allozyme loci in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Can. J. Genet. Cytol. **24:** 101—108 (1982a). — El-Kassaby, Y. A., Yeh, F. C. and Sziklai, O.: Inheritance of allozyme variants in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). Can. J. Genet. Cytol. **24:** 325—335 (1982b). — Furnier, G. R., Knowles, P., Aleksiuk, M. A. and Dancik, B. P.: Inheritance and linkage of allozymes in seed tissue of whitebark pine. Can. J. Genet. Cytol. **28:** 601—604 (1986). — Guries, R. P. and Ledig, F. T.: Inheritance of some polymorphic isoenzymes in pitch pine (*Pinus rigida* Mill.). Heredity **40:** 27—32 (1978). — Huang, M. R.: The application of isozyme analysis to research on genetic breeding of forest trees. Journal of Nnjing Institute of Forestry **3:** 121—127 (in Chinese) (1985). — Lewandowski, A. and Mejnartowicz, L.: Linkage analysis of allozyme loci in Polish larch (*Larix decidua* subsp. *polonica* (Racib.)(Domin). Hereditas **114:** 107—109 (1991). — Marty, T. L., O'Malley, D. M. and Guries, R. P.: A manual for starch gel electrophoresis: new microwave edition. Staff Paper Series 20, Dep. For., Univ. of Wisconsin-Madison (1984). — Mather, K.: The measurement of linkage in heredity. Methuen and Co. Ltd., London (1951). — Muona, O., Yazdani, R. and Lindqvis., G.: Analysis of linkage in *Picea abies*. Hereditas **106:** 31—36 (1987). — Na'iem, M., Inheritance and linkage of allozyme of megagametophyte of Japanese red pine plus-tree clones selected from natural stands. Ph. D. Thesis, University of Tsukuba, Japan (1991). — Na'iem, M., Tsumura, Y., Uchida, K., Nakamura, T. and Ohba, K.: Linkage of allozyme loci in Japanese red pine (*Pinus densiflora*). Can. J. For. Res. **23:** 680—687 (1993). — Na'iem, M., Tsumura, Y., Uchida, K., Nakamura, T., Shimizu, S. and Ohba, K.: Inheritance of isozyme variants of megagametophyte of Japanese red pine. J. Jpn. For. Soc. **71:** 425—434 (1989). — Niebling, C. R., Johnson, K. and Gerhold, H. D.: Electrophoretic analysis of genetic linkage in Scots pine (*Pinus sylvestris* L.). Bio-

chem. Genet. **25:** 803—814 (1987). — O'Malley, D. M., Allendorf, F. W. and Blake, G. M.: Inheritance of isozyme variation and heterozygosity in *Pinus ponderosa*. Biochem. Genet. **17:** 233—250 (1979). — O'Mally, D. M., Guries, R. P. and Nordheim, E. V.: Linkage analysis for 18 enzyme loci in *Pinus rigida* Mill. Theor. Appl. Genet. **72:** 530—535 (1986). — Ornstein, L.: Disk electrophoresis — I: background and theory. Ann. N. Y. Acad. Sci. **121:** 321—349 (1964). — Rudin, D.: Inheritance of glutamate-oxalate-transaminases (Got) from needles and endosperms of *Pinus sylvestris*. Hereditas **80:** 296—300 (1975). — Rudin, D.: Leucine-amino-peptidase (Lap) from needles and macrogametophytes of *Pinus sylvestris* L. — Inheritance of allozymes. Hereditas **85:** 219—226 (1977). — Rudin, D. and Ekberg, I.: Linkage studies in *Pinus sylvestris* L. — using macro gametophyte allozymes. Silvae Genet. **27:** 1—13 (1978). — Rudin, D. and Rasmuson, B.: Genetic variation in esterases from needles of *Pinus sylvestris* L. Hereditas **73:** 89—98 (1973). — Scandalios, J. G.: Genetic control of multiple molecular forms of enzymes in plants: a review. Biochem. Genet. **3:** 37—79 (1969). — Shiraishi, S.: Linkage relationships among allozyme loci in Japanese black pine, *Pinus thunbergii* Parl. Silvae Genet. **37:** 60—66 (1988a). — Shiraishi, S.: Inheritance of isozyme variation in Japanese black pine, *Pinus thunbergii* Parl. Silvae Genet. **37:** 93—100 (1988b). — Strauss, S. H. and Conkle, M. T.: Segregation, linkage and diversity of allozymes in knobcone pine. Theor. Appl. Genet. **72:** 483—493 (1986). — Suyama, Y., Tsumura, Y. and Ohba, K.: Inheritance of isozyme variants and allozyme diversity of *Abies mariesii* in three isolated natural forests. J. Jpn. For. Soc. **74:** 65—73 (1992). — Tomaru, N., Tsumura, Y. and Ohba, K.: Inheritance of isozyme variants in Korean pine (*Pinus koraiensis*). J. Jan. For. Soc. **72:** 194—200 (in Japanese) (1990). — Tsumura, Y., Uchida, K. and Ohba, K.: Genetic control of isozyme variation in needle tissues of *Cryptomeria japonica*. J. Hered. **80:** 291—297 (1989).

Identification of Races in Eucalyptus globulus ssp globulus Based on Growth Traits in Tasmania and Geographic Distribution

By G. J. Jordan, N. M. G. Borralho, P. Tilyard and
B. M. Potts

Cooperative Research Centre for Temperate Hardwood
Forstry,
University of Tasmania, P.O. Box 252c, Hobart, Tasmania,
Australia 7001

Summary

Canonical discriminant analysis of 432 open-pollinated families grouped into 46 collection localities covering the natural geographic range of *Eucalyptus globulus* ssp *globulus* was carried out on four year growth data from five trial sites in Northern Tasmania. Combining results from the analysis of growth responses with natural geographic boundaries and reported taxonomic groupings it was possible to identify 12 geographical races in the *E. globulus* ssp *globulus* base population. The three races from Victoria [(1) the Otway Ranges, (2) the Strzelecki Ranges and (3) South Gippsland], the (4) King Island, the (5) Furneaux Group, and (6) Central Western Tasmania races, showed relatively similar growth responses. Races from eastern Tasmania, [(7) Northeastern Tasmania, (8) Eastern Tasmania, (9) Jericho, and (10) Southeastern Tasmania] were distinct from the previous large group. Two small races, (11) Port Davey and (12) Lighthouse, Wilson's Promontory had very slow growth. The trees at the Lighthouse locality had a distinct shrub-like habit. The classification of four localities (South West Lavers Hill, Clarke Island, Dover and Recherche Bay) was doubtful. The variation in growth response across environments among the different races suggest that appropriate genetic grou-

pings (tentatively the 12 geographic races identified here) should be made prior to further genetic analysis of *E. globulus* ssp *globulus* breeding populations.

Introduction

In breeding programmes, accurate predictions of parental breeding values require correct identification of races (genetically and phenotypically distinct groups within a species; King and Stansfield, 1990) when family or individual selections are carried out across these groupings. In particular, if there are fewer parents from superior races in the breeding population, or if there is unbalanced representation of races across trials, biased estimates can occur with less selection pressure being allocated to the best geographic races resulting in sub-optimal genetic progress (Quaas and Pollack, 1981). Significant gains from direct race selection have also been reported (e.g. in *E. globulus*; Orme, 1988; Almeida, 1993). Unfortunately, it is
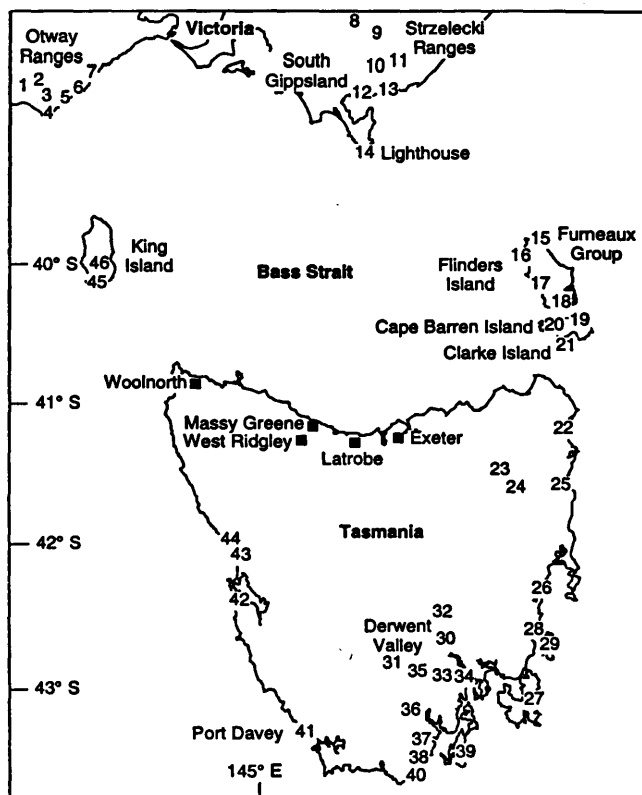
Figure 1. — Localities of natural populations of *Eucalyptus globulus* ssp *gobulus* and trials used in this analysis. Codes follow *table 1*. The collections cover virtually the whole range of the subspecies.

Locality	Code	Number of families
South West Lavers Hill	1	2
Otway State Forest	2	24
Cannan Spur	3	18
Parker Spur	4	36
Cape Patton	5	7
Jamieson Creek	6	7
Lorne	7	16
Jeeralang North	8	46
Jeeralang	9	3
Madalya Road	10	5
Bowden Road	11	5
Port Franklin	12	2
Hedley	13	7
Lighthouse, Wilsons Promontory	14	11
North Flinders Island	15	12
Central North Flinders Island	16	7
Central Flinders Island	17	13
South Flinders Island	18	10
North Cape Barren Island	19	10
West Cape Barren Island	20	27
Clarke Island	21	6
St Helens	22	6
Pepper Hill	23	4
Royal George	24	5
German Town	25	5
Mayfield	26	2
Tarrana	27	3
Triabunna	28	3
North Maria Island	29	5
Mt Dromedary	30	4
Ellendale	31	4
Jericho	32	7
Collinsvale	33	4
Hobart South	34	9
Moogara	35	19
Blue Gum Hill	36	3
South Geeveston	37	7
Dover	38	3
South Bruny Island	39	2
Recherche Bay	40	2
Port Davey	41	3
Macquarie Harbour	42	4
Little Henty River	43	11
Badgers Creek	44	8
South King Island	45	9
Central King Island	46	18

not always obvious how to best identify races. Races are most readily identified when they are geographically distinct. Classifications are usually based on obvious morphological or taxonomic differences, or on clear geographical boundaries. However, these classifications may fail to identify appropriate races for traits of interest to tree breeding. Thus, the inclusion of information about relative performance of populations in the traits of interest should improve the classification of races.

Eucalyptus globulus LABILL. ssp *globulus* (referred to as "ssp *globulus*" from here on) occurs naturally on mainland Tasmania, on the Bass Strait Islands and in southern Victoria (*Figure 1*). It has been introduced elsewhere in Australia, southern Europe, Asia, and North and South America, primarily as a source of pulp wood. Several breeding programs are currently selecting ssp *globulus* for better growth and fibre yield (COTTERILL et al., 1989; BORRALHO et al., 1993). They include material collected from native populations (e.g. ORME, 1978) or from local sources, generally of unknown origin. The geographical distribution of the subspecies, and the intrapopulation variability in capsule morphology have been well described

(KIRKPATRICK, 1975; JORDAN et al., 1993). Marked differences in growth between seed sources have been reported (ORME, 1988; VOLKER and ORME, 1988; VOLKER et al., 1990; ALMEIDA, 1993) although these studies were based on relatively few families and collection localities. Recently, two large collections were made by the CSIRO Tree Seed Centre in collaboration with several international forestry and pulp companies (*Figure 1*), covering the entire range of ssp globulus (GARDINER and CRAWFORD, 1987, 1988). Field trials have been based on this material in several countries, and variation in growth on a single site in Tasmania has been reported (POTTS and JORDAN, 1993).

Some geographic disjunctions can be used to divide the natural range of ssp *globulus*. Tasmania, Victoria and the Bass Strait islands are separated by sea. The eastern and western parts of the range in Tasmania are separated by long distances on land, as are the Otway Ranges and Gippsland. However, taxonomically distinct populations

Table 2. — Location, soil, climatic characteristics and abbreviations for trial sites.

Site	Code	Latitude (South)	Longitude (East)	Altitude	Soil type	Climatic averages		
						annual rainfall	temperatures °C warmest month	coldest month
Exeter	Ex	41° 17'	146° 51'	120 m	Sandy duplex	974 mm	16.5 °C	11.9 °C
Latrobe	La	41° 17'	146° 27'	100 m	Yellow podzol	953 mm	16.3 °C	12.0 °C
Massy Greene	MG	41° 05'	145° 54'	120 m	Kraznozem	1130 mm	16.0 °C	11.8 °C
Woolnorth	Wo	40° 49'	144° 53'	60 m	Yellow podzol	1163 mm	15.6 °C	12.2 °C
West Ridgely	WR	41° 08'	145° 48'	180 m	Kraznozem	1273 mm	15.6 °C	11.4 °C

293

seem to occur in continuous distributions in Flinders Island and Gippsland and there are no obvious geographic discontinuities in eastern Tasmania, which is a large part of the range (KIRKPATRICK, 1975; JORDAN et al., 1993). The present study, therefore, aims to classify seedlots from the natural range of ssp globulus into well defined groups based on clear geographic boundaries and on canonical discriminant analysis of the early growth of these seedlots across five trial sites in northern Tasmania. This classification into geographic races will be the basis for subsequent genetic analyses of early growth of these trials, and will be useful in comparing studies of different base populations.

Method

Seed Provenances

The two collections made by CSIRO Tree Seed Centre include open-pollinated seed from more than 600 individual trees in natural populations. The genetic material in these collections includes typical populations of ssp *globulus,* and populations taxonomically intermediate between this subspecies and mainland subspecies (JORDAN et al., 1993). Progeny trials from this collection have been established widely in Australia, Chile, Portugal, Spain and China. The genetic material is likely to be important in local breeding programs.

The families in the collection were grouped into localities (*Table 1*), defined as an arbitrary area of about 50 km². Localities were spread throughout the geographic range of ssp *globulus* (*Figure 1*). It is apparent from *table 1* that relatively high numbers of trees were sampled in some of the regions, particularly the Bass Strait islands, Otway Ranges and Gippsland.

Field trials

Five trials, established by North Forest Products in northern Tasmania (*Figure 1*), were used in these analyses (*Table 2*). All trials were disced and ploughed before trees were planted between July and August 1989 at spacing of 4 m x 2.5 m. Diammonium phosphate fertiliser (18 % N, 20 % P_2O_5) was applied to each seedling at planting (90 g at the Exeter trial, and 100 g at the others).

Between 448 and 549 open-pollinated families were included in each trial. Each trial was established in a resolvable incomplete block design (PATTERSON and WILLIAMS, 1976), with five replicates each containing between 21 and 28 incomplete blocks, which each contained between 20 and 25 families in two-tree contiguous plots (*Table 3*), giving a total of 10 trees per family in each trial.

Measurements

The height in dm (H_1) and diameter at breast height in dm (DBH_1) of each tree in the trials were measured by height pole and diameter tape respectively between May

and July 1993 at four years of age. The height (H_2) and DBH (DBH_2) of the second largest stem was measured in the case of multi-stemmed trees. Damaged trees were excluded from the analyses. Conic volume (V) in dm³ at four years was estimated as:

$$V = DBH_{1.}^2\left(13 + \frac{H_1 - 13}{3}\right) + DBH_{2.}^2\left(13 + \frac{H_2 - 13}{3}\right)$$

(1)

Transformed traits (the square of height and the square root of volume in each trial, resulting in a total of 10 variables) were used to optimise the normality and homogeneity of variance assumptions of the analyses. Family generalised least square means were calculated using restricted maximum likelihood methods (GENSTAT, 1990) following the model:

$$Y_{ijkl} = \mu + r_i + b_{ij} + f_k + p_{ik} + e_{ijkl}$$

(2)

where γ_{ijkl} is the phenotypic observation, μ is the trial overall mean, r_i is the fixed effect of the ith replicate, b_{ij} is the random effect of the jth block in replicate i, f_k is the fixed effect of the jth family p_{ik}, is the random effect of the kth plot in replicate i and e_{ijkl} is the remainder error.

Canonical Discriminant and Cluster Analysis

Multivariate comparisons between localities with more than three families were undertaken using canonical discriminant analysis (SOKAL and ROHLF, 1981) on the family means of transformed height and volume from each of the trials. Only the 432 families represented in all five Tasmanian trials were used (*Table 1*). Scores on the resulting standardised discriminant functions of all families (including those from localities with less than three families) were derived and locality means of these scores were calculated. The relative importance of the major variables in differentiating localities in the discriminant space was summarised by vectors indicating the direction of variation. The lengths of the vectors were proportional to the unvariate F -values between populations, and the directions were determined by the standardised canonical coefficients. Populations were classified using average linkage clustering (SNEATH and SOKAL, 1973) of the mean scores on the discriminant functions, so that the distances between localities were Mahalanobis' distances (PHILLIPS et al., 1973). SAS (SAS Institute Inc., 1990) was used for all calculations.

Multivariate Analysis of Variance

Comparisons were made between proposed geographic races based on the canonical discriminant and cluster analyses with multivariate analysis of variance (MANOVA) based on family least square means using SAS (SAS Institute Inc., 1990). Geographic races containing more than one locality were compared using a nested design with geographic races as a fixed effect and localities within geographic races as a random effect, and contrasts were made between pairs of geographic races with HENDERSON's Type III sums of squares (e.g. SEARLE, 1987), and the locality within geographic race effect as the error. Localities were compared with a single stratum design, and geographic races containing only one locality, and doubtful localities, were contrasted with the pooled effect for the localities in their respective geographically nearest geographic race. The significance of these contrasts given by the F-tests

Table 3. — Trial design features, including numbers of replicates (reps) and incomplete blocks (blocks), and overall means with standard deviations for height and estimated volume at 4 years.

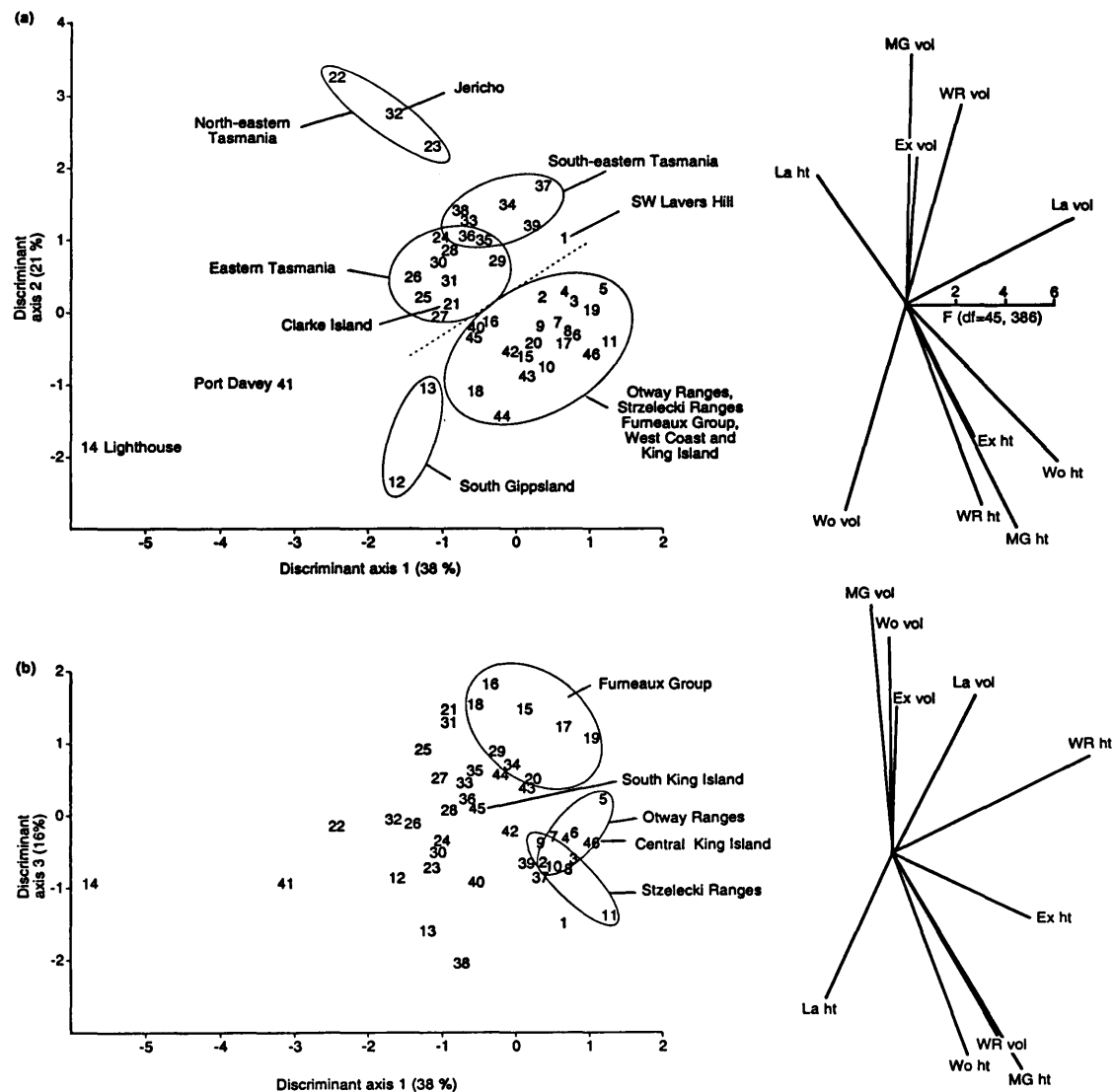| Site | \--------- Numbers of \-------- | | | | height ± sd (m) | volume ± sd (dm³) |
	families	reps	blocks per rep	families per block		
Ex	551	5	28	20	7.01 ± 0.91	12.8 ± 5.0
La	569	5	25	24	6.87 ± 1.85	10.7 ± 6.6
MG	596	5	24	25	10.47 ± 1.16	60.7 ± 22.1
Wo	494	5	25	20	6.94 ± 0.92	15.4 ± 7.0
WR	450	5	23	20	9.10 ± 0.94	38.3 ± 14.6

Figure 2. — Standardised locality mean scores on the first three discriminant axes from analysis of growth traits of *Eucalyptus globulus* ssp *globulus*. 2a. — Discriminant axis 1 versus Discriminant axis 2. 2b. — Discriminant axis 1 versus Discriminant axis 3. Vectors showing the direction of variation of the growth traits are shown on the right hand side of each plot. These are proportional in length of the F -value between localities.

may be overestimated since the geographic race groupings were partly derived using the same data as the MANOVA's.

Results and Discussion

Canonical Discriminant and Cluster Analysis

Figure 2 shows the locality mean scores on the first three axes generated by the canonical discriminant analyses. The first and second discriminant axes (*Figure 2a*), which accounted for 59 % of the variation, separated the slow growing Lighthouse (code 14 in *Table 1*) and Port Davey (41) localities and, to a lesser extent, two localities from South Gippsland (Port Franklin, 12, and Hedley, 13) from all others. A second group including Clarke Island (21) and all of the eastern Tasmanian localities (22 to 39), except Recherche Bay (40) lay above a line oblique to the two discriminant axes in *Figure 2a*. A group containing Recherche Bay and most of the localities from the Otway Ranges (2 to 7), Furneaux Group (15 to 20), the Strzelecki Ranges (8 to 11), King Island (45 to 46) and western Tasmania (42 to 44) lay below this line. South

West Lavers Hill (1) was closer to the eastern Tasmanian localities than any of the other Victorian localities. The western Tasmanian localities were differentiated from most of the Victorian and Bass Strait localities by having lower scores on both axes. Two localities from northern Tasmania (St Helens, 22 and Pepper Hill, 23) and one from central eastern Tasmania (Jericho, 32) were differentiated from the other localities in eastern Tasmania by high scores on the second axis. The southeastern Tasmanian localities (33 to 39), except Recherche Bay (40), tended to have higher scores on both axes than the localities from central eastern Tasmania (24 to 31).

The Furneaux Group localities were differentiated from the Otway and Strzelecki Ranges localities by high values on the third discriminant axis (*Figure 2b*). The Strzelecki Ranges locations were weakly differentiated from the Otway Ranges localities by a combination of the first and third axes (*Figure 2b*).

The total multivariate variation between localities is summarised in the cluster analysis (*Figure 3*). The groups

Mahalanobis' Distance

Figure 3 (dendrogram) labels:

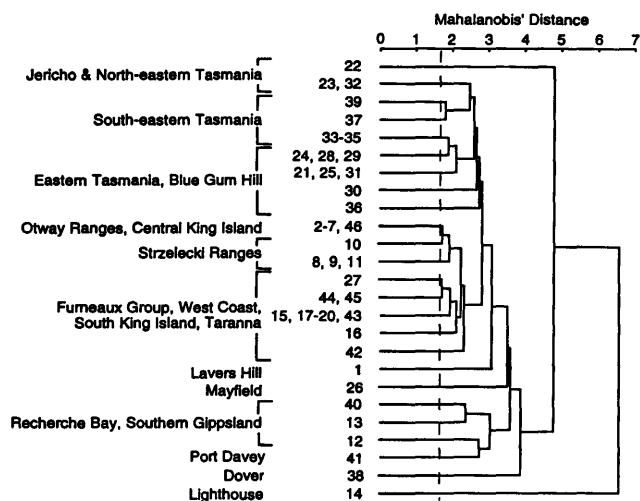| Label	Codes
Jericho & North-eastern Tasmania	22, 23, 32
South-eastern Tasmania	39, 37
	33-35
	24, 28, 29
Eastern Tasmania, Blue Gum Hill	21, 25, 31, 30, 36
Otway Ranges, Central King Island	2-7, 46
Strzelecki Ranges	10, 8, 9, 11
	27
Furneaux Group, West Coast, South King Island, Taranna	44, 45, 15, 17-20, 43, 16, 42
Lavers Hill	1
Mayfield	26
Recherche Bay, Southern Gippsland	40, 13
Port Davey	12, 41
Dover	38
Lighthouse	14

Figure 3. — Average linkage cluster analysis of standardised locality mean scores on discriminant axes from Analysis 1. Codes are from *table 1*.

described above were apparent, except (i) that the Furneaux Group localities (15 to 20) were poorly differentiated from the western Tasmanian localities (42 to 44), (ii) the King Island localities (45 and 46) did not form a distinct group, (iii) the Blue Gum Hill locality (38) was distinct from the other localities in south-eastern Tasmania, (iv) the Taranna locality (27) clustered with the western Tasmanian and Bass Strait Island localities rather than the other eastern Tasmanian locality, (v) the southern Gippsland localities (12 & 13) did not form a cluster and (vi) the St Helens locality (22) appears to be an outlier. The results shown in *figures 2* and *3* were robust, since essentially the same groupings were produced by analyses of different subsets of the variables, analyses excluding various outlying localities and cluster analyses over different numbers of discriminant axes (data not shown).

Differentiation of Major Groups and Geographic Races

Four major groups (*Table 4*), which conform well with geographic regions and taxonomic variation, can be differentiated by the canonical discriminant and cluster analyses.

Group 1

The first major group includes localities from the Otway Ranges, Strzelecki Ranges, South Gippsland, the Furneaux Group, King Island and western Tasmania. This is a region which contains both core populations of ssp *globulus* and intergrade populations between core ssp *globulus* and other subspecies (KIRKPATRICK, 1975; JORDAN et al., 1993). Although the analysis clearly separates the South Gippsland localities from the rest of the zone of intergradation it is likely that a significant proportion of this difference is due to inbreeding effects in the seedlots used. Seed from these two localities was collected from small remnant populations (i.e., individuals or small groups of trees which were previously part of larger and more continuous stands.) Growth rates are known to be reduced in remnant populations of ssp *globulus*, probably due to increased inbreeding depression (POTTS and JORDAN, 1993).

Six geographic races can be distinguished within this major group of localities (*Table 4*). The Otway Ranges race is geographically distinct, and except for South West Lavers Hill, was discriminated well in the analysis, with

Table 4. — Proposed division of *Eucalyptus globulus* ssp *globulus* into groups, geographic races and aberrant localities on the basis of geographic distribution and growth in five trials in Tasmania. The mean tree height at four years in each trial is given.

Race	Localities	Heights (m)				
		Ex	La	MG	Wo	WR
Group 1						
1. Otway Ranges	1 to 7	7.38	7.08	11.10	7.37	9.40
2. Strzelecki Ranges	8 to 11	7.35	6.98	12.03	6.99	9.71
3. South Gippsland	12 & 13	6.63	6.45	10.05	6.46	8.46
4. Furneaux Group	15 to 21	6.98	6.54	10.41	7.33	9.17
5. King Island	45 & 46	7.06	7.02	10.40	7.36	9.12
6. Central Western Tasmania	42 to 44	6.81	6.45	10.40	7.36	9.15
Group 2						
7. Northeastern Tasmania	22 & 23	6.58	7.15	9.90	5.69	7.44
8. Eastern Tasmania	24 to 31	6.79	6.68	10.20	6.51	8.50
9. Southeastern Tasmania	33 to 40	7.23	7.31	10.30	6.69	9.03
10. Jericho	32	6.86	7.38	9.71	5.54	8.02
Group 3						
11. Port Davey	41	5.29	5.76	7.81	5.29	8.21
Group 4						
12. Lighthouse	14	3.51	3.23	5.45	3.74	5.80
Aberrant localities within races						
Lavers Hill (Group 1)	1	8.05	7.52	11.73	6.78	9.27
Clarke Island (Group 1)	21	6.49	9.78	9.78	6.60	8.63
Dover (Group 2)	38	7.50	8.10	10.53	6.54	8.75
Recherche (Group 2)	40	6.32	7.33	10.45	6.74	8.97

high growth rates at all sites (*Table 4*). The Strzelecki Ranges race did not differ significantly in growth responses from the Otway Ranges race (*Table 5*). The South Gippsland race had generally slower growth than the nearby Strzelecki Ranges race (*Table 4*). The relationship between South Gippsland and the Strzelecki Ranges could be distorted by inbreeding effects (see above) and the multivariate differences were not significant (*Table 5*). However, capsule morphology suggests that these two regions are genetically distinct, since the Strzelecki Ranges populations appear to be morphologically intermediate between ssp *globulus* and ssp *pseudoglobulus*, whereas the South Gippsland populations match the core phenotype of ssp *globulus* (JORDAN et al., 1993). Although the two localities within this race were clearly distinct in *figures 2* and *3*, they were not significantly different (MANOVA, p > 0.3). The Furneaux Group race was distinct from its neighbouring races, South Gippsland, King Island and Northern Tasmania, (*Table 5*), even though the northern (15 and 16) Flinders Island localities appear to be intergrade populations, and the other localities (17 to 20) match core ssp *globulus* (JORDAN et al., 1993). The Furneaux Group race had moderate growth at all sites, except at Woolnorth where these localities were relatively fast growing (*Table*

Table 5. — Percentage probability values of pairwise contrasts between proposed races (with more than one locality) of *Eucalyptus globulus* ssp *globulus* based on multivariate analysis of variance of transformed volume and height at five sites. These comparisons are suitable for a priori pairwise comparisons, a posteriori comparisons would require significant differences at least at the 0.1 % level.

Race	Code	ST	SG	FU	KI	WT	NE	ET	SE
Otway Ranges	OT	24	0.8	0.01	14	0.5	0.01	0.3	0.01
Strzelecki Ranges	ST	.	7	0.1	16	7	0.01	0.1	0.01
South Gippsland	SG	.	.	0.2	8	7	0.01	1	0.06
Furneaux Group	FU	.	.	.	0.2	20	0.01	0.06	0.01
King Island	KI	.	.	.	.	14	0.01	0.7	0.02
Central Western Tasmania	WT	.	.	.	.	.	0.01	0.3	0.01
Northeastern Tasmania	NE	.	.	.	.	.	.	0.2	0.3
Eastern Tasmania	ET	.	.	.	.	.	.	.	5
Southeastern Tasmania	SE	.	.	.	.	.	.	.	.

4). The two King Island localities were distinct from each other (*Figures 2* and *3*), and showed intermediate growth rates at most sites (*Table 4*), but may have been affected differentially by inbreeding. The locality (46) with more families had affinity to the Otway Ranges and Strzelecki Ranges localities. These families were also collected from remnant populations, but the collection (45) with fewer families produced by far the highest proportion of abnormal seedlings in the CSIRO collection suggesting that they came from particularly inbred populations (POTTS and JORDAN, 1993) and were grouped into a single King Island race. Although this King Island race was not significantly different in growth response from the Otway Ranges race (*Table 5*), its geographic isolation suggests that it should be treated separately. Finally localities from Central Western Tasmania were not clearly distinct from the Bass Strait and Strzelecki Ranges races (*Table 5*), but are clearly geographically isolated.

Group 2

Growth traits (*Figure 2*) showed that the localities from eastern Tasmania formed a major group with generally slower growth than those of Group 1 (*Table 4*). These form a region of core populations of ssp *globulus* (JORDAN et al., 1993). Four geographic races in this group could be distinguished on the basis of growth and geographic distribution. The Northeastern Tasmania race includes the two northernmost localities (St. Helens, 22 and Pepper Hill, 23) and is highly distinct from the other northern and central localities in eastern Tasmania (*Figures 2* and *3*). Although the St. Helens locality appeared as an outlier in *figure 3*, it was not significantly different from the Pepper Hill locality (MANOVA, p > 0.08). One locality from central Tasmania (Jericho, 32) was clearly distinct from all other Tasmanian localities (MANOVA p < 0.001) and a Jericho race is proposed. There was more or less continuous variation among the remainder of the eastern and southern Tasmanian localities. However, there appeared to be at least as much variability among the eastern Tasmanian localities as among the Bass Strait Island, Western Tasmanian, Strzelecki and Otway Ranges races combined (*Figure 2*). Thus, the remaining localities in eastern Tasmania were divided into two races, Eastern Tasmania (24 to 31) and Southeastern Tasmania (33 to 40), as apparent in *figure 2a* and *table 4*. These two races were distinguished by their faster relative growth on the drier sites (Ex, La). The northern races were clearly distinct from the central and southern geographic races, but the central and southern races were only marginally distinct (*Table 5*). The exact delimitation of races in the Derwent Valley (localities 32 to 35) is debatable and may require further data.

Groups 3 and 4

Two localities (Port Davey, 41 and Lighthouse, 14) can be considered as distinct groups and geographic races because of their extreme and distinct growth performance. The Port Davey race was distinct, with very slow growth at all sites (*Table 4*), and significantly different from all other localities (MANOVA; p < 0.001). Although this locality is poorly represented in this analysis (only three families) and, therefore, the relationships with other localities were poorly determined, other features suggest that it is distinct. It is small and highly isolated and POTTS and JORDAN (1993) reported that several families showed evidence of previous hybridisation (possibly with *E. ovata* or

E. brookeriana). The Lighthouse locality clearly produced the slowest growing trees at all sites (MANOVA; p < 0.001), but this population has a unique mallee form, precocious flowering, precocious vegetative phase change and thick leaves which have presumably evolved in response to its exposure to strong winds and salt spray (HASAN, 1993).

The growth of four localities (South West Lavers Hill, Clarke Island, Dover and Recherche Bay) appeared distinct from those of the other localities in their respective geographic races, although differences were not significant (MANOVA; p > 0.1). Further studies are required to determine if these differences are the result of inbreeding depression, sampling errors or true genetic differences. South West Lavers Hill was slower growing than the other Otway Ranges localities, particularly at Woolnorth (*Table 4*), but the seed was collected from remnant populations and only two families were used in the present analysis. The Clarke Island locality was, in general, slower growing than the rest of the Furneaux Group and intermediate between this geographic race and the eastern Tasmanian geographic races in *figure 2*. This agrees with its geographic position, intermediate between the rest of the Furneaux Group and eastern Tasmania. However, the locality is also a remnant population with high proportions of abnormal seedlings, which suggests that the population is highly inbred (POTTS and JORDAN, 1993). The Dover (38) and Recherche Bay (40) localities were distinct from the other southeastern Tasmanian localities although the estimates were based on only three and two families respectively.

Despite the general opinion that there is little geographic variation within ssp *globulus* for growth traits compared to other temperate eucalypts (VOLKER and ORME, 1988; RAYMOND, 1989), significant differences in performance between localities, both in eastern Tasmania, and in the Bass Strait/Victorian region have been reported (WOOLASTON et al., 1991). Thus, the differentiation in growth found between races identified in the present study is likely to be significant.

The four major groups of geographic races described above conform well with the major taxonomic groupings of JORDAN et al. (1993), which suggests that the classification for growth traits proposed here may have some taxonomic basis. Thus, all of the Group 2 races have core ssp *globulus* capsule phenotypes, and all of the Group 1 races, except South Gippsland, King Island and most of the Furneaux Group, have *globulus* intergrade capsule morphology. The King Island populations were intermediate in capsule morphology between intergrade and core phenotypes.

The classification of seedlots into geographic races found in this study is based on trials covering a considerable range of environmental conditions in northern Tasmania, and should provide a reasonable classification for Tasmanian conditions. However, environmental conditions in other parts of the world where *E. globulus* ssp *globulus* is grown differ markedly from those in Tasmania. Thus, analyses of geographic races may need to be extended to these areas before genetic analyses of data are undertaken, although the conformity with the taxonomic classification of populations (JORDAN et al., 1993) suggests that the classification presented here is likely to be robust.

Conclusions

In most cases, geographically isolated regions could be differentiated on their growth response. Localities in the main range of ssp. *globulus* on the east coast of Tasmania were relatively variable compared with the main group of Victorian and Bass Strait island localities, and could be separated into four major groups. On the basis of similarities in growth response in five Tasmanian trials and geographic consistency, 12 geographic races of ssp *globulus* were identified (*Table 4*).

References

Almeida, M. H. R. N. R.: Estudo da Variabilidade Geográfica em *Eucalyptus globulus* Labill. Unpublished PhD thesis, Universidade Técnica de Lisboa (1993). — Borralho, N. M. G., Cotterill, P. P. and Kanowski, P. J.: Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. Can. J. For. Res. **23**: 648—656 (1993). — Cotterill, P. P., Dean, C., Cameron, J. and Brindbergs, M.: Nucleus breeding: a new strategy for rapid improvement under clonal growth. In: Proceedings of the IUFRO Conference on Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal Growth and Seedling Forestry. Pattaya, Thailand. Gibson, G. L., Griffin, A. R. and Matheson, A. C. (eds): 39—51. Oxford Forestry Institute, Oxford, U. K. and Winrock International, Arlington, Virginia (1989). — Gardiner, C. A., and Crawford, D. F.: 1987 Seed collections of *Eucalyptus globulus* subsp. *globulus* for tree improvement purposes. Unpublished Report, CSIRO Division of Forest Research, Canberra (1987). — Gardiner, C. A., and Crawford, D. F.: 1988 seed collections of *Eucalyptus globulus* subsp. *globulus* Labill. for tree improvement purposes. Unpublished Report, CSIRO Division of Forestry and Forest Products, Canberra (1988). — GENSTAT 5: Genstat 5, Release 2. Reference Manual Supplement. Oxford University Press, Oxford (1991). — Hasan, O.: The Effect of Paclobutrazol on Flowering Activity and Gibberellin Levels in *Eucalyptus* nitens and *Eucalyptus*

globulus. Unpublished PhD. thesis, University of Tasmania (1993). — Jordan, G. J., Potts, B. M., Kirkpatrick, J. B., and Gardiner. C. A.: Variation in the *Eucalyptus globulus* complex revisited. Aust. J. Bot. **41**: 763—785 (1993). — King, R. C. and Stansfield, W. D.: A Dictionary of Genetics. Oxford University Press, New York (1990). — Kirkpatrick, J. B.: Geographical Variation in *Eucalyptus globulus*. Bulletin No. 47, Forestry and Timber Bureau. Australian Government Publishing Service, Canberra (1975). — Orme, R. K.: *Eucalyptus globulus* provenances. In: Proceedings of the Third World Consultation on Forest Tree Breeding, Canberra: 207—221. CSIRO, Division of Forest Research, Canberra (1978). — Orme, R. K.: Progress with *Eucalyptus globulus* provenance research. Silvicultura **31**: 483—486 (1988). — Patterson, H. D. and Williams, E. R.: A new class of resolvable incomplete block designs. Biometrika **63**: 83—92 (1976). — Phillips, B. F., Campbell, N. A. and Wilson, B. R.: A multivariate analysis of geographic variation in the welk *Dicathais*. J. Ep. Mar. Biol. Ecol. **11**: 27—69 (1973). — Potts, B. M. and Jordan, G. J.: Variation in a base population trial of *Eucalyptus globulus* subsp. *globulus* in Tasmania. In: Research Working Group No. 1 of the Australian Forestry Council, Forest Genetics, Proceedings of Twelfth Meeting, Canberra; February 1993: 87—89. Australian Forestry Council, Canberra (1993). — Quaas, R. L. and Pollack, E. J.: Modified equations for sire models with groups. J. Dairy Sci. **64**: 1868—1870 (1981). — Raymond, C. A.: Developing breeding populations for temperate eucalypts in relation to natural populations. In: Proceedings of the IUFRO Conference on Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal Growth and Seedling Forestry, Pattaya, Thailand. Gibson, G. L., Griffin, A. R. and Matheson, A. C. (eds): 423—424. Oxford Forestry Institute, Oxford, U. K. and Winrock International, Arlington, Virginia (1989). — SAS Institute Inc.: SAS/STAT User's Guide Version 6, Volume 2. SAS Institute Inc., Cary, NC (1990). — Searle, S. R.: Linear models for unbalanced data. John Wiley and Sons, New York (1987). — Sneath, P. H. A., and Sokal, R. R.: Numerical Taxonomy. W. H. Freeman and Co., San Francisco (1973). — Sokal, R. R., and Rohlf, F. J.: Biometry. 2nd Edn. W. H. Freeman and Co., San Francisco (1981). — Volker, P. W., Dean, C. A., Tibbits, W. N. and Ravenwood, I. C.: Genetic parameters and gains expected from selection in *Eucalyptus globulus* in Tasmania. Silvae Genetica **39**: 18—21 (1990). — Volker, P. W. and Orme, R. K.: Provenance trials of *Eucalyptus globulus* and related species in Tasmania. Aust For. **51**: 257—265 (1988). — Woolaston, R., Whiteman, P. H. and Cameron, J. N.: Genetic analyses of four year diameter measures for *Eucalyptus globulus* growing across four sites in Victoria, Australia. In: Intensive Forestry: The Role of Eucalypts. Proceedings of the IUFRO symposium, P2.02-01 Productivity of Eucalypts, 2 to 6 September 1991, Durban, South Africa. Schönau, A. P. G. (ed.): 371—381. ICFR, Durban (1991).

Effects of Sexual Reproduction at Different Latitudes on Performance of the Progeny of Picea abies

By T. Skrøppa[1]), T. Nikkanen[2]), S. Ruotsalainen[3]) and Ø. Johnsen[1])

Abstract

Controlled crosses of the same combinations were performed in a Norway spruce seed orchard in northern Finland and in 1 of 2 orchards in southern Finland. Seedlings from 11 family pairs were cultivated and cold acclimated in a phytotron together with control provenances and were frozen in artificial freezing tests at different temperatures. The seedlings from the crosses at the northern location were generally more frost hardy than their full-sibs from the southern crosses and were also taller. The controlled cross seedlings were less frost hardy than natural stand seedlings originating from the same latitude as their parents. A close relationship was found between the hardiness of the control provenances and their latitude. The results indicate that adaptive properties of Norway spruce seedlings to some extent depend on the climatic conditions at the site where the reproduction is performed.

Introduction

Recent results have shown that seedlings from seeds produced after controlled crosses in Norway spruce (*Picea abies* (L.) Karst.) seed orchards or clonal archives may not

[1]) The Norwegian Forest Research Institute, 1432 Ås, Norway
[2]) The Finnish Forest Research Institute, Punkaharju Research Station, 58450 Punkaharju, Finland
[3]) The Finnish Forest Research Institute, Kolari Research Station, 95900 Kolari, Finland