same order as for the randomised block analysis (see *Figure 2.).*

The competition terms will correct the effects to the competition level of the trial mean, but when grown in a monoculture, the best varietes would produce a more competitive environment than that of the trial average and so will not perform as well as in the trial. KEMPTON suggested the treatment effects would be appropriate to that of the variety grown in a monoculture if the effects are divided by 1-$\varkappa$, where $\varkappa$ is the competition coefficient in our data, where $\varkappa = -0.54$, this is equivalent to multiplying the effects by 0.65. Ignoring this factor would give estimates of the effects that were much too large.

A further bias occurs when the best varieties are selected from a varietal trial. Those varieties that produce yields above their true potential are more likely to be selected than those performing poorly. This selection bias was discussed by PATTERSON and SILVEY (1980) and COTTERILL, CORRELL and BOARDMAN (1982). Unfortunately all three sources of bias from a randomised block trial tend to exaggerate the varietal effects.

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Variation of Eucalyptus camaldulensis from North Australia grown in Israel*)

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Summary

Variation of *E. camaldulensis* was studied in 71 families from 31 seed sources in North Australia. Clinal variation along latitudinal and longitudinal gradients occurs with regard to several of the characters investigated. Factor and cluster analyses with nine traits tend to group the seed sources according to major drainage divisions of North Australia: Timor Sea and Gulf of Carpentaria. Some provenances which occupy abnormal positions on the graphs are interpreted as Late Tertiary or Pleistocene relicts; the similarity between the Timor Sea and Gulf of Carpentaria provenances, on the one hand, and seed sources from the interior with drainage to inland lakes (Western Plateau, Lake Eyre), on the other, is apparently due to the disjunction of a formerly continuous distribution area as the result of climatic changes and/or modifications of drainage patterns.

In field trials, yields at 6 years of age ranged from 48.9 $m^3\ ha^{-1}$ to as little as 3.8 $m^3\ ha^{-1}$. The Finke River, N. T., family 10489-J1235 is apparently from an elite tree with low provenance-site interaction. Considerable variation in yield between families from the same seed origin points to the possibility of significant genetic gains by selection of suitable seed trees of the most promising provenances. The importance is stressed of juvenile-mature correlations for early screening of high-yielding seed sources and families.

Key words: Eucalyptus camaldulensis, geographic variation, provenance trials, progeny tests.

Zusammenfassung

In Israel wurde die Variation von *Eucalyptus camaldulensis* bei 71 Familien aus 31 Herkünften aus Nordaustralien untersucht. Klinale Variation entlang von Breitengrad- und Längengradgradienten trat in Bezug auf einige der untersuchten Merkmale auf. Die Faktoren- und die Cluster-Analyse mit neun Merkmalen weisen auf eine Gruppierung der Herkünfte im Zusammenhang mit dem wesentlichen Einzugsbereich der zur See hin entwässernden Flüsse von Nordaustralien hin: Timor See und Golf von Carpentaria. Einige Provenienzen, die ungewöhnliche Positionen in den Graphiken besetzen, werden für spätterziäre oder pleistozäne Relikte gehalten. Die Verschiedenheit zwischen den Provenienzen vom Timor See und vom Golf von Carpentaria auf der einen Seite und den Herkünften aus den abflußlosen Gebieten des Landesinneren (Western Plateau, Lake Eyre) ist wahrscheinlich auf

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eine Disjunktion zurückzuführen, die dieses früher kontinuierliche Verbreitungsgebiet als Ergebnis von klimatischen Änderungen und/oder von Änderungen der Art der Entwässerung geteilt hat.

In den Feldversuchen ergaben sich Erträge, im Alter von sechs Jahren, von 48,9 m³ pro ha bis herunter zu 3,8 m³ pro ha. Die Familie 10489-J1235 vom Finke River, N. T., stammt vermutlich von einem Elitebaum ab mit geringer Herkunft-Standort-Interaktion. Die beachtliche Variation im Ertrag zwischen Familien gleicher Herkunft weist auf die Möglichkeit hin, erhebliche genetische Gewinne durch Selektion von geeigneten Mutterbäumen der versprechendsten Herkünfte zu erreichen. Es wird hervorgehoben, daß die Jugend/Alters-Korrelationen für die Früherkennung von gutwüchsigen Herkünften und Familien bedeutsam sind.

Introduction

During the last 15 years numerous papers have appeared that demonstrate convincingly the occurrence of variation as related to seed source in *Eucalyptus camaldulensis* DEHNHARDT; many of these papers were critically reviewed by ELDRIDGE (1975). Whereas the existence of a north-south cline of variation is, in spite of some discontinuities (e.g. GRUNWALD and KARSCHON, 1974), by now well established (KARSCHON, 1967, 1974; PRYOR and BYRNE, 1969; BURLEY *et al.*, 1971), variation from east to west is so far poorly understood. Also, there is less published information available on variation of the species in the summer rainfall part of its area of distribution in the north compared with the better known winter rainfall part in the south of the continent.

Large-scale seed collections in 1972—73 from four drainage divisions (Department of Minerals and Energy, 1975) in the northern part of Queensland, the Northern Territory and the Kimberley region of Western Australia by the Forest Research Institute of the Forestry and Timber Bureau (now the CSIRO Division of Forest Research) in Canberra, have made it possible to fill part of this gap in our knowledge.

Materials and Methods

Seed of 71 trees from 31 North Australian provenances (*Table 1, Fig. 1*) was sown at Ilanot (32° 18' N, 34° 54' E) in April 1974 and April 1975, and nursery stock was raised in containers according to current practice.

The following determinations were made on nursery stock to discriminate between seed sources: Petiole length, base angle at convex side of midrib, length and width of leaf blade, oil gland density and leaf colour were recorded on the 5th—7th leaf of 20—50 plants of each half-sib family. Oil gland density was counted under a magnification of x20 on the convex side of the midrib, in the area of maximum width of the blade, of a field of 23.3 mm². Colour was determined according to the Munsell system (Munsell Color Co., 1952); for statistical analysis the index of fading (NICKERSON, 1936) was calculated as the colour deviation from the arbitrarily set standard, 2.5 G 8/8.

Sclerophylly, *i.e.* the dry-matter content per unit area

Table 1. — Seed origins.

No.	Seed origin	Number of seed trees	Location	Lat. N ° '	Long. E ° '	Altitude m	Mean max. warmest month °C	Mean min. coolest month °C	Mean annual rainfall mm	Drainage division*
1	10489	1	Finke River, N.T.	25 41	134 51	335	35.8	4.7	127	LE
2	10494	3	SW of Alice Springs, N.T.	24 30	133 15	549	35.1	3.8	252	LE
3	10496	1	Roe Creek, N.T.	23 43	133 43	762	35.1	3.8	252	LE
4	10498	1	W of Alice Springs, N.T.	23 43	133 46	762	35.1	3.8	252	LE
5	10507	1	N of Tennant Creek, N.T.	18 38	133 56	366	37.1	10.6	352	WP
6	10517	1	Fergusson River, N.T.	14 04	131 59	213	38.9	12.2	628	TS
7	10531	1	Napperby Creek, N.T.	22 49	132 36	564	35.5	4.4	267	WP
8	10532	1	Chainman Creek, N.T.	14 37	132 07	91	37.7	15.3	963	TS
9	10533	1	Victoria River, N.T.	15 36	131 07	30	39.6	11.1	594	TS
10	10536	3	Dunham River, W.A.	15 47	128 43	46	36.6	18.9	693	TS
11	10540	2	Ord River, W.A.	17 29	127 57	366	37.7	8.9	479	TS
12	10543	1	Fitzroy River, W.A.	18 11	125 36	152	40.5	11.1	519	TS
13	10544	4	Lennard River, W.A.	17 23	124 45	61	36.1	14.4	627	TS
14	10550	2	Isdell River, W.A.	16 57	125 34	335	37.7	13.3	963	TS
15	10557	1	Drysdale River, W.A.	15 40	126 23	396	37.7	13.3	963	TS
16	10558	10	Gibb River, W.A.	16 08	126 30	427	37.7	13.3	963	TS
17	10571	2	Mary River, W.A.	18 44	126 52	305	37.7	8.9	479	TS
18	10574	1	Sturt Creek, W.A.	19 34	127 41	305	38.1	11.0	360	WP
19	10576	1	Yalloogarie Creek, N.T.	21 49	131 10	518	36.7	8.5	272	WP
20	10911	3	Emu Creek, Petford, Qld.	17 20	144 58	534	29.6	10.4	860	GC
21	10912	5	Walsh River, Qld.	17 03	144 32	335	29.6	10.4	860	GC
22	10913	2	W of Almaden, Qld.	17 20	144 39	549	29.6	10.4	860	GC
23	10920	1	Crooked Creek, Qld.	18 17	143 14	305	36.2	11.4	823	GC
24	10922	1	S of Stirling, Qld.	17 20	141 30	150	34.6	14.8	944	GC
25	10923	6	Gilbert River, Qld.	17 10	141 45	30	34.6	14.8	944	GC
26	10924	2	Wyabba Creek, Qld.	16 43	142 00	30	34.6	14.8	944	GC
27	10927	4	Leichhardt River, Qld.	19 48	140 07	180	38.0	10.3	468	GC
28	10928	2	Fullerton River, Qld.	20 42	141 10	150	38.0	10.3	468	GC
29	10929	2	Flinders River, Qld.	20 30	142 15	180	38.0	10.3	468	GC
30	10930	2	Flinders River, Qld.	20 40	142 38	213	37.4	8.1	486	GC
31	10931	3	Sandy Creek, Hughenden, Qld.	20 43	144 22	348	37.4	8.1	486	GC

* GC - Gulf of Carpentaria; LE - Lake Eyre; TS - Timor Sea; WP - Western Plateau.

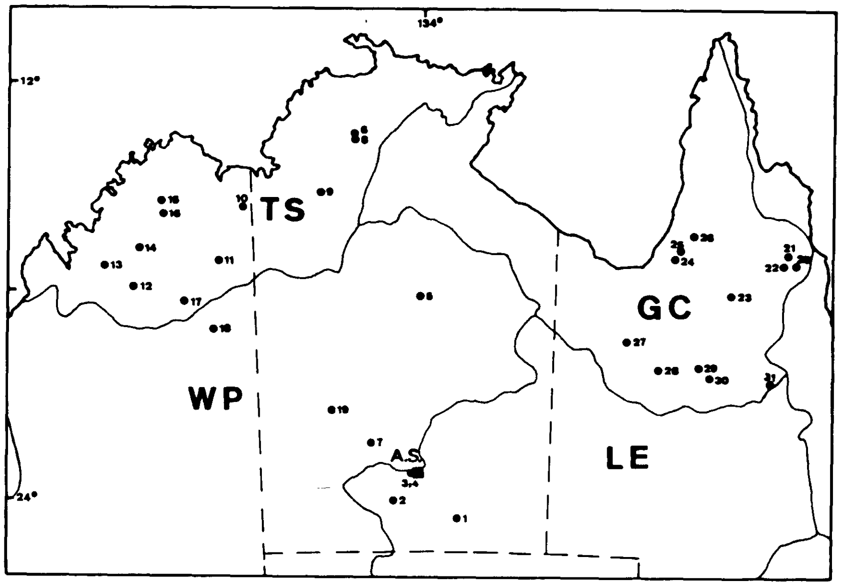

Fig. 1 — Location of seed sources (for details, see *Table 1)* and boundaries of drainage divisions (Department of Minerals and Energy, 1975). GC - Gulf of Carpentaria; LE - Lake Eyre; TS - Timor Sea; WP - Western Plateau. A. S. - Alice Springs, N. T.

(Stocker, 1971), was determined in March 1975 and February 1976 on leaf disks of 38.5 mm² and 63.6 mm², respectively, from 30—40 plants per family (one leaf per plant).

Epicuticular waxes were determined in July 1975 and 1976 on 2-cm² sections of one intermediate leaf each from 15 plants per family by dissolving the wax in 10 cm³ chloroform, filtration through Whatman No. 2 paper, evaporation, and weighing of the residue.

The morphology of the epicuticular waxes of the 4th—5th (opposite) or 8th—11th (alternate) leaves from 15 families of 14 seed sources was examined with a scanning electron microscope; leaf disks were affixed to polished carbon disks with rubber cement and coated with a gold-palladium alloy (60:40) about 200 Å thick (Hanover and Reicosky, 1971).

Table 2. — Mean values and standard deviations for nine traits in 31 seed sources.

Seed origin	Petiole length mm	Leaf length cm	Leaf width cm	Base angle °	Oil glands cm^{-2}	Lignotubers %	Sclerophylly mg cm^{-2}	Wax mg dm^{-2}	Index of fading
10489	7.9	8.47	2.93	36.17	981.0	11.3	7.81	20.00	41.0
10494	9.7	9.23	2.89	34.05	957.2	21.3	7.16	20.33	43.9
10496	4.7	4.40	1.35	28.50	796.2	7.2	7.81	15.00	41.0
10498	7.0	6.10	1.24	23.87	750.2	23.5	7.11	12.00	36.0
10507	7.1	9.27	2.02	29.16	1,727.0	29.4	5.50	22.33	46.8
10517	6.4	6.46	1.20	26.83	1,370.7	37.0	3.60	8.50	52.0
10531	3.9	3.83	0.82	22.87	900.2	15.6	5.86	14.33	52.0
10532	5.4	6.65	1.43	27.67	1,113.9	18.3	5.66	11.50	48.5
10533	4.7	5.01	1.21	23.33	1,341.8	46.7	6.08	9.60	48.5
10536	9.7	8.33	2.10	31.53	1,202.5	43.4	5.97	13.00	48.5
10540	6.3	6.53	1.19	25.66	1,347.4	35.0	5.78	12.33	41.5
10543	8.7	8.24	2.12	34.50	1,245.6	45.9	4.63	12.66	46.0
10544	11.2	10.08	2.37	32.04	1,107.8	36.4	5.50	12.40	50.0
10550	8.4	7.31	1.13	25.42	1,117.2	31.4	5.22	12.66	46.0
10557	5.9	6.88	1.29	30.17	687.2	22.2	5.88	10.16	47.0
10558	9.5	8.23	1.77	30.03	1,261.4	27.2	6.09	14.50	51.0
10571	6.3	8.17	1.29	24.85	1,243.1	37.4	5.98	16.66	44.8
10574	8.5	9.80	2.20	28.39	1,414.0	33.3	5.33	15.50	44.2
10576	5.4	8.40	1.70	28.50	1,031.0	15.2	7.55	16.83	46.4
10911	6.0	6.37	1.13	26.15	791.2	64.4	5.43	9.16	40.9
10912	9.8	10.76	2.46	31.27	695.8	48.9	6.37	11.83	48.6
10913	5.4	6.70	1.11	17.00	505.3	65.0	5.50	10.33	49.0
10920	6.3	6.81	1.09	23.90	636.2	41.7	4.76	13.66	46.0
10922	3.7	4.78	1.19	25.17	814.6	39.7	5.68	12.83	46.0
10923	9.9	9.60	2.51	30.28	788.1	54.1	5.64	13.10	48.6
10924	6.3	7.10	1.21	24.84	1,137.1	51.0	4.21	13.00	46.5
10927	7.6	9.00	2.13	28.88	1,181.4	62.3	7.00	18.66	42.3
10928	5.6	6.18	1.12	25.04	856.8	18.6	7.83	13.83	44.0
10929	4.6	6.30	1.08	26.00	767.8	43.4	6.46	13.83	47.8
10930	5.8	6.66	1.40	27.05	854.8	55.1	6.80	14.66	43.5
10931	10.3	10.83	2.37	30.76	777.0	57.0	6.44	20.22	43.5
Mean	7.0	7.50	1.65	27.74	1,013.0	36.7	6.02	14.04	45.9
S.D.	2.0	1.81	0.60	3.95	279.3	16.2	1.03	3.44	3.6

Experimental plantations of 12 provenances (27 families) and 18 provenances (29 families) were established on red sandy loam at Ilanot in the central Coastal Plain and on brown rendzina at Tirosh (31° 45' N, 34° 55' E) in the Judean Foothills in December 1974 and October 1975, respectively. The layout was a randomized-block design with four replications at Ilanot and six replications at Tirosh, each plot consisting of nine trees spaced 3 × 3 m apart, *i.e.* 1,111 trees per ha; cultivation was by dry-farming. Mean annual rainfall is 603 mm at Ilanot and 424 mm near Tirosh falling mainly in winter. Tree heights and number of surviving trees were recorded each year, and D. B. H. was recorded beginning from the third year. Tree volumes were calculated by assuming a form factor of 0.4 irrespective of seed origin (Karschon, 1974).

Results

Table 2 reports the provenance means of leaf characters and lignotubers of the 31 seed sources under investigation *(Table 1, Fig. 1).* As shown by statistical analyses, between-provenance variation of all measured traits was highly significant ($P \leqq 0.001$).

The matrix of correlation coefficients between measured traits and parameters describing the seed origin *(Table 1)* is given in *Table 3.* Whereas variation of leaf size and shape (length and width of the blade, base angle, and petiole length) is not clinal, there is evidence of variation in relation to latitude and longitude of seed origin, of several characters. Sclerophylly and amount of epicuticular waxes increase, and the lignotuber percent and index of fading decrease, with latitude; at the same time, lignotuber percent increases with longitude, whereas oil gland density decreases. Effects of altitude on lignotuber percent and index of fading are similar to those of latitude. Significant correlations were also obtained between several characters and climatic factors.

Table 3. — Matrix of correlation coefficients for seed origin parameters and nine traits of 31 provenances.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. Latitude	1.00	.13	.55**	-.11	-.85**	-.81**	-.08	-.05	.25	.18	-.29	-.43*	.72**	.63**	-.58**
2. Longitude		1.00	-.06	-.54**	-.11	.15	-.16	-.01	-.04	-.24	-.57**	.52**	.14	.07	-.18
3. Altitude			1.00	-.39*	-.70**	-.39*	-.16	-.20	-.12	-.14	-.31	-.36*	-.38*	.16	-.44*
4. Mean max. temp.				1.00	.13	-.24	-.05	-.05	-.06	.12	.56**	-.23	-.09	.14	.17
5. Mean min. temp.					1.00	.77**	.29	.25	-.02	.01	.23	.44*	-.58**	-.42*	.56**
6. Mean rainfall						1.00	.07	.00	-.24	-.21	-.19	.43*	-.56**	-.59**	.44*
7. Petiole length							1.00	.85**	.79**	.69**	.14	.23	-.08	.25	.04
8. Leaf length								1.00	.83**	.66**	.18	.28	-.01	.46**	.02
9. Leaf width									1.00	.86**	.13	.06	.25	.55**	-.08
10. Base angle										1.00	.15	-.14	.20	.41*	-.05
11. Oil glands											1.00	-.10	-.31	.20	.20
12. Lignotubers												1.00	-.38*	-.21	.07
13. Sclerophylly													1.00	.47**	-.51**
14. Wax														1.00	-.29
15. Index of fading															1.00

* - significant at P = 0.05; ** - significant at P = 0.01.

The nine measured traits *(Table 2)* were analyzed by factor analysis (Morrison, 1967) with nine factors; four factors were retained which account for 86% of the total variation. The loadings of the four factors obtained after varimax rotation *(Table 4)* show that the first factor is typified by leaf size and shape (petiole length, blade length and width, base angle), which are independent of latitude and longitude of seed origin *(Table 3)*. Factor 2 is defined by ecologically significant traits—sclerophylly, epicuticular waxes and index of fading, which are related to latitude of seed provenance. Factors 3 and 4 are typified by lignotuber percent and oil gland density, respectively, both of which are related to longitude of seed origin *(Table 3)*. The scores for factors 2, 3 and 4 in relation to location of seed origin are presented in *Fig. 2*. Whereas factor 1 cannot be readily interpreted, factor 2 defines a latitudinal cline; factors 3 and 4 show a readily interpretable pattern which can be related to the two major drainage divisions of North Australia — the Timor Sea and Gulf of Carpentaria drainage systems (Department of Minerals and Energy, 1975).

Cluster analysis (SAS, 1979) of the 31 provenances based on nine traits produced two major groupings which correspond essentially to the two major drainage divisions represented in our study — Timor Sea with 11 provenances, and Gulf of Carpentaria with 12 provenances *(Table 1, Fig. 1)*. The Timor Sea cluster *(Fig. 3,* left) includes two seed sources each from the Gulf of Carpentaria and Western Plateau drainage systems, while the Gulf of Carpentaria grouping *(Fig. 3,* right) includes one Timor Sea provenance and the remaining provenances from the Western Plateau and Lake Eyre drainage divisions.

Table 4. — Factor analysis of nine traits for 31 seed sources.

Traits	Factor			
	1	2	3	4
Petiole length	0.91	-0.08	0.19	0.04
Leaf length	0.90	0.06	0.25	0.13
Leaf width	0.95	0.18	-0.06	0.04
Base angle	0.84	0.07	-0.32	0.08
Oil glands	0.13	-0.11	-0.08	0.95
Lignotubers	0.10	-0.10	0.94	-0.11
Sclerophylly	0.12	0.71	-0.46	-0.34
Wax	0.45	0.62	-0.23	0.33
Index of fading	0.06	-0.88	-0.07	0.09
Variance explained by each factor	3.48	1.73	1.37	1.18

In all 15 leaf samples examined *(Table 5)* the epicuticular waxes are of the plate type (Hallam and Chambers, 1970), although the size and shape of the plates vary *(Figs. 4—5)*.

Table 6 presents the growth of 27 half-sibs from 12 provenances at Ilanot at 6 years of age, with trees from locally selected seed known to originate from the southern parts of Australia (Abd-Alla *et al.*, 1980; Karschon, 1970) serving as control. Volumes ranged from 56.6 m^3 ha^{-1} to as little as 3.8 m^3 ha^{-1}; the fastest growing Australian family was from the Finke River, N. T. (10489-J1235), yielding 48.9 m^3 ha^{-1}. In some cases there was considerable variation among families from the same seed source; for instance, yields of six half-sibs from the Gilbert River, Qld. (10923) ranged from 28.2 m^3 ha^{-1} to 11.5 m^3 ha^{-1}. The correlation between yield per ha in the 6th year and height growth in the first year was highly significant ($r = 0.74$**).

Results obtained after four years at Tirosh *(Table 7)* were fairly similar to those obtained at Ilanot *(Table 6)*, the growth of the Finke River family (10489-J1235) being second only to that of a half-sib from the Victoria River, N. T. (10533-JT231). Yield at 4 years of age was significantly related to tree height at the age of two years ($r = 0.80$**), but not at one year of age. In contrast to the situation at Ilanot, there was a positive correlation ($r = 0.56$**) between yield per ha at 4 years of age and latitude of seed origin; height and D. B. H. were inversely related to longitude of seed origin ($r = -0.38$* and -0.46*, respectively), but there was no significant relation between yield and longitude.

Discussion and Conclusions

There has so far been little information published on patterns of variation of *E. camaldulensis* in the northern part of its area of distribution, north of the parallel of the Tropic of Capricorn (23° 30' S), although some tropical provenances were included in morphological studies by various authors (Andrew, 1973; Burley *et al.*, 1971; Hallam and Chambers, 1970; Karschon, 1967, 1971; Pryor and Byrne, 1969; see also Eldridge, 1975). Chemotaxonomical studies of northern seed sources by Banks and Hillis (1969) and Abd-Alla *et al.* (1980) are also relevant. The chromosome number $2n = 22$ is the same in provenances from tropical and subtropical latitudes (Grunwald and Karschon, 1979).

For technical reasons it was not possible to raise nur-

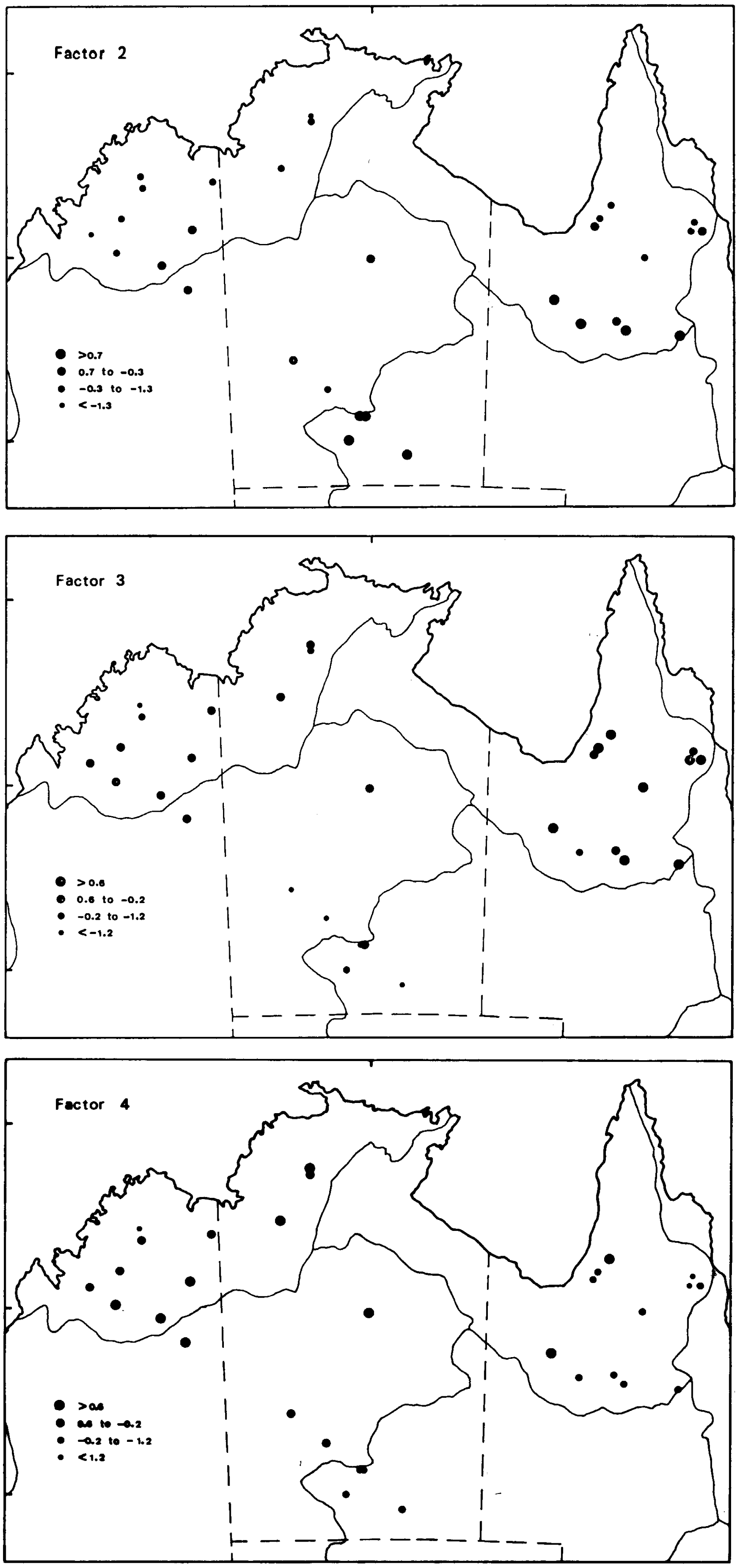

Fig. 2. — Scores of factors 2, 3 and 4 as related to geographical location of seed origin.

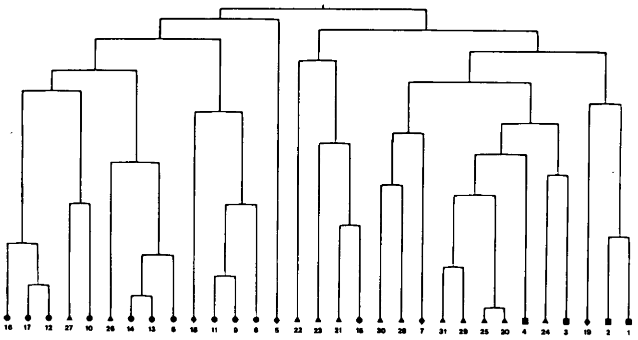

Fig. 3. — Cluster analysis of 31 seed sources based on Euclidian distances among nine standardized variables. Drainage divisions are indicated as follows: ▲ - Gulf of Carpentaria; ■ - Lake Eyre; ● - Timor Sea; ◆ - Western Plateau.

Table 5. — Epicuticular plate waxes observed in selected seed sources.

Seed source and family	Drainage division*	Seed source and family	Drainage division*
10494-J1247	LE	10571-JT331	TS
10494-J1248	LE	10574-JT341	WP
10498-J1256	LE	10911-J1529	GC
10517-J1303	TS	10912-J1538	GC
10532-JT226	TS	10920-J1560	GC
10543-JT269	TS	10927-J1583	GC
10544-JT278	TS	10928-J1591	GC
10557-JT304	TS		

* GC - Gulf of Carpentaria; LE - Lake Eyre; TS - Timor Sea; WP - Western Plateau.

sery stock (and to establish provenance trials) of all the seed available in the same year, yet an endeavour was made to obtain, by sowing in two successive seasons, as complete a coverage possible of the area of seed collection *(Fig. 1).* Since statistical analysis of morphological variation performed separately for each season of sowing produced identical trends, results presented in *Tables 2—4* and *Figs. 2—3* refer to all 31 seed sources comprising 71 families *(Table 1, Fig. 1).* Yield data from the field trials *(Tables 6—7)* were, of course, analyzed separately owing to different site conditions, growth rate and age of trees.

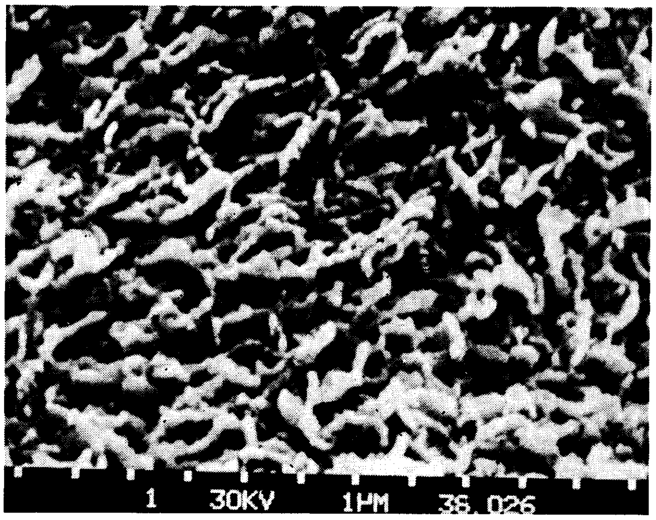

Fig. 4. — Epicuticular plate wax of half-sib from Crooked Creek, Qld. (10920-J1560). x7,000 .

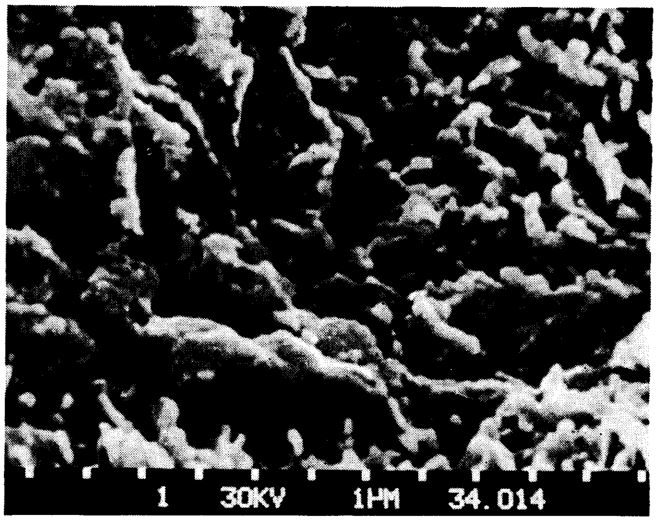

Fig. 5. — Epicuticular plate wax of half-sib from Sturt Creek, W. A. (10574-JT341). x7,000.

As mentioned earlier, all the families in this study were found to have epicuticular waxes of the plate type *(Table 5, Figs. 4—5);* however, HALLAM and CHAMBERS (1970) found tube and plate waxes in what they refer to as *E. camaldulensis* var. *obtusa* Blakely from north of Darwin, N. T., and Port Hedland, W. A., and plate waxes in three unnamed provenances from the Gulf of Carpentaria drainage division of Queensland. In a previous study (C. GRUNWALD, unpublished data), tubes and plates were found in three, out of 14, population from various parts of Austra-

Table 6. — Performance of 27 families from 12 seed sources at Ilanot*.

Seed source and family	Age 6				Age 1
	Volume $m^3\ ha^{-1}$	Height m	D.B.H. cm	Number of trees/ha	Height m
local	56.6a	10.9a-b	12.2a	1,080a-b	2.2a
10489-J1235	48.9a-b	11.4a	11.4a-b	1,080a-b	1.8a-d
10558-JT316	37.2b-c	9.6a-d	10.3a-c	1,049a-b	1.8a-d
10927-J1588	32.6b-d	9.7a-c	9.6a-d	1,080a-b	2.0a-c
10494-J1246	31.1b-d	9.3a-d	9.5a-d	1,111a	2.1a-b
10494-J1247	31.1b-d	9.4a-d	9.6a-d	1,111a	2.3a
10923-J1571	28.2b-d	9.0a-e	9.6a-d	988a-c	1.8a-d
10923-J1570	27.5c-e	8.8a-e	9.2a-d	1,080a-b	1.6a-d
10931-J1599	26.3c-e	8.6b-e	9.2a-d	1,049a-b	1.2b-d
10544-JT278	25.5c-e	8.2b-e	8.5b-e	1,049a-b	1.7a-d
10923-J1572	25.1c-e	8.9a-e	9.0a-d	956a-c	1.5a-d
10558-JT315	25.0c-e	9.0a-e	9.0a-d	1,018a-b	1.4a-d
10931-J1598B	24.5c-e	8.7a-e	8.9a-d	1,080a-b	1.7a-d
10923-J1569	22.1c-e	9.4a-d	8.7a-d	957a-c	1.5a-d
10494-J1248	21.4c-e	9.0a-e	9.4a-d	833b-c	1.4a-d
10927-J1587	19.8c-e	8.2b-e	8.2b-e	1,049a-b	1.4a-d
10544-JT279	19.8c-e	8.4b-e	8.8a-d	895a-c	1.7a-d
10912-J1539	19.3c-e	8.8a-e	10.0a-d	772c	1.8a-d
10931-J1600	18.9c-e	8.1c-e	8.2b-e	1,049a-b	1.4a-d
10558-JT309	18.3c-e	7.8c-e	8.4b-e	988a-c	2.0a-c
10558-JT312	17.7c-e	6.2e-f	6.4d-e	1,080a-b	1.4a-d
10923-J1573	16.2c-e	8.2b-e	7.8b-e	988a-c	1.2b-d
10558-JT310	16.0c-e	7.8c-e	8.7a-d	895a-c	1.2b-d
10536-JT244	13.4d-e	7.5c-f	7.1c-e	1,018a-b	1.2b-d
10923-J1574	11.5d-e	7.6c-f	6.8d-e	1,018a-b	1.4a-d
10507-J1269	11.1d-e	7.5c-f	7.2c-e	926a-c	1.0d
10574JT341	10.8d-e	6.7e-f	6.4d-e	988a-c	1.1d
10576-JT348	3.8e	5.0f	5.0e	772c	1.0d
S.D.	11.2	1.3	1.5	94	0.4

* Means not sharing a common letter are significantly different at P = 0.05, using Duncan's Multiple Range Test.

Table 7. — Performance of 29 families from 18 seed sources at Tirosh*.

Seed source and family	Age 4				Age 2
	Volume $m^3\ ha^{-1}$	Height m	D.B.H. cm	Number of trees/ha	Height m
10533-JT231	20.6a	7.3a-c	8.2a	1,070a-b	4.5a
10489-J1235	19.4a-b	8.0a	8.3a	1,049a-b	4.5a
10930-J1598A	19.4a-b	7.6a-b	8.2a-b	1,090a-b	4.2a-e
10498-J1256	16.4a-c	7.0a-d	7.9a-b	1,090a-b	4.2a-e
10494-J1246	16.0a-d	7.0a-e	8.0a-b	1,070a-b	4.1a-e
10930-J1596	15.3a-e	6.6b-f	7.5a-c	1,049a-b	4.1a-e
10543-JT269	14.5a-f	7.3a-c	7.4a-c	1,090a-b	4.4a-c
10571-JT331	13.9b-f	6.3b-h	7.8a-b	1,111a	4.1a-e
10536-JT242	11.2c-g	6.8a-f	6.6a-e	1,111a	4.3a-d
10544-JT281	10.4c-h	6.8a-f	7.0a-d	1,008a-c	3.7a-f
10927-J1588	8.4c-i	6.4b-h	6.3b-f	1,090a-b	4.0a-e
10558-JT307	8.2d-i	6.5b-g	6.6a-e	946a-c	3.5b-h
10911-J1530	7.2e-i	5.9d-j	5.4d-h	988a-c	3.8a-f
10558-JT308	6.9f-i	6.1c-i	6.2c-f	1,070a-b	3.7a-f
10911-J1529	6.0f-i	6.2b-i	5.2d-h	1,029a-c	4.4a-b
10544-JT278	5.8f-i	5.6d-j	5.5c-g	1,090a-b	3.5a-h
10927-J1589	5.6f-i	5.4f-k	5.2d-h	1,070a-b	3.6a-f
10544-JT279	4.8g-i	5.0g-k	5.2d-h	1,111a	3.6a-g
10911-J1531	4.5g-i	5.6d-j	4.8e-h	1,049a-b	4.2a-e
10558-JT313	4.4g-i	5.4f-k	5.5c-h	1,070a-b	3.6a-h
10931-J1598B	4.0g-i	4.9h-k	5.1e-h	988a-c	3.4c-h
10558-JT314	3.9g-i	5.5e-j	5.2d-h	1,008a-c	3.4d-h
10923-J1569	3.1g-i	5.0h-k	4.4g-i	1,029a-c	3.3e-h
10912-J1540	2.5g-i	5.0g-k	4.0g-i	988a-c	3.3e-h
10912-J1542	2.2g-i	4.7j-k	4.6e-i	864b-c	3.1f-h
10912-J1539	1.8h-i	5.0g-k	4.6e-i	802b-c	2.6h-i
10924-J1580	1.6h-i	4.5j-l	3.8g-i	823b-c	2.6h-i
10913-J1543	1.2h-i	4.0k-l	3.4h-i	1,008a-c	2.7g-i
10922-J1568	0.7i	3.2l	2.8i	761c	2.0i
S.D.	6.1	1.2	1.6	95	0.6

* Means not sharing a common letter are significantly different at P = 0.05, using Duncan's Multiple Range Test.

lia, *viz.* Agnew. W. A. (7052), the Todd River near Alice Springs, N. T. (6788), and Broken Hill, N. S. W. (formerly referred to as var. *subcinerea* Blakely). Differences in wax morphology from the general area of Alice Springs are particularly noteworthy, viz. 6788 with tubes and plates (see above), and 10494 and 10498 with plates only *(Table 5).* It may, therefore, be premature to draw definite conclusions on the geographical distribution of wax features in *E. camaldulensis.*

When analyzing patterns of variation of a species over an area extending over more than 11 degrees of latitude and 20 degrees of longitude *(Table 1, Fig. 1),* the question arises as to the existence of north-south and/or east-west clines. As shown in *Table 3,* variation of only part of the traits can, indeed, be interpreted as clinal. In agreement with earlier findings (KARSCHON, 1967, 1971) lignotuber percent, oil gland density and index of fading decrease with latitude, and epicuticular waxes increase with latitude; the increase from north to south of sclerophylly is directly related to dry-matter content (C. GRUNWALD, unpublished data) and, hence, to frost resistance (GRUNWALD and KARSCHON, 1977). The increase with longitude of lignotuber percents confirms earlier findings (KARSCHON, 1967, 1971), but the decrease from west to east of oil gland density contradicts earlier results (KARSCHON, 1967) where Western Australia was represented by only four seed sources from the Indian Ocean drainage division (which is not included in the present study). The correlations with latitude and longitude of seed origin of the traits examined are reflected in the factor analysis *(Table 4),* where factor 2 is typified by characters related to latitude, and factors 3 and 4 — by characters related to longitude.

Factor and cluster analyses based on nine traits provide a deeper insight into patterns of variation in North Australia *(Figs. 2—3).* Both methods discriminate quite well between provenances from the Timor Sea and Gulf of Carpentaria drainage divisions. However, there are several exceptions which call for some comment.

Let us first consider the seed sources with exoreic drainage, *i. e.* external drainage by rivers which reach the sea. The Wyabba Creek, Qld. (10924) and Leichhardt River, Qld. (10927) provenances, which belong to the Gulf of Carpentaria drainage, display affinity to the Timor Sea drainage provenances, whereas the Drysdale River, W. A. (10557) provenance from the Timor Sea drainage has a high degree of resemblance to the Gulf of Carpentaria seed sources. Since it is safe to exclude the possibility of dysgenic selection owing to the remoteness of the sites, this may be due either to evolution along separate lines not conforming to the present drainage systems, or to their relict character. We are, of course, unable to provide supporting evidence for the first hypothesis. With regard to the second hypothesis reference is made to an earlier paper (KARSCHON, 1971) postulating that *E. camaldulensis* originated in the Late Tertiary or Early Pleistocene in inland northern Queensland, and that during the Pleistocene migration from the centre of origin was wave-like (BURBIDGE, 1960), the species advancing during wet (Pluvial) phases and retreating during arid (Interpluvial) phases, with some relicts persisting in favourable ecological niches such as along watercourses. (Obviously, this hypothesis of possible evolutionary history to explain genetic variation in *E. camaldulensis* is necessarily speculative and not subject to verification by experiment.)

With regard to seed sources with endoreic drainage, *i.e.* internal drainage by rivers which do not reach the sea, two of the Western Plateau drainage division provenances — Sturt Creek, W. A. (10574) and N of Tennant Creek, N. T. (10507) — show affinity to the Timor Sea provenances but occupy fairly isolated positions in the left part of the cluster *(Fig. 3).* Sturt Creek is located just south of the watershed separating the Timor Sea and Western Plateau drainage divisions; since the major drainage systems of the area in the Late Tertiary were similar to the present-day drainage pattern (PATERSON, 1970), it may be that the affinity between the Sturt Creek and Timor Sea provenances is due to the disjunction, as the result of arid cycles in the Pleistocene and Early Holocene, of a formerly continuous population extending over both sides of the divide, with laterization of the Sturt plateau region pointing to its wetter climate in the past. The other two Western Plateau drainage provenances — Napperby Creek, N. T. (10531) and Yalloogarie Creek, N. T. (10576) — have a high degree of resemblance to the Gulf of Carpentaria provenances. Relative uptilting at the margin of the Barkly Tableland (see below) and establishment of internal drainage north of the MacDonnell Ranges (MABBUTT, 1962) may have cut off these populations from the Gulf of Carpentaria system.

The Lake Eyre drainage division is represented in our study by four seed sources from the surroundings of Alice Springs, N. T. All show affinity to the Gulf of Carpentaria provenances but tend to concentrate toward the extreme right of the cluster *(Fig. 3),* with the seed sources from the Finke River (10489) and from SW of Alice Springs (10494) being very similar. Establishment of the present internal drainage occurred at the time of subsidence of the Lake Eyre basin and uplifting along the margins of the Barkly Tableland (Mabbutt, 1962). The affinity of the Lake Eyre and Gulf of Carpentaria drainage provenances may, therefore, be due to the fact that in Late Tertiary and Early Pleistocene times both belonged to the same drainage division. An analogous case was described from the Near East where the occurrence of *Acacia gerrardii* Benth. in the Negev and Sinai deserts is confined to an area which formed, until the Late Pleistocene, part of a single drainage system, when some of the summer-dry rivers (wadis) were captured by the younger hydrographic system of the newly formed Jordan Rift Valley (Halevy and Orshan, 1972).

To sum up, the major finding of our study is the close relation between seed provenance of *E. camaldulensis* and drainage divisions in North Australia (and possibly also in other parts of its area of distribution). The notion that 'boundaries between river systems can be expected to form boundaries between ecotypes' was already propounded by Larsen (1964), and a division of the species into provenance groups corresponding to drainage systems was given by Turnbull (1973; see also FAO, 1979) as a guide for provenance trials.

Supporting evidence was presented by Banks and Hillis (1969), who found a close relationship between seed origin and phytochemical pattern; grouping of the samples on the basis of polyphenol composition led to the recognition of a southern and northern division, each of which consisted of several phytochemical provinces that conform to the drainage system pattern. Of their three regions we are concerned with in this study, provenances from the Timor Sea drainage were readily identifiable chemically and geographically, but poor correlations between phytochemical patterns and seed origin were found for the Gulf of Carpentaria and 'Interior', *i.e.* Western Plateau and Lake Eyre, drainage divisions; this was attributed to inadequate sampling in the former and the uncoordinated drainage patterns in the latter, which had resulted in isolated populations (Banks and Hillis, 1969).

Additional support is provided by the work of Andrew (1973), some of whose 'ecotypes' correspond in fact to drainage systems, whereas the cluster analysis of Burley *et al.* (1971) failed to discriminate between drainage divisions of North Australia because of inadequate distribution of seed sources, coefficients of determination indicating the amounts of variation explained by longitude of seed origin being very low. In our study the distinct groupings corresponding to the contemporary (Holocene) Timor Sea and Gulf of Carpentaria drainage systems were, in spite of the irregularities discussed above, clearly identified by factor and cluster analysis *(Figs. 2—3)* and at least some of these irregularities could be explained by past (Tertiary-Pleistocene) drainage patterns which justify the inclusion of the seed sources from the interior in the Timor Sea and Gulf of Carpentaria groupings. Thus, our experimental evidence clearly supports the conclusions of Larsen (1964), Banks and Hillis (1969) and Turnbull (1973) of drainage systems as an important factor for describing variation in *E. camaldulensis*, provided that due consideration is given to boundary changes of drainage divisions and climatic changes during geological eras.

In our field trials *(Tables 6—7)* the outstanding performance of the Finke River, N. T., family 10489—J1235 is noteworthy although not entirely unexpected, since this is the southernmost provenance included in the study and located outside the tropics *(Table 1, Fig. 1)*. (It remains to be seen if the Victoria River, N. T. family 10533-JT231 will maintain its lead at Tirosh.) The success of the Finke River family is in agreement with earlier findings (Karschon, 1974) that under subtropical conditions, and particularly in winter-rainfall Mediterranean climates, yields are positively related to latitude of seed provenance; it is, however, noteworthy that four families from the same general area as the Finke River, *e.g.* SW of Alice Springs (10494) and W of Alice Springs (10498), had distinctly lower yields. Apparently the Finke River family is not only well adapted to the latitudes of Israel but the seed tree is a valuable elite tree whose properties and low provenance-site interaction show up only in provenance trials, Considerable variation in performance was recorded between families from the same seed source, and depending upon the site class, tree height at one or two years of age was again found to be useful to predict yields (Karschon, 1974).

So far, little has been published abroad on the performance of the seed sources under investigation in this study. The outstanding growth in tropical countries of the Petford, Qld., provenance is, of course, already well documented (Doran and Boland, 1978; Lacaze, 1977), but not unexpectedly yields of three families from Emu Creek, Petford (10911) at Tirosh were, at best, medium *(Table 7)*. The Gilbert River, Qld. (10923) seed source shows particular promise in Upper Volta (FAO, 1979). The Gibb River, W. A. (10558), provenance*) is reported by Doran and Boland (1978) to be of superior growth in Thailand, Nepal and Laos; in our trials, yields of different families of this seed source ranked second at Ilanot *(Table 6)* but occupied only the 12th place at Tirosh *(Table 7)*. Between-family variation in performance again suggests that considerable genetic gains could be realized in developing tropical countries by selecting not only the most suitable seed sources, but also superior seed trees (Karschon, 1974).

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*) For a discussion of the water relations of this seed source, see Grunwald and Karschon (1982).

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Genetic Structures and Expected Genetic Gains from Multitrait Selection in Wild Populations of Douglas fir an Sitka spruce II. Practical application of index selection on several populations

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Summary

The paper reports the use of a series of multiple trait selection indexes to maximise expected gains following selection in some Douglas fir and Sitka spruce populations. The vector of genotypic values of an individual is derived from performances of its open pollinated half sibs, from its provenance, and from the phenotypic and additive genetic covariance matrices between some economically important characteristics. The problem was to derive a linear combination of these genotypic values which would maximise gain in desirable characteristics (growth, flushing) and minimise the increase in undesirable ones (sinuosity, budset branching).

Many weighting coefficients were tested and the one providing the most desirable outcome was chosen. The resulting distribution of selected individuals among provenances and progenies is given.

Multitrait index selection appears to be useful in practical selection, and the genetic gains are substantial even when starting from wild populations. The problems of clonal seed orchard constituted of clones selected in different populations are discussed with respect to variations of genetic structure between populations.

Key words: Multitrait selection, *Picea sitchensis, Pseudotsuga menziesii*, Index selection, Genetic gains.

Zusammenfassung

In der Arbeit wird über die Verwendung einer Serie multipler Merkmals-Selektionsindices berichtet, um den nach Selektion zu erwartenden genetischen Gewinn in einigen Douglasien- und Sitkafichtenpopulationen zu maximieren. Der Vektor genotypischer Werte eines Individuums wird von der Erscheinung seiner frei abgeblühten Halbgeschwister, von seiner Provenienz und von den phänotypischen und additiven genetischen Kovarianzmatrizen zwischen ökonomisch wichtigen Merkmalen abgeleitet. Das Problem bestand darin, eine lineare Kombination dieser genotypischen Werte zu erzielen, bei der ein genetischer Gewinn erwünschter Merkmale (Wachstum, Austrieb) maximiert und gleichzeitig der Anstieg unerwünschter (Krummwüchsigkeit, Blütenansatz, Astigkeit) auf ein Minimum herabgesetzt wird.

Zahlreiche gewogene Koeffizienten wurden getestet und derjenige, der für die Auswertung am effektivsten war, ausgewählt.

Die daraus resultierende Verteilung selektierter Individuen in Provenienzen und Nachkommenschaften ist gegeben.

Die Index-Selektion auf multiple Merkmale erschien in der praktischen Selektion brauchbar, und die genetischen Gewinne waren beträchtlich, selbst wenn man von Wild-