Provenance Variation in Eucalyptus camaldulensis Dehnh. in California*)

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Summary

In California, the Lake Albacutya provenance of river red gum was clearly superior in volume growth to 22 other provenances collected throughout the range of the species in Australia. It had at least 2.5 times the volume of the plantation mean at 5.5 years, consistent with its performance in other countries with Mediterranean climates like California's. Other provenances from southeastern Australia, particularly those in the Murray River basin, also performed well.

The Murray River trees tended to be more crooked and have more forking than those from other areas, and also were among the most heavily flowering in the plantation. The Lake Albacutya trees were somewhat straighter and less forked than those from the Murray River drainage proper.

All successful provenances had a high rainfall pattern correlation (RPC), a statistic defined as the correlation of monthly precipitation at provenance origin with precipitation at the planting site. Cluster analysis on monthly precipitation, mean maximum temperature, and length of frost season linked provenances from the Murray River drainage and Lake Albacutya. Successful provenances had an RPC $>$ 0, long frost periods $>$ 120 days, and low summer mean maximum temperatures $<$ 34° C. When the planting site was included in the cluster analysis, it also joined the Lake Albacutya and Murray River group. RPC and the multivariate techniques provide a basis for objectively recognizing homoclimes.

Key words: geographic variation, *Eucalyptus camaldulensis,* Lake Albacutya, biomass fuel, stem form.

Zusammenfassung

In einem Provenienzversuch in Kalifornien (USA) mit 23 Herkünften von *Eucalyptus camaldulensis* aus dem natürlichen Verbreitungsgebiet der Art in Australien, war die Herkunft Lake Albacutya den 22 anderen im Wachstum eindeutig überlegen. Diese hatte im Alter von 5½ Jahren mindestens 2,5 mal soviel Holz produziert wie das Versuchsflächenmittel ausmachte. Dies entspricht zugleich der Wachstumsleistung beim Versuchsanbau in anderen Ländern, die ein ähnliches Klima haben wie Kalifornien. Andere Herkünfte aus Südost-Australien, besonders solche aus dem Murray-River-Becken, zeigten ebenfalls eine gute Leistung.

Die Bäume vom Murray River tendierten zu einer mehr gekrümmten und Zwiesel-Stammform als die aus anderen Regionen, und zählten außerdem zu den blühfreudigsten der Versuchsflächen. Die Lake Albacutya-Bäume waren etwas geradschäftiger und weniger verzwieselt als die vom Murray River.

Alle erfolgreichen Herkünfte zeigten eine enge Korrelation mit dem Niederschlagsmuster (RPC), eine Statistik, die als eine Korrelation zwischen dem monatlichen Niederschlag am Ursprungsort der Herkunft und dem Niederschlag am Versuchsflächen-Standort definiert ist. Eine Cluster-Analyse des monatlichen Niederschlages, des mittleren Temperatur-Maximums und der Länge der Frostperiode verband die Herkünfte vom Murray-River-Becken und vom Lake Albacutya. Erfolgreiche Herkünfte hatten eine RPC von über 0, lange Frostperioden über 120 Tage und niedrige maximale Sommerdurchschnittstemperaturen von unter 34° C. Wenn der Standort der Versuchsfläche in die Cluster-Analyse mit einbezogen wurde, verband dies ebenfalls die Lake Albacutya- und die Murray River-Gruppe. Die RPC und das multivariate Verfahren liefern eine Basis, um Zonen gleicher Klimabedingungen objektiv erkennen zu können.

Introduction

River red gum (*Eucalyptus camaldulensis* Dehnh.) has been introduced throughout the Mediterranean basin and various parts of Africa and southern Asia to produce wood for fuel, posts, poles, construction timbers, and hardboard flooring (FAO 1979). Its popularity can be attributed to its rapid growth in subhumid climates that are characterized by extended dry seasons and moderate to high temperatures. In the subhumid coastal zone of California there are considerable acreages of land not currently in productive use, but suitable for the establishment of eucalypt plantations. Demand for biomass fuel for home heating and for cogenerating plants is growing, and eucalypts, such as river red gum, could fill a real need.

Species trials established in 1964 by the U.S. Forest Service at Concord, California, indicated that river red gum grew well and suffered no noticeable damage from drought or frost (King and Krugman, 1980). Even better growth might be expected because provenances of river red gum are known to differ considerably in performance (Eldridge, 1975). Only one seed source was included in the initial trials at Concord. Therefore, a provenance trial was initiated in 1976 in order to better evaluate adaptability and growth. Presented here are the 5.5 year results of that provenance trial and recommendations for seed sources for commercial planting in central California. Six to ten years is the anticipated rotation for eucalypt fuel biomass production in California, so results at 5.5 years can be extrapolated to rotation age with little risk.

Materials and Methods

Seed from 23 natural stands of river red gum were obtained from the Forestry and Timber Bureau (now CSIRO Division of Forest Research), Canberra, Australia. The stands covered a wide range of latitude, longitude, elevation, and climate (*Table 1*). Seed were stratified for 60 days, and in June 1975 were germinated in flats under a mist system. They were transplanted into Tinus[2]) containers (20 cm deep, volume of 340 cc) at the cotyledon stage, and outplanted between February 18 to 26, 1976.

*) Based on a thesis by the senior author presented to North Carolina State University in partial fulfillment of the requirements for the degree of Master of Science.

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[2]) Trade names and commercial enterprises or products are mentioned soley for information. No endorsement by the U.S. Department of Agriculture is implied.

Table 1. — Geographic and climatic data for river red gum provenances.

	Provenance[1]	Australian Seed Lot No.	IFG[2] Lot No.	Number of Trees[3]	Latitude (°S)	Longitude (°E)	Elevation (m)	Natural Region	Average Max. Temp. of Warmest Month (°C)	Average Min. Temp. of Coldest Month (°C)	Length of Frost Period (days)	Total Annual Rainfall (mm)	Rainfall Pattern Correlation[4] (r)
A	Lake Albacutya, Vict	S 6845	L	10	35°50'	142°00'	60	SUB-HUMID	30.7	3.8	150	419	0.88
B	Hamilton, Vict	S 6844	K	10	37°16'	142°17'	305	TEMPERATE	26.3	4.4	125	617	0.87
C	Nathalia, Vict	S 6846	M	10	36°00'	145°10'	150	SUB-HUMID	30.4	4.6	138	431	0.80
D	Angaston, SA	S 6965–74	AC	10	34°30'	139°00'	610	TEMPERATE	25.1	4.8	149	1190	0.94
E	Darlington Pt., NSW	S 6990	AF	8	34°34'	146°01'	90	SUB-HUMID	31.8	3.6	153	407	0.37
F	Forbes, NSW	S 6956	X	10	33°20'	147°59'	240	SUB-HUMID	33.3	3.5	133	557	0.00
G	Port Lincoln, SA	S 6975–79	AD	5	34°40'	135°50'	30	TEMPERATE	25.2	8.0	0	484	0.96
H	Petford, Qld	S 6953	U	5	17°20'	144°57'	520	SUB-MONSOON	34.8	9.3	9	786	−0.76
I	Mundiwindi, WA	S 7037	AK	4	23°05'	120°08'	305	ARID	38.1	5.2	65	263	−0.67
J	+9 mi. S. Agnew, WA	S 7106	AR	2	28°30'	121°00'	455	ARID	35.9	5.7	76	220	−0.33
K	Todd River, Alice Springs, NT	S 6788	I	10	23°38'	133°35'	580	ARID	35.2	3.8	102	267	−0.87
L	Onslow, WA	S 7030	AI	3	22°02'	115°01'	30	ARID	35.7	10.8	0	264	−0.05
M	Adavale Rd., Quilpie, Qld	S 6963	AB	3	26°35'	144°18'	190	SEMI-ARID	36.8	5.4	92	502	−0.81
N	Pentland, Qld	S 6945	R	1	20°35'	145°27'	455	SEMI-ARID	36.1	11.9	7	486	−0.75
O	Hughenden, Qld	S 6949	T	5	20°43'	144°21'	395	SEMI-ARID	37.4	8.1	7	486	−0.75
P	Wiluna, WA	S 7046	AM	10	26°34'	120°03'	490	ARID	37.2	4.9	24	225	−0.21
Q	Temple Bar Creek, Alice Springs, NT	S 6716	H	1	23°50'	133°50'	550	ARID	35.2	3.8	102	267	−0.87
R	20 mi. S. Agnew, WA	S 7052	AO	5	28°15'	120°40'	335	ARID	35.9	5.2	76	220	−0.33
S	Charleville Rd., Quilpie, Qld	S 6871	P	10	26°52'	144°49'	225	SEMI-ARID	36.8	5.4	92	502	−0.81
T	Thargomindah, Qld	S 6872	Q	4	27°58'	143°43'	120	ARID	36.7	5.8	37	272	−0.82
U	Three Springs, WA	S 7084	AQ	4	29°20'	115°35'	305	SUB-HUMID	35.4	7.0	0	394	0.87
V	Katherine, NT	S 6869	N	10	14°25'	132°15'	110	MONSOON	38.0	13.2	0	951	−0.83
W	Newcastle Waters, NT	S 7080	AP	10	17°30'	133°30'	215	SUB-MONSOON	39.1	11.1	0	456	−0.78

[1]) State Abbreviations: Victoria (Vict), South Australia (SA), New South Wales (NSW), Queensland (Qld), Western Australia (WA), Northern Territory (NT).
[2]) Institute of Forest Genetics lot number.
[3]) Number of trees represented in seed collection.
[4]) The correlation coefficient between mean monthly precipitation at Concord and at the provenance origin. Provenance with a positive or zero correlation have winter rainfall maximum, those with negative coefficients, a summer maximum.

The climate of the planting site at Concord, although located only 32 km east of San Francisco, is typical of many dry, inland areas of California. It is separated from the coast by a range of low hills. The long-term mean annual precipitation is 366 mm, almost all during the winter months (U.S. Department of Commerce, 1964). During the decade 1968 to 1978, precipitation ranged from 150 to 500 mm per year (U.S. Department of Commerce, 1969—1978). From May through September less than 20 mm of rain falls, with peak rainfall of 83 mm in January alone. The mean annual temperature is 14.2° C, ranging from 6.9° C for the coldest month to 20.7° C for the warmest (U.S. Department of Commerce, 1964). The mean daily minimum for January, the coldest month, is 2.9° C and the lowest records are about −7.2° C. The mean daily maximum for July, the warmest month, is 32.9° C and the highest recorded temperatures are about 45.6° C. The elevation of the planting site is 62 m, and soils tend to be deep, well-drained clay or loam of good agricultural quality.

The site was disced after the autumn rains began in 1975 and rototilled just prior to planting in February, 1976. Planting holes were prepared with a power-driven augur. Spacing was 3.05 m × 3.05 m. Grass in the first 9 blocks was controlled with simazine [3]), sprayed just after planting and again in September 1977. Block 10, later dropped from the analysis, was sprayed with devrinol. Open-ended, cardboard milk cartons were placed over seedlings to reduce damage from drying winds and from rodents. The area was disced in March or April of 1977, 1979, and 1980 for fire protection. Seedlings were hand-irrigated with about 4 liters of water per seedling at the time of planting and monthly in the first year during the dry season.

[3]) This publication does not represent a recommendation for the pesticides reported, nor does it imply that they have been registered by tie appropriate government agency.

The year of planting and the following year were two of the worst drought years on record in California.

The planting design was a randomized complete block with 10 blocks. In each block, each provenance was represented by a 4-tree row plot. Two of the 10 blocks were affected by competing herbaceous vegetation and had relatively high mortality (28%) compared to the others (7%). These two blocks were omitted from the analysis.

Survival and second-year heights were recorded in 1977 In June of 1981, 5.5 years after planting, measurements were taken on height and diameter at breast height, using a height-pole and diameter-tape. Relative volume was estimated by V = (diameter)^2 × (height), an index rather than a true measure of yield. Straightness was scored from 1 to 5. In scoring, an attempt was made to distribute the scores more or less normally; the average score, 3, occurs about 40% of the time, scores 2 and 4, 20% of the time each, and scores 1 and 5, 10% of the time each. Reproductive output was determined by estimating the proportion of the crown that supported capsules or flowers: if less than one-third of the crown supported capsules or flowers, it was considered to be light, one-third to two-thirds was medium, and over two-thirds was heavy. Forking was recorded in terms of the number of stems forked at the base and those forked higher in the tree. Basal forking is, perhaps, an indication of dieback from frost damage in the year of establishment.

Statistical analyses were made on the plot means with the Statistical Analysis System computing package (Helwig and Council, 1979). The analysis of variance and Duncan's

Table 2. — Provenance means for relative volume, height at 1.5 years and 5.5 years, dbh, straightness, and forking.

	Provenance	Volume (cu m)	Height 1.5 (m)	Height 5.5 (m)	DBH (cm)	Straightness	Trees forked at base (%)	Trees forked above base (%)
A	Lake Albacutya	.0684 a	1.32 abc	7.17 a	9.5 a	2.4 ghij	3.1 c	34.4 abcde
B	Hamilton	.0570 ab	1.23 bcde	5.97 bc	8.9 ab	2.6 efghij	3.1 c	52.0 ab
C	Nathalia	.0463 abc	1.58 ab	5.78 bcd	7.8 abc	2.9 cdefg	0.0 c	47.6 abc
D	Angaston	.0462 abc	1.15 bce	5.85 bcd	8.5 ab	2.4 ghij	6.3 bc	40.5 abc
E	Darlington Point	.0421 bcd	1.26 bcde	6.32 ab	7.6 abcd	2.6 efghij	12.5 abc	40.5 abc
F	Forbes	.0297 cde	0.98 cdef	5.40 bcde	7.2 bcde	2.5 efghij	9.4 abc	43.8 abc
G	Port Lincoln	.0270 cde	0.91 cdef	4.94 cdef	7.1 bcde	2.1 j	10.4 abc	58.0 a
H	Petford	.0253 cde	1.77 a	5.99 bc	6.2 cdef	3.2 bc	0.0 c	30.0 abcde
I	Mundiwindi	.0230 cde	0.91 cdef	4.98 cdef	6.0 cdef	3.4 ab	12.5 abc	22.9 bcde
J	Agnew	.0224 cde	1.02 cdef	4.85 def	6.1 cdef	3.0 bcdef	15.7 abc	20.9 cde
K	Alice Springs	.0215 cde	1.10 bcdef	4.54 ef	5.7 cdef	2.8 cdefgh	18.8 abc	7.3 de
L	Onslow	.0201 de	1.02 cdef	4.36 ef	6.0 cdef	2.5 fghij	24.9 abc	4.1 e
M	Quilpie	.0200 de	0.89 cdef	5.19 cdef	5.8 cdef	3.1 bcd	9.4 abc	25.0 bcde
N	Pentland	.0194 de	1.10 bcdef	4.85 def	5.8 cdef	2.6 efghi	3.1 c	52.0 ab
O	Hughenden	.0191 de	1.20 bcdef	4.79 def	5.8 cdef	2.8 cdefgh	15.6 abc	41.6 abc
P	Wiluna	.0180 de	0.72 f	4.99 cdef	5.5 cdef	3.8 a	6.3 bc	31.3 abcde
Q	Alice Springs	.0173 de	0.81 def	4.89 def	5.3 ef	3.0 bcde	6.3 bc	35.4 abcd
R	Agnew	.0170 de	1.26 bcde	4.82 def	5.5 def	2.9 cdef	16.6 abc	27.0 bcde
S	Quilpie	.0148 e	0.97 cdef	4.55 ef	5.5 def	2.2 ij	13.5 abc	32.1 abcde
T	Thargomindah	.0146 e	1.04 cdef	4.18 f	5.1 ef	2.3 hij	25.0 abc	21.9 bcde
U	Three Springs	.0124 e	0.77 ef	4.29 f	5.2 ef	2.7 defgh	6.3 bc	25.0 bcde
V	Katherine	.0107 e	0.98 cdef	4.36 ef	4.6 f	3.0 bcde	6.3 bc	25.0 bcde
W	Newcastle Waters	.0098 e	0.88 cdef	4.14 f	4.3 f	2.7 defgh	28.0 abac	27.1 bcde
	Error Std. Sev.	.0221	0.56	0.92	1.9	0.6	16.8	25.4

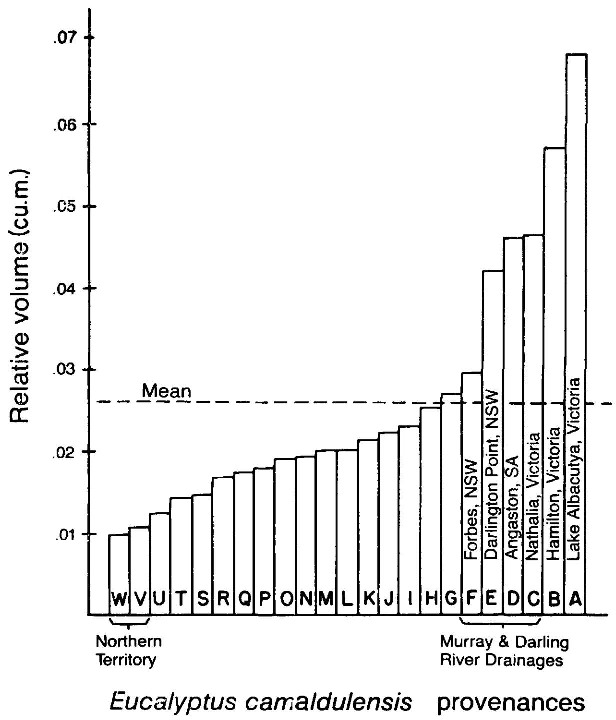

Figure 1. — Relative volume of 23 provenances of river red gum grown in California. Letters (A, B, . . . , W) refer to provenances listed in *Table 1.*

New Multiple Range Test were used to separate and rank provenances. SAS stepwise regression and cluster analysis (PROC CLUSTER) were used to describe provenance performance based on climatic variation at the provenance origin.

Results

Provenance mean height at 5.5 years ranged from 4.1 to 7.2 m, and relative volume from 0.010 to 0.068 cu m. The largest tree was 12.1 m tall and 19.8 cm dbh. Significant differences were found among provenances for volume, diameter, height, straightness, forking, and flowering (*Table 2* and *Fig. 1*)

Despite extensive overlap in volume growth, as indicated by Duncan's New Multiple Range Test, there seems to be a major gap that separates provenances from the Murray River system and adjacent areas in southeastern Australia, which rank as the top five, from the rest of Australia, which do poorly in comparison (*Table 2*). The top five provenances are Lake Albacutya, Hamilton, and Nathalia in Victoria, Angaston in South Australia, and Darlington Point in New South Wales. In the ranking of provenance means for diameter growth, the same five provenances are joined in the top group by two other provenances that are in or near the Murray River basin, one to the northeast at Forbes, New South Wales, and the other to the west at Port Lincoln, South Australia (*Table 2*). Provenances from more distant areas are inferior and do not differ significantly from each other. The provenances also fall into two groups for height, but there is more overlap (*Table 2*). Though trees from Port Lincoln are superior in diameter growth, they are not sufficiently superior in height growth to be included in the top group for volume production. The Petford provenance is superior in height growth but only average in diameter growth, resulting in only mediocre volume production. The Forbes provenance is marginally superior for both diameter and height but its mean volume production is sufficiently low to exclude it from the top group.

Two provenances from Western Australia, Wiluna and Mundiwindi, were the straightest, followed by the Petford and Quilpie sources from Queensland and the Katherine and Alice Springs sources from the Northern Territory. Although the provenances from southeastern Australia were superior for growth traits, they fall within the most crooked group, except for Lake Albacutya. It was average with regard to straightness, ranking 9 out of 23.

The provenances from southeastern Australia as a whole tend to have 12.5% or less basal forking. Eight of the remaining 17 provenances have more than 12.5% basal forking (*Table 2*). Basal forking may indicate susceptibility of young seedlings to freezing, and its low incidence in the provenances from southeastern Australia is reasonable because they originated from the latitudes with the coldest climates (*Table 1*). However, this group surpasses most other provenances in forking above the base (greater than 34.4% forked).

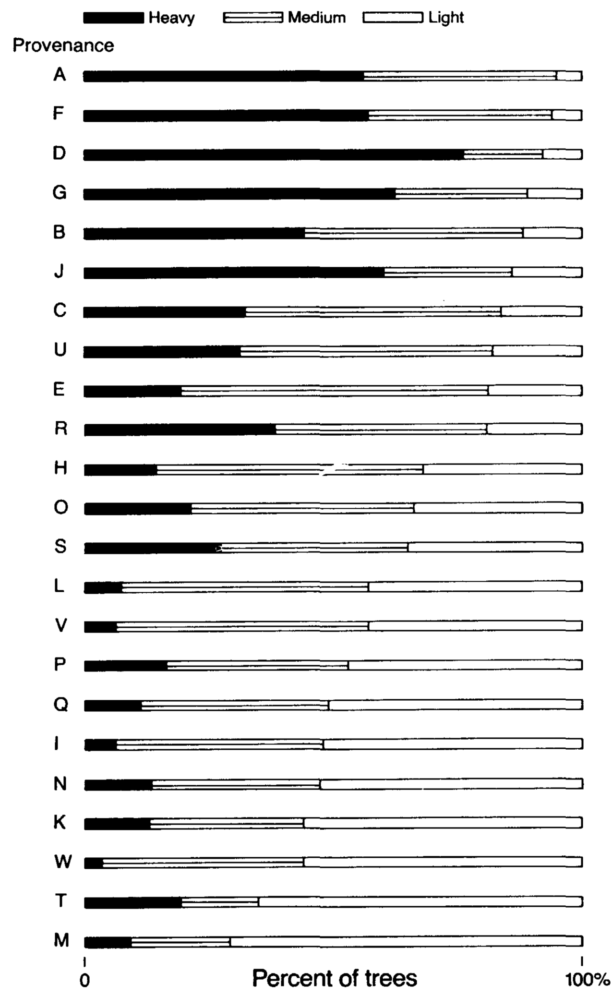

Figure 2. — Flowering classes of river red gum at 5.5 years of age. Letters (A, B, . . . , W) refer to provenances listed in *Table 1.*

Table 3. — Correlations among growth and form characteristics in river red gum, based on provenance means (in parentheses) and trees within provenances.

	Dbh	Height 1.5	Height 5.5	Straightness	Flowering	Basal Forking	Forking Above Base
Volume	0.88	0.66	0.79	-0.06	-0.37	-0.50	0.44
Dbh		--- 0.66	(0.93) 0.87	(0.33) -0.08	(-0.68) -0.34	(0) -0.04	(0.35) 0.12
Height 1.5			(0.59)	-0.13	-0.29	---	---
Height 5.5				(0.06) -0.22	(-0.51) -0.33	(0) -0.05	(0.04) -0.02
Straightness					(-0.53) 0	(0) 0.13	(0.84) 0.24
Flowering						(0) 0.02	(-0.65) -0.02
Basal Forking							(0) -0.03

Flowering was moderate to heavy in over 80% of the trees from southeastern Australia. Three provenances from Western Australia also had more than 80% of their trees in the moderate to heavy flowering category, while provenances Thargomindah and Quilpie from Queensland had less than 40% (*Fig. 2*).

Provenance means for height at 5.5 years were fairly well correlated with height after two growing seasons ($r = 0.59$; *Table 3*). All five of the provenances from southeastern Australia ranked near the top after only two seasons. Provenances from Agnew in Western Australia, Hughendon and Pentland in Queensland, and Alice Springs in the Northern Territory fell from the upper ranks over time, while those from Port Lincolm and Forbes improved significantly. The tallest provenance at 1.5 years was from Petford, but it subsequently dropped to third place.

Correlations among provenance means revealed only weak correlations between stem straightness or forking on the one hand, and growth on the other. The tendency was for negative associations. The combined association of crooked stems and forking with growth meant that the Murray River group had relatively poor form. The most heavily flowering provenances tended to be slower-growing. Correlations among individuals within provenances were generally similar in sign to those among provenance means but much weaker, suggesting few barriers to simultaneously selecting for superior growth and good form.

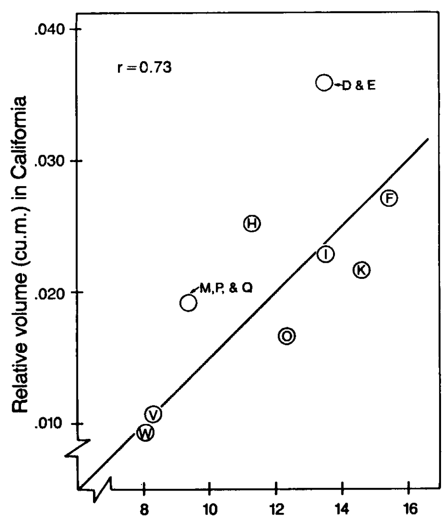

Figure 3. — Correlation between volume of river red gum provenances at 5.5 years in California and volume growth to 10 years in Pakistan. Letters (D, E, . . . , W) refer to provenances listed in *Table 1*.

Discussion

Provenances from the Murray and Darling River system and peripheral areas of Victoria, South Australia, and New South Wales had superior growth in our California planting, as well as on sites with summer drought in Greece (Panetsos, 1970), Israel (Karschon, 1974; Moreshet, 1981), Italy (Giordano, 1974), Morocco (Destremau *et al.*, 1973), Rhodesia (Barrett and Carter, 1976), Zambia, Spain, Algeria, and Portugal (Lacaze, 1977). Even in Pakistan, with a monsoon climate but with a winter precipitation maximum, results from an irrigated trial reported by Siddiqui *et al.* (1979) are similar to those in California. For 9 seed sources common to both tests, the correlation between relative volume in California and volume per hectare per year at 10 years of age in Pakistan was $r = 0.73$ ($P < 0.05$; *Fig. 3*).

The Lake Albacutya provenance is consistently outstanding in Mediterranean climates like California's, which may be attributed to its adaptation to a low summer rainfall regime. The Lake Albacutya population is located around the margin of a lake bed that is usually dry.

In our trial, the Lake Albacutya provenance had 20% greater volume than the Hamilton, Victoria provenance, the next best, which is on the Glenelg River system that flows southward away from the Murray River. The Lake Albacutya provenance was 161% better than the mean of all provenances and was 6 times or 598% better than the worst provenance, Newcastle Waters, Northern Territory. Even in the two replications omitted because of weed competition, the Lake Albacutya provenance performed outstandingly well. When those two replications were included, the Lake Albacutya provenance had 63% more volume than the next best provenance and was 200% better than the plantation mean. River red gum was recommended for California based on the growth of a seed source of unknown origin received from Brazil (King and Krugman, 1980). After 6 years at Concord, height of that provenance was 6.2 m and dbh was 6.6 cm compared to 7.2 m and 9.5 cm for the Lake Albacutya provenance after only 5.5 years, which included two of the severest drought years in California's recorded history.

It might be anticipated that the best provenances for California are those whose climate-of-origin correspond most closely in pattern to that at Concord. We calculated the correlation between monthly rainfall at a meteorological station representing each of the 23 provenance origins (HALL, 1972) with monthly rainfall at Concord during the decade 1969—1978 (U.S. Department of Commerce, 1969—1978), keeping in mind the opposition of the seasons in the Northern and Southern Hemispheres; i.e., January in California corresponds to July in Australia, February with August, etc. A simple correlation coefficient was then calculated from the 12 pairs of observations for each provenance and the Concord planting site. The correlations express the similarity between the rainfall pattern at Concord and the pattern at each of the 23 provenance locations. The correlations ranged from 0.96 between Concord and Port Lincoln, South Australia, a summer dry locality, to −0.87 between Concord and Alice Springs, Northern Territory, which has a summer rainfall maximum (*Table 1*). These rainfall pattern correlations (RPC) explained much of the variation among provenances in volume (*Table 4*). Nevertheless, the relationship did not appear smooth (*Fig. 4*). Provenances from areas with an RPC of zero or less did uniformly poorly. Provenances from areas with an RPC of circa 0.8, ranged from poor to exceptionally good, with no obvious relationship between volume and RPC. The poor performance of provenances such as Three Springs, Western Australia, with an RPC of 0.87, must be explained by other factors.

Table 4. — Correlations between provenance growth and form characteristics and the climate at provenance origin[1]).

	Volume	Dbh	Height 5.5	Basal Forking	Forking Above Base
Latitude	0.72***	0.79***	0.58**	-0.31	0.47*
Longitude	0.42*	0.40	0.51*	--	--
Elevation	-0.12	-0.09	0.05	--	--
Mean Maximum Temperature	-0.75***	-0.83***	-0.60**	0.44*	-0.60**
Mean Minimum Temperature	-0.46*	-0.50*	-0.46	--	--
Length of Precipitation	0.69***	0.70***	0.67***	-0.29	0.22
RPC	0.72***	0.76***	0.54***	-0.41	0.45

[1]) Significance indicated by: ***, P < 0.01; **, 0.01 < P < 0.05; *, 0.05 < P <0.10.

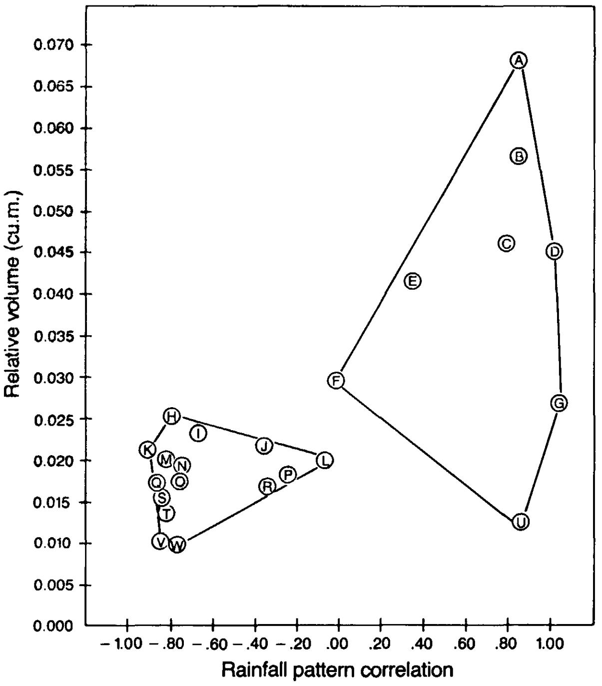

Figure 4. — Relationship of provenance mean volume of river red gum at 5.5 years in California to rainfall pattern correlation, a statistic correlating monthly rainfall at provenance origin with rainfall at the planting site. Letters (A, B, . . . , W) refer to provenances listed in *Table 1*.

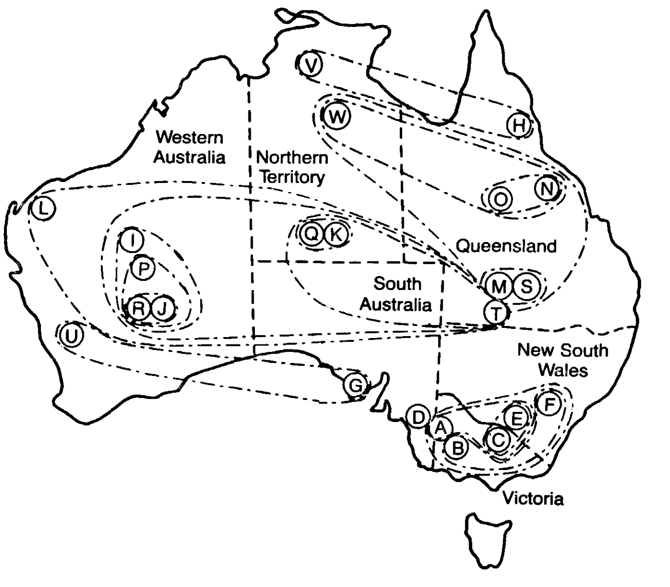

Figure 5. — River red gum locations in Australia, clustered by rainfall amount and pattern. Letters (A, B, . . . , W) refer to provenances listed in *Table 1*.

Cluster analysis was used to examine the 23 provenances for evidence of regions of similar rainfall patterns (*Fig. 5*). The degree of similarity among provenances was expressed by pairwise Euclidean distances that were based on the monthly rainfall values. It was arbitrarily decided to terminate the clustering process at six clusters because these clusters represented six easily described rainfall regions (*Fig. 5*), climates with a winter rainfall maximum and high, medium, or low total precipitation, and those with a summer maximum and either high, medium, or low total precipitation. Summer rainfall predominates in northern latitudes and winter rainfall in southern latitudes; the highest rainfall is found along the coast in both regions, while the lowest rainfall is found inland. Monthly rainfall for the provenances within each cluster were averaged and plotted over the twelve months (*Fig. 6*) for comparison with the rainfall pattern at Concord. The top seven provenances for growth at Concord were all in the clusters with highly positive RPC values, the three winter rainfall clusters.

Growth was also correlated strongly with provenance latitude, length of the frost period, and mean maximum temperature in the warmest month (*Figs. 7—9, Table 4*). However, the relationships with latitude and frost period, in particular, do not appear smooth (*Figs. 7, 8*). Provenances that did best in Concord came from temperate latitudes in Australia (> 32° S) with mainly winter rainfall (RPC > 0), long frost periods (> 120 days), and low summer maximum temperatures (< 34° C). For comparison, the planting site is located at 38°01' N, has a frost period of 125 days (U.S. Department of Commerce, 1974) and mean maximum temperature of the warmest month is 30.3° C (U.S. Department of Commerce, 1964).

It is apparent that the occurrence of winter rainfall and the length of the frost period at the provenance origin,

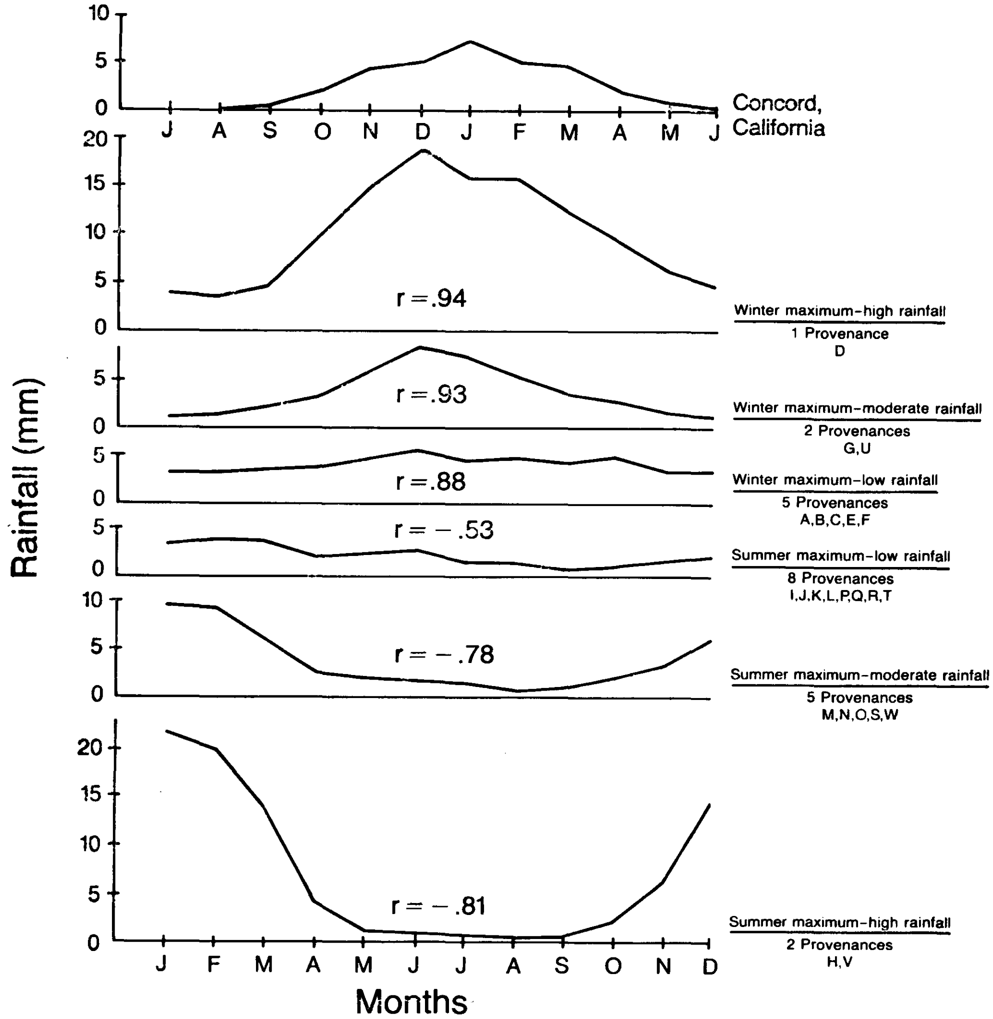

Figure 6. — Monthly rainfall for six river red gum provenance clusters and the Concord, California planting site. Letters (A, B, . . . , W) refer to provenances listed in *Table 1*.

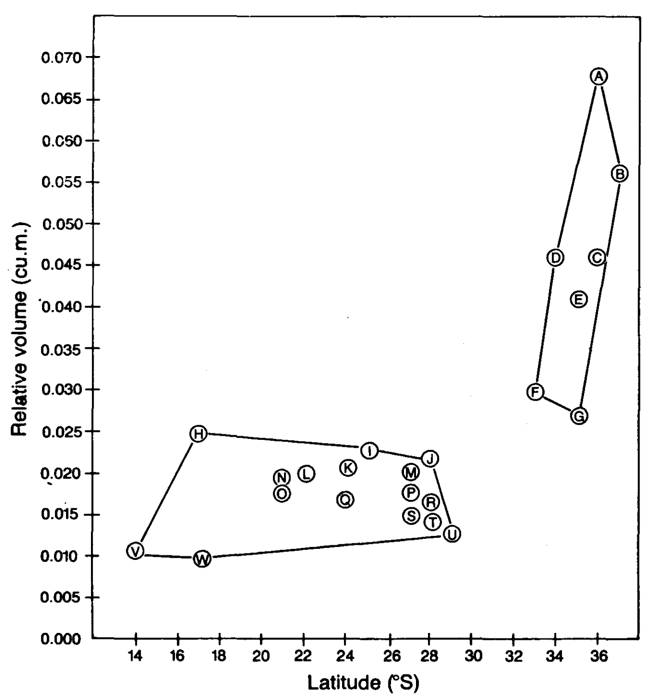

Figure 7. — Relationship of river red gum provenance mean volume at 5.5 years in California with latitude of origin. Letters (A, B, . . . , W) refer to provenances listed in *Table 1*.

when combined, account for most of the observed provenance variation in growth response at Concord, although both maximum temperature and latitude are predictive. Based on rainfall pattern correlation alone, the Three Springs, Western Australia provenance should do well at Concord. Its poor growth is rationalized with reference to the complete lack of frost in its native habitat.

It is reasonable to expect a greater degree of frost tolerance among the more southerly provenances, because some of the northern provenances never experience frost in their native regions. Frost is a definite factor at Concord; in December 1972, temperatures dropped below freezing for nine consecutive nights, reaching a low of −9° C (U.S. Department of Commerce, 1969—1978). Pryor and Byrne (1969) found that seedlings of southern provenances of river red gum were more frost resistant than northern provenances, but Awe and Shepherd (1975) claimed to find the opposite relationship.

It is conceivable that the southeast Australian provenances, which are adapted to striking deep roots rapidly, were successful in California because they were able to exploit deep moisture during the dry season. Provenances from Lake Albacutya and Nathalia, Victoria (Murray River drainage) germinated more vigorously than northern provenances when tested on a soil brought to field capacity and then left with no additional application of moisture, simulating a winter rainfall pattern (Awe *et al.*, 1976). They

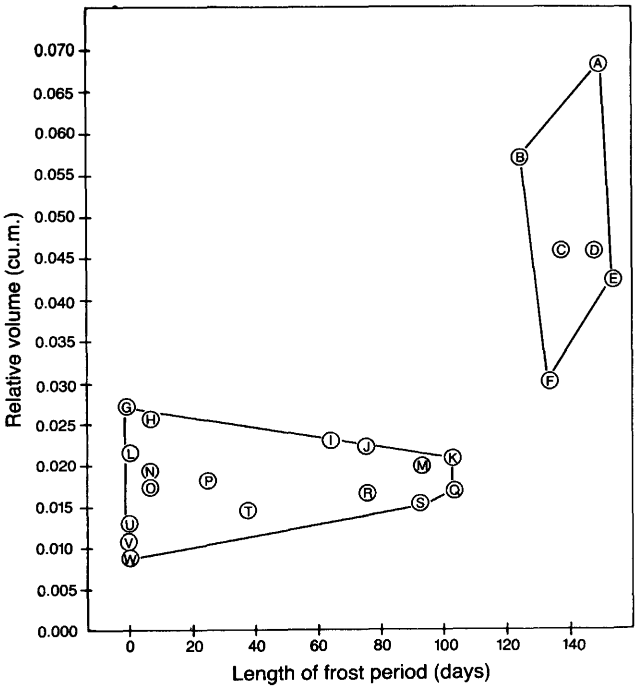

Figure 8. — Relationship of river red gum provenance mean volume at 5.5 years in California with length of frost period at the provenance origin. Letters (A, B, . . . , W) refer to provenances listed in *Table 1.*

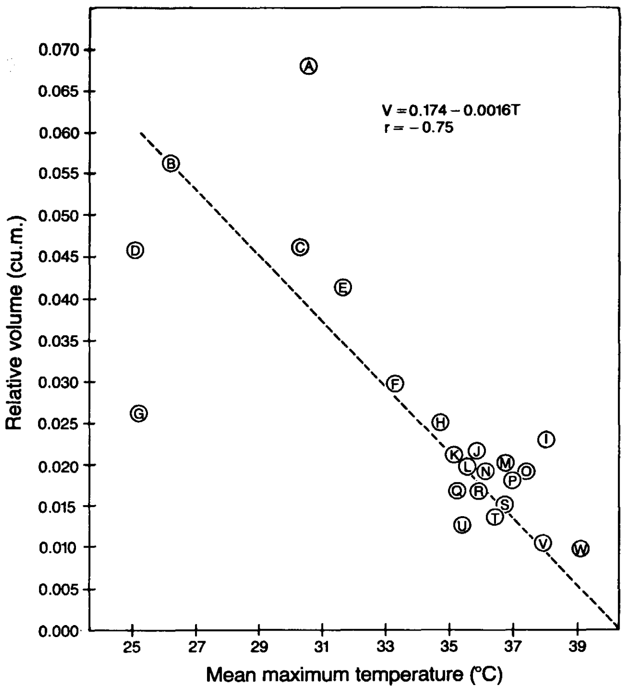

Figure 9. — Correlation of river red gum provenance mean volume at 5.5 years in California with mean maximum temperature in the warmest month at the provenance origin. Letters (A, B, . . . , W) refer to provenances listed in *Table 1.*

also produced the greatest root dry weight and number of roots (Awe *et al.*, 1976; Moreshet, 1981).

The provenance from Three Springs, Western Australia is adapted to the same rainfall pattern as the southeast Australian provenances, and yet it ranks third from the bottom in growth response. This may be due to the fact that there is no frost period in Three Springs, although the percentage of forking at and above the base, common signs of frost damage, are quite low and do not indicate that it has experienced cold damage. Trees from this provenance show an affinity for Western Australian flooded gum (*E. rudis* Endl.) and may be hybrids, accounting for their deviant behavior. Similarly, the Petford, Queensland provenance, which performs much better in height growth than expected for a provenance of its latitude, length of frost period, and rainfall pattern, shows evidence of introgression with forest red gum (*E. tereticornis* Sm.), according to Pryor and Byrne (1969).

Paradoxically, the Port Lincoln source, which is native to a frost-free climate, performs as well as most of the other winter rainfall provenances in diameter growth. The Port Lincoln provenance had a high root:shoot ratio, even higher than seedlings from Lake Albacutya, when grown in Israel (Sands, 1981), a factor that, perhaps, contributed to its success at Concord. The Port Lincoln provenance is unique: it consists of just a few trees growing on a limestone outcrop, an unusual site for the species. It grows well on soils of high pH in Pakistan (Quadri, 1983) and in Italy (Lacaze, 1977; Turnbull, 1973). It deserves attention for its potential on calcareous soils.

River red gum may not be the ideal species for all sites in California. For example, it was outproduced by manna gum (*E. viminalis* Deane et Maid.) on some sites (Standiford and Donaldson, 1982). However, when river red gum is planted, the Lake Albacutya provenance should be used, based on our results and its consistently superior performance in countries which, like California, have Mediterranean climates. It may also prove particularly valuable on saline soils (Sands, 1981). Its tendency to crookedness should be little deterrent for its use as fuel biomass. Other provenances should be introduced from the Murray River, Wimmera River, and adjacent drainages to increase the genetic base. More intensive sampling of this area may reveal provenances of equal or better performance than those already tested. Mother-tree identities should be retained in future testing to facilitate selection within provenance collections. Gains can almost certainly be made by selection within provenances, since Karschon (1974) has already demonstrated the existence of within-stand variation. Incidentally, the concurrence of results among countries with Mediterranean climates suggests that progress could be made by exchange of selected materials.

Acknowledgements

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Unsound Seeds in Conifers: Estimation of Numbers of Lethal Alleles and of Magnitudes of Effects Associated with the Maternal Parent

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Abstract

A model is developed for estimating the genetic load and the magnitude of maternal environmental effects in conifers from observed proportions of unsound seeds produced. Results indicate that maternal effects typically account for 5—30% of seed mortality. The average number of lethals carried is around 10, consistent with previous estimates. Observations relating to variances in proportions of unsound seeds lead to the conclusion that the average genetic load, and hence the mutation rate, probably varies over different forest locations. Implications for sampling methodology are presented.

Key words: unsound seed, lethal alleles, maternal effects, genetic load.

Zusammenfassung

In der vorliegenden Arbeit wird ein Modell entwickelt, welches bei Koniferen sowohl zur Schätzung der genetischen Belastung als auch zur Schätzung des Ausmaßes mütterlicher Umwelteffekte dienen kann. Hierbei wird der beobachtete Anteil der produzierten nicht lebensfähigen Samen genutzt. Die Ergebnisse weisen darauf hin, daß 5—30% der Samen-Mortalität durch Effekte des Samenelters verursacht werden. Die mittlere Anzahl von Letal-Allelen liegt bei 10, was früheren Untersuchungen nicht widerspricht. Beobachtungen hinsichtlich der Varianzen in den Anteilen nicht lebensfähiger Samen lassen den Schluß zu, daß die mittlere genetische Belastung, und daher die Mutationsrate, wahrscheinlich über die verschiedenen Standorte variiert. Folgerungen für die Stichprobennahme werden ebenfalls dargestellt.

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Introduction

Observations of high proportions of unsound seeds produced by conifers, especially following self-pollination, have led to surprisingly high estimates of the average number of recessive embryonic lethal alleles carried by individual trees (see FRANKLIN, 1970, for review). However, effects that are external to the embryonic genotypes also determine seed viability. Such effects as the age and vigor of the maternal parent, the water and nutrient supply to the female reproductive organs, and the maternal parent's resistance to pests all influence seed development. Although some interaction between the maternal support apparatus and the embryonic developmental capacity may exist, we wish to consider only those effects on female fecundity that can be considered to be independent of the embryonic genotype. In this paper we propose a model that incorporates embryonic genetic effects and maternal effects. We present analyses of data on proportions of unsound seeds for *Pinus taeda* and *Pinus virginiana* observed by BRAMLETT (personal communication) and by BRAMLETT and PEPPER (1974). Our results indicate that maternal effects typically account for 5 to 30 percent of the mortality and that the number of embryonic lethals is therefore lower than previously estimated. However, the estimated reduction is slight, typically no more than 10% relative to estimates obtained from models that do not incorporate maternal effects.

Previous investigations have placed the average number of lethals per tree at about 10, though there seems to be considerable variation around this mean number. For instance. SORENSEN (1969) estimated numbers of lethals in 35 sample trees to range from a low of 3 to a high of 27, with a mean number of 11.2 and a variance of 32. We shall argue that variances which exceed the associated means suggest that the lethal load varies from one location to another in the forest. This variation in lethal load implies that the forest from which the samples were drawn has a hetero-