pantar	9	0.0611	0.78	65
Wetar	7	0.0222	6.69	56
All islands	4	0.0167	10.46	63

$N_{p(1)}$ = number of private alleles; p(1) = mean frequency of private alleles; $(N_m)_{est}$ = mean number of migrants.

Table 6. — Multi-locus estimates of outcrossing rate (t) and WRIGHT's fixation index ($F = 1 - H_o/H_e$, $F_e = (1 - t)/(1 + t)$) for 2 populations of *E. urophylla*.

population	mean t (± se)	family range	F	F_e
13 Alor 1	0.90 ± 0.19*	0.83–0.96	0.236[a] ± 0.108	0.053
24 Wetar 4	0.91 ± 0.04**	0.86–0.96	0.365[b] ± 0.109	0.047

*) variable loci: MDH-1, IDH-1, PGD-1, GPI-2, EST-1.
**) variable loci: MDH-1, MDH-2, IDH-1, PGD-1, GPI-2, EST-1.
[a]) rejection of the null hypotheses that F = 0 at 5% level;
[b]) at 1% level.

there were other eucalypts in the vicinity. *E. urophylla* hybridizes naturally with *E. alba* REINW. ex BLUME in narrow overlap zones at low (Flores, Timor) and high altitudes (Wetar); however, *E. alba* does not occur above about 450 m on Mt Egon (J. DORAN and B. GUNN, pers. comm.). MARTIN and COSSALTER (1975 to 1976) state that from phenotypic appearance hybrids in nature are rare as adult trees, but from morphological studies of progeny it appears that the actual rate of hybridization may be quite high suggesting selective abortion of hybrids subsequent to germination.

Population Timor 2 from Mt Mutis also separates from the rest of the populations. It possesses the private allele UGP-2_6 and has a higher frequency of the alleles PGD-1_4 (0.582, all others $\leq$ 0.293) and UGP-2_5 (0·205, all others $\leq$0.078).

The cluster analysis does not show close relationships between populations from each geographic area (e.g. between those from each of the major mountain areas on Flores). Similarly there is no clear pattern with respect to altitude. On Wetar populations from the east (wet) and west (dry) of the island are not differentiated isozymically. The only significant correlations between estimates of genetic diversity (A, P, H_e, H_o) and geographical parameters (latitude, longitude, altitude) were between P and longitude ($r = 0.422$, $p < 0.05$) and H_o and longitude ($r = 0.624$, $p < 0.005$). This suggests a gradient of increasing genetic diversity from west to east.

Gene flow between populations on each island (*Table 5*) is sufficiently high to prevent local differentiation, through migration of alleles. All the estimates of N_m are greater than 1 with the exception of Pantar. Migration of alleles between islands was also high, but generally less than that between populations, as might be expected. Only Timor (UGP-2_6, EST-1_5), Lomblen (GPI-2_1), and Alor (IDH-1_2) had alleles that did not occur on other islands. There were no alleles present in more than one population on an island that were private to that island.

Mating system

The multi-locus estimates of outcrossing indicate that *E. urophylla* is a predominantly outcrossing species· Estimates of t (*Table 6*) are among the highest recorded for any species in the genus studied to date, equalled only by seed orchard material of *E. regnans* (MORAN, BELL and GRIFFIN, 1989) where t = 0.91. For natural populations, in which trees might be expected to breed with near relatives resulting in greater effective inbreeding, the rates reported here are remarkable, although seed was collected from widely spaced individuals in each of the populations.

Variation in t between individual trees was low. Estimates of the fixation index F were positive, and there was a deficiency of heterozygotes in the progeny compared to HARDY-WEINBERG expectations. The values of F are much higher than those expected under inbreeding equilibrium (F_e) given the levels of t (*Table 6*) suggesting breeding between close relatives rather than selfing.

Discussion

The occurrence of *E. urophylla* on islands might suggest greater barriers to gene flow between populations than in other eucalypts whose populations may be separated by other vegetation (including other *Eucalyptus* species) and non-forest habitat barriers, but not by open sea. Absolute distances between islands are far greater than the distance that pollen might normally be carried by insect vectors, but it is possible that wind-blown insects could carry pollen between islands or that birds are effective pollinators. Alternatively, the species may have become established on each island within a relatively short period of time from the same original genetic stock, colonising similar habitats and so limiting further differentiation of populations. The exception to this might be Wetar. In environmental terms Wetar is not greatly different to the other islands, although there is evidence that some populations occur on drier sites and there has been much less modification of stands by man (fire is far less frequent and cutting is quite restricted; B. Gunn and M. Mc Donald, pers. comm., 1990). The fragmentation of the species' distribution on all other islands has possibly taken place quite recently, although it is probably insufficient to lead to population differentiation as all remnants are relatively large and some gene flow between them may be expected. The high estimates of gene migration on Timor and Alor support this view. Large populations also have greater resistance to genetic drift due to lower probability of genetic bottlenecks; small genetic differences between large populations possibly attest to relatively similar selective pressures (Loveless and Hamrick, 1984).

There is a contrast between clear provenance variation in trials and the great degree of phenotypic variation in a number of field characters (Martin and Cossalter, 1975 to 1976; Pinyopusarerk et al., 1993; L. D. Pryor, pers. comm., 1993) and rather unstructured isozyme differentiation. In particular there is no pattern in allele frequencies or measure of genetic diversity that relates to the striking correlation between altitude and fruit size in west Timor and Wetar (Moura, 1977) or the clearly superior growth rates reported for low altitude provenances on Flores (see Eldridge et al., 1993; Charomaini, 1990). Canonical variate analysis of seedling characters distinguished populations from Wetar from all others (Pinyopusarerk et al., 1993). This was attributed to the particular environmental conditions on Wetar (shallow soils on steep slopes, climatic stresses).

Genetic distances between the major clusters of populations are small. In a southern temperate species of *Eucalyptus* (*E. delegatensis*), Moran (unpublished data), using isozymes, found 2 distinct clusters (distance between groups D = 0.035 (Moran, Bell and Prober, 1990)) that corresponded to the 2 major parts of the species' distribution (New South Wales/Victoria and Tasmania) and to a similar clustering based on morphological characters (Boland and Dunn, 1985). Similar correspondence between morphological data and allelic frequencies has been found in *E. nitens* (Cook, 1989), although there are other eucalypts in which classification of taxa below the species level is not supported by isozyme analyses (e.g. *E. caesia* (Moran and Hopper, 1983) and *E. crucis* (Sampson, Hopper and James, 1988)). The clusters of populations of *E. urophylla* generated by analysis of their isozyme genotypes loosely match those found using seedling characters (Pinyopusarerk et al., 1993). However, excluding the anomalous populations of Flores 5 and Timor 2, the distance between the major clusters of *E. urophylla* (Wetar, Alor 1 and Timor 5 vs the rest; see *Figure 2*) is small (D = 0.01). In this case, isolation and the differences in genomes between geographic areas has not led to the same degree of differentiation in isozymes as in morphological features. Although 2 new species are proposed based on morphological studies of adult material (*E. wetarensis* (Wetar material) and *E. orophila* (from high altitudes on Timor) — Pryor et al., submitted), there is no strong evidence from this study of isozyme variation to support the establishment of new species or varieties.

The origins of *Eucalyptus* in eastern Indonesia are unclear. Two explanations are possible — recent (in geological terms) long-distance dispersal from northern Australia and/or New Guinea, or a much more ancient occupation. The presence of the genus on any of the islands between Wetar/Timor and New Guinea (Irian Jaya) has not been established. The most westerly known population of *E. pellita*, a close relative of *E. urophylla*, is in eastern Irian Jaya, some 1400 km east of Timor, although suitable environments for *E. pellita* and *E. urophylla* certainly exist in the western part of Irian Jaya and their presence there cannot be ruled out. Migrations westwards from the Australian-New Guinea continent may have been possible from the early Pliocene (Audley-Charles, 1981).

Alternatively, progenitors of *E. urophylla* may have been present on Timor since before Timor, considered Gondwanic in origin, collided with the southern edge of the Laurasian Inner Banda Arc (which includes all the other islands carrying *E. urophylla)* about 3 million years ago (Audley-Charles, 1981). According to palynological evidence from a deep sea core taken to the south-west of Timor, Myrtaceae (presumed to be *Eucalyptus)* and *Casuarina* became dominant in the early part of the Pleistocene at about the same time (Zaklinskaya, 1978). The volcanic islands of the Inner Banda Arc that currently carry populations of *E. urophylla* are possibly of much more recent origin (late Miocene), and colonisation has taken place recently, but presumably before the late Pleistocene when the deep trench that separates Timor from the Inner Banda Arc was formed by down-faulting (Audley-Charles, 1981). The distribution of alleles is consistent with this hypothesis; Timor and nearby Alor populations contain more of the total number of alleles present in the species (89%) than any other island (Wetar 83%, Pantar 60%, Lomblen 60%, Adonara 59%, Flores 81%). Presumably there has been sufficient time for much of the original allelic composition of the species to be dispersed throughout the distribution.

The apparent absence of *Transversaria* from the Northern Territory of Australia (and possibly also from the western parts of New Guinea) suggests that climatic change has since occurred to restrict the section to its current distribution (eastern Indonesia, New Guinea, eastern seaboard of Australia and southwest Western Australia). Presumably the intensity of the dry season in monsoonal northern Australia is too severe for the species in this group.

The high estimates of outcrossing rate in the 2 populations sampled demonstrate that *E. urophylla* is a predominantly outbreeding species. There is an apparent lack of neighbourhood structure, as there is very little variation in individual tree outcrossing rates; pollen pools are presumably homogeneous (an assumption of the mixed

mating model — BROWN, BARRETT and MORAN, 1985). Even though there may be local groupings of close relatives in eucalypt populations, collecting seed from widely spaced trees may have resulted in effective sampling of local subpopulations. The values of the fixation index suggest some inbreeding, but because of the high outcrossing rates this is likely to represent mating between close relatives rather than selfing. *E. urophylla* has unspecialized flowers, and is presumably pollinated by a wide range of flying insects. High levels of homozygosity in progeny compared to parents have been described for other eucalypts (e.g. *E. delegatensis* (MORAN and BROWN, 1980), *E. stoatei* (HOPPER and MORAN, 1981)), indicating selection against homozygotes between seed set and sexual maturity. The reasonable levels of genetic diversity found in *E. urophylla* suggest that normal breeding strategies (see ELDRIDGE et al., 1993) that have been applied to other species in the genus will be appropriate.

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References

ADAMS, W. T., STRAUSS, S. H., COPES, D. L. and GRIFFIN, A. R.: Population Genetics of Forest Trees. Kluwer Academic, Dordrecht and Boston (1992). — ARADHYA, K. M. and PHILLIPS, V. D.: Genetic variability in fourteen provenances of *Eucalyptus* species in Hawaii. Silv. Genet. **42**, 9—15 (1993). — AUDLEY-CHARLES, M. G.: Geological history of the region of Wallace's Line. In: Wallace's Line and Plate Tectonics. T. C. WHITMORE (ed). Clarendon Press, Oxford. pp. 24—35 (1981). — BOLAND, D. J., BROOKER, M. I. H., CHIPPENDALE, G M., HALL, N., HYLAND, B. P. M., JOHNSTON, R. D., KLEINIG, D. A. and TURNER, J. D.: Forest Trees of Australia. CSIRO/Nelson Melbourne (1984). — BOLAND, D. J. and DUNN, A.: Geographic variation in alpine ash (*Eucalyptus delegatensis* R. T. BAKER). Aust. For. Res. **15**, 155—171 (1985). — BROWN, A. H. D., BARRETT, S. C. H. and MORAN, G. F.: Mating system estimation in forest trees: models, methods and meanings. In: Population Genetics in Forestry. H. GREGORIUS (ed.). Springer-Verlag, Berlin. pp. 32—49 (1985). — BROWN, A. H. D., CLEGG, M. T., KAHLER, A. L. and WEIR, B. S.: Plant population genetics, breeding, and genetic resources. Sinauer Associates, Sunderland, Massachussetts (1990). — BROWN, A. H. D., MATHESON, A. C. and ELDRIDGE, K. G.: Estimation of the mating system of *Eucalyptus obliqua* L'HERIT. by using allozyme polymorphisms. Aust. J. Bot. **23**, 931—949 (1975). — BURGESS, I. P. and BELL, J. C.: Comparative morphology and allozyme frequencies of *Eucalyptus grandis* HILL et MAIDEN and *E. saligna* SM. Aust. FOR. Res. **13**, 133—149 (1983). — BURGESS, I. P., BELL, J. C. and VAN WYK, G.: The identity of trees currently known as *Eucalyptus grandis* in the Republic of South Africa based on isozyme frequencies. S. Afr. For. J. **135**, 24—30 (1985). — CHAROMAINI, M.: Geographic variation of juvenile leaf morphological characteristics of *Eucalyptus urophylla* from Eastern Nusa Tenggara islands grown in south Sumatra. Indones. For. Res. Bull. **530**, 1—10 (1990). — CHIPPENDALE, G. M.: *Eucalyptus*. In: Flora of Australia. Vol. 19. Myrtaceae — *Eucalyptus, Angophora*. Australian Government Publishing Service, Canberra (1988). — COATES, D. J. and SOKOLOWSKI, R. E.: Geographic patterns of genetic diversity in karri (*Eucalyptus diversicolor* F. MUELL.). Aust. J. Bot. **37**, 145—156 (1989). — COOK, I.: Morphological and isozyme variation in *Eucalyptus nitens*. Unpublished MSc Thesis, University of Melbourne (1989). — DORAN, J. C., WILLIAMS, E. R. and BROPHY, J. J.: Patterns of variation in the leaf oils of *Eucalyptus urophylla, E. pellita* and *E. scias*. (submitted). — ELDRIDGE, K. G., DAVIDSON, J., HARWOOD, C. E. and VAN WYK, G.: Eucalypt domestication and breeding. Clarendon Press, Oxford (1993). — FRIPP, Y. J.: Allozyme variation and mating system in two populations of *Eucalyptus kitsoniana* (LUEHM.) MAIDEN. Aust. For. Res. **13**, 1—10 (1982). — GUNN, B. V. and MCDONALD, M. W.: *Eucalyptus urophylla* seed collections. Forest Genetic Resources Information, No. 19. FAO, Rome (1991). — HOPPER, S. D.: and MORAN, G. F.: Bird pollination and the mating system of *Eucalyptus stoatei*. Aust. J. Bot. **29**, 625—638 (1981). — JACOBS, M. R.: Eucalypts for planting. FAO Forestry Series, No. 11. FAO, Rome (1981). — JOHNSON, L. A. S. and HILL, K. D.: New taxa and combinations in *Eucalyptus* and *Angophora* (Myrtaceae). Telopea **4**, 37—108 (1990). LOVELESS, M. M. and HAMRICK, J. L.: Ecological determinants of genetic structure in plant populations. Ann. Rev. Ecol. Syst. **15**, 65—95 (1984). — MARTIN, B. and COSSALTER, C.: Les eucalypts des iles de la Sonde. Bois For. Trop. **163**, 3—25; **164**, 3—14; **165**, 3—20; **166**, 3—22; **167**, 3—24; **168**, 3—17; **169**, 3—13 (1975-1976). — MORAN, G. F.: Patterns of genetic diversity in Australian tree species. New Forests **6**, 49—66 (1992). — MORAN, G. F. and BELL, J. C.: *Eucalyptus*. In: Isozymes in Plant Genetics and Breeding. Part B. S. D. TANKSLEY and T. J. ORTON (eds). Elsevier, Amsterdam. pp. 423—441 (1983). — MORAN, G. F., BELL, J. C. and GRIFFIN, A. R.: Reduction in levels of inbreeding in a seed orchard of *Eucalyptus regnans* F. MUELL. compared with natural populations. Silv. Genet. **38**, 32—36 (1989). — MORAN, G. F. BELL, J. C. and PROBER, S.: The utility of isozymes in the systematics of some Australian tree groups. Aust. Syst. Bot. **3**, 47—57 (1990). — MORAN, G. F. and BROWN, A. H. D.: Temporal heterogeneity of outcrossing rates in alpine ash (*Eucalyptus delegatensis* R. T. BAK). Theor. Appl. Genet. **57**, 101—105 (1980). — MORAN, G. F. and HOPPER, S. D.: Genetic diversity and the insular population structure of the rare granite rock species, *Eucalyptus caesia* BENTH. Aust. J. Bot. **31**, 161—172 (1983). — MORAN, G. F. and HOPPER, S. D.: Conservation of the genetic resources of rare and widespread eucalypts in remnant vegetation. In: Nature conservation: the role of remnants of native vegetation. D. A. SAUNDERS, G. W. ARNOLD, A. A. BURBRIDGE and A. J. M. HOPKINS (eds). Surrey Beatty, Sydney. pp. 151—162 (1987). — MOURA, V.P.G.: Altitudinal variation in *Eucalyptus urophylla* S. T. BLAKE. Unpublished MSc. thesis, University of Melbourne (1977). — NEI, M.: Estimation of average heterozygosity and genetic desitance from a small number of individuals. Genetics **89**, 583—590 (1978). — PETERS, G. B., LONIE, J. S. and MORAN, G. F.: The breeding system, genetic diversity and pollen sterility in *Eucalyptus pulverulenta*, a rare species with small disjunct populations. Aust. J. Bot. **38**, 559—570 (1990). — PINYOPUSARERK, K., GUNN, B. V., WILLIAMS, E. R. and PRYOR, L. D.: Comparative geographical variation in seedling morphology of three closely related red mahoganies, *Eucalyptus urophylla, E. pellita* and *E. scias*. Aust. J. Bot. **41**, 23—34 (1993). — PROBER, S. M., TOMPKINS, C., MORAN, G. F. and BELL, J. C.: The conservation genetics of *Eucalyptus paliformis* L. LOHNSON and BLAXELL and *E. parvifolia* CAMBAGE, two rare species from south-eastern Australia. Aust. J. Bot. **38**, 79—95 (1990). — PRYOR, L. D. and JOHNSON, L. A. S.: A classification of the eucalypts. ANU Press, Canberra (1971). — PRYOR, L. D., WILLIAMS, E. R. and GUNN, B. V.: A morphometric analysis of *Eucalyptus urophylla* and some related taxa. (submitted). — RITLAND, K.: Genetic differentiation, diversity and inbreeding in the mountain monkeyflower (*Mimulus caespitosus*) of the Washington Cascades. Can. J. Bot. **67**, 2017—2024 (1989). — RITLAND, K. and JAIN, S.: A model for the estimation of outcrossing rate and gene frequencies using n independent loci. Heredity **47**, 35—52 (1981). — SAMPSON, J. F., HOPPER, S. D. and JAMES, S. H.: Genetic diversity and the conservation of *Eucalyptus crucis* MAIDEN. Aust. J. Bot. **36**, 447—460 (1988). — SAMPSON, J. F., HOPPER, S. D. and JAMES, S. H.: The mating system and population genetic structure in a bird-pollinated mallee, *Eucalyptus rhodantha*. Heredity **63**, 383—393 (1989). — SLATKIN, M.: Rare alleles as indicators of gene flow. Evolution **39**, 53—65 (1985). — SWOFFORD, D. L. and SELANDER, R. B.: BIOSYS-1: a computer program for the analysis of allelic variation in population genetics and biochemical systematics. Illinois Natural History Survey, Champaign, Illinois. 43 p. (1989). — TURNBULL, J. W.: Geographic variation in *Eucalyptus cloeziana*. Unpublished PhD thesis, Australian National University, Canberra (1980). — TURNBULL, J. W. and BROOKER, M. I. H.: Timor Mountain Gum, *Eucalyptus urophylla* S. T. BLAKE. Forest Tree Leaflet Series No. 214. CSIRO, Melbourne (1978). — YEH, F. C., BRUNE, A., CHELIAK, W. M. and CHIPMAN, D. C.: Mating system of *Eucalyptus citriodora* in a seed-production area. Can. J. For. Res. **13**, 1051—1055 (1983). — ZAKLINSKAYA, E. D.: Palynological information from late Pliocene-Pleistocene deposits recovered by deep-sea drilling in the region of the island of Timor. Rev. Palaeobot. Palynol. **26**, 227—141 (1978).