

sing male gametes also primarily occurs in the polyembryonic stage. There is no good genetic evidence of effective competition in the haploid pollen stage up to fertilisation for conifers, even when selfing is involved.

A question not addressed by this study is whether the genotype of the female parent influences the selection between pollen gametes. In many crosses the male contributing to each embryo could not be determined unequivocally with the isozyme markers available. Studies in progress will hopefully rectify these problems and also allow sampling at a number of points between pollination and the maturation of the embryo.

The polymix mating design for progeny testing select clones is attractive because it costs less in terms of labour and resources than equivalent series of single-pair matings. If pollen parents are not equally represented in the progeny of each female parent then breeding value estimates may be biased. Similarly in a clonal seed orchard situation the selection already proven to exist against selfed embryos may operate against particular outcross combinations. On the positive side there is potential to look for correlations between gametophytic selection and sporophytic performance (TER-AVANESIAN 1978, OTTAVIANO *et al.* 1980): do the best pollen competitors exhibit the best adult growth?

We conclude that our results show sufficient evidence of non-random contribution of pollens to viable seed formation to warrant further study. In particular, results should be obtained for a larger sample of pollen donors and seed parents. Nevertheless, in this study at least, such effects are not so strong as to affect the utility of the polymix mating design in practical tree breeding. One approach to overcome the problem of non-random contribution would be to use a large number of pollens in mixture, thereby reducing the influence of any one male with unusual competitive ability. The disadvantage of such a solution would be the reduced chances of identification of male parents of superior progeny using genetic markers.

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Provenance Productivity in *Eucalyptus camaldulensis* Dehnh. and its Implications to Genetic Improvement in the Savanna Region of Nigeria

By G. O. OTEGBEYE¹

Forestry Research Institute of Nigeria

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Abstract

A 13-year provenance trial of *Eucalyptus camaldulensis* DEHNH. at Afaka was analysed for height and girth growth.

¹ Principal Research Officer, Forestry Research Institute of Nigeria, Savanna Forestry Research Station, P. M. B. 1039, Samaru-Zaria, Nigeria.

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The best provenances were those from the northern parts of Australia while the poorest came from the south. Petford provenance outranked all the other provenances in both characteristics examined. It was closely followed by Katherine provenance.

The variation pattern tends to suggest the existence of two separate eco-physiological groups in the species. There were, however, detectable differences among members of the same group. The provenances of *Eucalyptus camaldulensis* from the northern parts of Australia are better adapted to the ecological situation of the Savanna region of Nigeria.

The extremely high variability in height and girth growth among the provenances examined indicates that both provenance and individual tree selection methods can be used in the genetic improvement of this species. Girth growth will be more responsive to genetic improvement than height growth.

The variation pattern obtained was similar to the one reported by JACKSON and OJO (1973) indicating that early results from a provenance trial of such highly variable provenances can be used to predict relative performance at more advanced ages.

Key words: *E. camaldulensis*, provenance, height, girth, selection, genetic improvement.

Zusammenfassung

Es wurde ein 13 Jahre alter Provenienzversuch von *Eucalyptus camaldulensis* DEHNH. in Afaka auf Höhen- und Dickenwachstum hin, untersucht. Zwischen den 16 untersuchten Provenienzen gab es bezüglich der beiden Wachstumsmerkmale hoch signifikante Unterschiede. Die Herkunft trug zu 28,3% bei der Höhe und zu 27,5% beim gemessenen Umfang in Brusthöhe zur Gesamtvariation bei. Einzelbaumunterschiede machten bei der Höhe 58% und beim Umfang in Brusthöhe 65,6% der Variation aus.

Die besten Provenienzen stammten aus dem nördlichen Australien, während die schlechtesten aus Südaustralien kamen. Die Herkunft Petford war für beide Merkmale die beste, dichtgefolgt von der Herkunft Katherine.

Das Variationsmuster tendierte dahin, bei dieser Art die Existenz zweier separater ökophysiologischer Gruppen anzunehmen. Jedenfalls gab es nachweisliche Unterschiede zwischen Mitgliedern der gleichen Gruppe. Die Provenienzen von *Eucalyptus camaldulensis* aus Nordaustralien sind an die ökologische Situation in der Savannenregion Nigerias besser angepaßt.

Die extrem hohe Variabilität beim Höhen- und Dickenwachstum bei den untersuchten Herkünften zeigte, daß sowohl die Auswahl von Herkünften, als auch die Selektion von Einzelbäumen zur genetischen Verbesserung dieser Art herangezogen werden kann. Dabei ist das Dickenwachstum für die genetische Verbesserung mehr verantwortlich als das Höhenwachstum.

Das erhaltene Variationsmuster war dem von JACKSON und OJO (1973) berichteten ähnlich, wobei es anzeigt, daß Frühstest-Resultate eines Provenienzversuches mit derart variablen Provenienzen benutzt werden können, um die relative Leistungsfähigkeit im fortgeschrittenen Alter vorzusagen.

Introduction

The Savanna region of Nigeria covers a total area of about 777,000 square kilometres. A wide range of soil types and climatic conditions therefore exists within the region. Generally, annual rainfall decreases from south to north. Five major vegetation zones can be identified within the region. These zones include (and in order of dryness) Derived savanna, Southern Guinea Savanna, Northern Guinea Savanna, Sudan Savanna and Sahel Savanna. There is no

sharp transition between the zones but they are not homogeneous (KEMP, 1969).

Past cultivation, fire and grazing have very much affected the natural vegetation of the region. Thus it is incapable of meeting the rapidly increasing requirements for all classes of forest products. The tree species indigenous to this region are very slow growing, hence introduction trials of exotic tree species together with planting trials of selected indigenous species were started on some savanna sites many years ago (KENNEDY, 1932; AINSLIE, 1935). The scope of the trial programmes has since been increased. KEMP (loc. cit.) gave the objectives of the programme for each of the five savanna ecological zones earlier on identified. Generally, the objectives include identifying fast-growing tree species for the production of fuelwood, building poles, timber and pulp.

Through the various species trials, *Eucalyptus camaldulensis* was identified as one of the fast-growing exotic tree species that can be used for future plantations in the savanna region of Nigeria (KEMP, 1969). It has also been identified as one of the most successful fast-growing species in the Sudan Savanna Zone (KEMP, 1970). It, however, grows relatively poorly in the more southernly parts of the country, especially in the Derived Savanna Zone. Plantations of this species have, however, been established on the Jos Plateau.

Eucalyptus camaldulensis, which is loosely referred to as the 'river red gum', is naturally found in the Australian mainland where it occurs throughout apart from the southern parts of Western Australia and a broken fringe along the east coast (HALL *et al.*, 1970). Outside Australia, it is one of the most planted species. In its natural habitat, it is a species characteristic of water courses (PRYOR and BYRNE, 1969) where it produces a moderately hard and useful timber. It tolerates a wide range of environmental conditions.

A great amount of morphological variation exists in *Eucalyptus camaldulensis*. This allowed BLAKELY (1955) to identify the existence of five varieties in the species. However, PRYOR and BYRNE (1969) indicated that many more of such varieties could be added if one were to consider the variation as such. Instead, they suggested the existence of two different forms, those found in the northern parts of Australia belonging to one form and the Southern population belonging to the other. However, variation still exists within each form (BANKS and HILLIS, 1969; BURLEY *et al.*, 1971; KARSCHON, 1967).

A seed source trial of *Eucalyptus camaldulensis* was undertaken in 1967 in the savanna region of Nigeria. The entire study has been described by JACKSON and OJO (1973). Early results so far published indicate that Petford and Katherine provenances are best suited to the savanna region of Nigeria except where plantations are irrigated. Mundiwindi provenance was identified to be best for irrigated plantations in arid environments.

In this paper, the *Eucalyptus camaldulensis* provenance trial at Afaka is analysed through the thirteenth year of its establishment. An attempt is made to relate the results so obtained to the fifth-year growth at all the trial locations and thereby make appropriate recommendation for plantation establishment in the savanna areas of Nigeria. The implications of the results to genetic improvement of the species are also discussed.

Table 1. — Sources of sixteen *Eucalyptus camaldulensis* seed lots tried at Afaka.

Seed Source	Latitude	Longitude	Altitude (m)	Rainfall (mm)	Max. Temp. ¹ °C	Minimum Temp. ² °C
Petford, Q	17° 20' S	144° 57' E	518	716	34.8	9.3
Bullock Creek, Q	20° 49' S	144° 48' E	327	463	37.4	8.0
Katherine, N.T.	14° 20' S	132° 15' E	110	958	38.0	13.2
Eulo, Q	28° 04' S	145° 41' E	190	320	36.0	11.0
Mundiwindi, W.A.	23° 05' S	120° 08' E	300	269	38.0	5.2
Willuna, W. A.	26° 34' S	120° 03' E	490	249	37.2	4.8
Tennant Creek, N.T.	19° 30' S	134° 0' E	340	422	37.6	11.1
Newcastle Waters, N.T.	17° 30' S	133° 30' E	210	483	39.1	11.1
Darlington Point, N.S.W.	34° 34' S	141° 01' E	90	385	31.8	3.6
Alice Springs, N.T.	23° 38' S	133° 35' E	580	252	35.2	3.8
Bourke, N.S.W.	30° 13' S	145° 58' E	110	919	36.7	4.9
Walpole Island, N.S.W.	34° 10' S	141° 30' E	90	247	28.3	5.4
Silverton, N.S.W.	31° 54' S	141° 13' E	210	234	32.5	5.1
Woolpooer, V.	37° 0' S	142° 0' E	300	606	26.3	4.4
Mengers Hill, S.A.	34° 30' S	139° 0' E	610	1182	25.0	4.8
Lake Albacutya, V.	35° 50' S	142° 0' E	70	347	30.7	3.8

1. Average daily maximum temperature of warmest month.

2. Average daily minimum temperature of coolest month.

Materials and Methods

Seed Sources. Sixteen *Eucalyptus camaldulensis* seed sources were represented in the study in each of seven trial locations. Information on the sources is given in Table 1. The seed lots were supplied by the Centre National de Recherches Forestieres, Nancy, and were among collections made by the Forestry and Timber Bureau, Canberra, Australia (JACKSON and OJO, 1973).

Nursery Procedure. The seeds were sown in March, 1967 in seed trays at Savanna Forestry Research Nursery, Samaru. Four weeks after germination, the resultant seedlings were pricked out into polythene pots of height 20 cm and diameter 7.5 cm. A potting medium of 4 parts river sand and 3 parts of rotted cow manure was used while 3.5 kg 15-15-15 compound fertilizer and 360 gm dieldrin 2% dust was added to every cubic metre of the medium.

Planting Sites. The seedlings were planted in July, 1967 at Afaka, Kabama (Northern Guinea Zone) and Yambawa (Sudan Zone) while planting was done in August, 1967 at TaHoss, Vom, Barakin Ladi (Jos Plateau) and Malam Fatori (Lake Chad Basin). The trials on the Jos Plateau were sited in the areas typical of the Derived Savanna vegetation while that of Malam Fatori is an example of a very arid area. Information on the trial locations is given in Table 2.

The experimental design used in each trial was a balanced lattice with five replications, except in the Vom trial where a randomized block design with four replications was used. This was due to shortage of seedlings for that trial location (JACKSON and OJO, 1973). There were thirty-six trees per plot.

Measurements. Only the trial at Afaka was assessed at 13 years. The results obtained were, however, compared with the reported results for the entire trial through the fifth year. Sixteen trees per plot were assessed for height and girth-at-breast height. Height was measured with Haga altimeter while girth was measured with a tape. The sixteen measurement trees were normally restricted to the inner trees in each plot. However, where it was not possible to obtain such number of trees, appropriate number of trees were selected at random from outside ones in that particular plot to make up the required sixteen trees.

Data Analysis. Although the experimental design was that of a balanced lattice with five replications per plot, the analysis followed that of a randomized block design. The conditions for a balanced lattice design were no longer obtainable at the trial location. Two of the sixteen provenances were well represented in only three of the original five blocks while the remaining fourteen were well represented in all the five blocks. Analysis of variance had to be performed in two stages because of the situation stated above and so as to cover all the blocks and provenances.

The first stage of the analysis involved all the fourteen provenances that were represented in all the five blocks. The second stage involved the best two and the worst two provenances obtained from the first stage of the analysis and the two provenances (Petford and Lake Albacutya) that were represented in only three blocks and therefore had to be excluded from the first analysis. For the purpose of the first analysis, five blocks were used while, obviously, only three blocks were considered in the second analysis.

Table 2. — Trial locations of the *Eucalyptus camaldulensis* provenances tested in the Savanna region of Nigeria.

Location	Latitude	Longitude	Altitude (m)	Rainfall (mm)	Maximum Temp. ¹ °C	Minimum Tem. ² °C
Afaka, Kaduna State	10° 37' N	7° 17' E	600	1290	35	15
Kabama, Kaduna State	11° 8' N	7° 42' E	640	1120	36	14
TaHoss, Plateau State	9° 38' N	8° 44' E	1250	1350	31	13
Barakin Ladi, Plateau State	9° 32' N	8° 54' E	1300	1350	31	13
Vom, Plateau State	9° 43' N	8° 47' E	1250	1380	31	13
Yambawa, Kano State	12° 10' N	9° 0' E	400	840	38	13
Malam Fatori, Borno State	13° 35' N	13° 22' E	300	214 ³	40 ³	15 ³

1. Mean maximum temperature of hottest month.

2. Mean minimum temperature of coldest month.

3. Source: Sikes, 1972.

In both analyses, Random Model was used, that is all components were assumed random except the mean. Expectation of mean squares was determined following the rules described by SCHULTZ (1955). The format used is shown in Table 3.

Results and Discussion

A highly detectable degree of variation was found among the sixteen provenances tested for height and girth growth (Tables 4 and 5). Bullock Creek provenance had the best performance among the fourteen provenances analysed in the first analysis (Table 6). However, when Duncan's Multiple range test was used to test for significant differences among the provenance means, there was no detectable difference between the means of Bullock Creek

and Katherine provenances for the two growth characteristics. In the second stage of the analysis involving the best two provenances (Bullock Creek and Katherine), the worst two provenances (Wohlpooper and Mengers Hill) obtained from the first analysis, and the Petford and Lake Albacutya provenances, Petford provenance was found to excel the other provenances in both height and girth growth. Mengers Hill still had the least performance.

Generally, the provenances from the northern parts of Australia performed better than those from the southern parts of the country. This trend might be due to the climatic differences among the two groups, the northern parts having predominantly summer rainfall while the southern parts have winter rainfall. The general experience in the introduction of exotic trees to Nigeria is that

Table 3. — Form of analysis of variance. Random Model.

Source	df	Mean Square	Expected Mean Square
Block (b)	b-1	MS _b	$\sigma_e^2 + t\sigma_{pb}^2 + tp\sigma_b^2$
Provenance (p)	p-1	MS _p	$\sigma_e^2 + t\sigma_{pb}^2 + tb\sigma_p^2$
Provenance x Block	(p-1)(b-1)	MS _{pb}	$\sigma_e^2 + t\sigma_{pb}^2$
Tree (Provenance x Block)	t(p-1)(b-1)	MS _{t(pb)}	σ_e^2

a

b = number of blocks

p = " " provenances

t = " " trees/plot

$$\sigma_{pb}^2 = \frac{MS_{pb} - MS_{t(pb)}}{t}$$

$$\sigma_p^2 = \frac{MS_p - MS_{pb}}{tb}$$

Table 4. — Analysis of variance for height and girth-at-breast height (GBH) for 13-year-old trees of fourteen provenances of *Eucalyptus camaldulensis* tested at Afaka.

Source of variation	df	MEAN SQUARE ^a	
		HEIGHT	GBH
BLOCK	4	310.714 **	1376.99 **
PROVENANCE	13	648.91 **	5220.02 **
PROVENANCE X BLOCK	52	57.62 **	329.41 **
ERROR	980	17.24	160.79

^a ** Statistically significant at 1% level.

almost without exception species from predominantly winter rainfall areas do very badly compared to those from areas with summer rainfall (JACKSON and OJO, 1973). The species from a particular rainfall pattern can be expected to have become adapted to that type of rainfall pattern through the process of natural selection that have probably operated over a long period of time.

The results tend to confirm the existence of eco-physiological differences between the northern and southern populations of *Eucalyptus camaldulensis*. This lends credence to the existence of the two separate forms suggested by PRYOR and BYRNE (1969). However, there were detectable differences among provenances within each group. Petford

Table 5. — Analysis of variance for height and girth-at-breast height (GBH) for 13-year-old trees of six provenances of *Eucalyptus camaldulensis* tested at Afaka.

Source of variation	df	HEIGHT	GBH
BLOCKS	2	44.14 *	412.99
PROVENANCES	5	1506.96 **	7029.34 **
PROVENANCE X BLOCK	10	32.23 **	447.32 **
ERROR	252	11.84	156.58

^a * Statistically significant at 5% level.
** Statistically significant at 1% level.

provenance was found to outrank all other provenances examined for the two growth characteristics, attaining a mean 13-year height of about 26.4 m and a mean girth of about 69.5 cm. It was followed by Katherine provenance with a mean 13-year height of about 23.1 m and a mean girth of 67.5 cm. Katherine provenance also has a better form than Bullock Creek (JACKSON and OJO, 1973).

A similar variation pattern has been reported on 5-year-old trees of the same study (JACKSON and OJO, loc. cit.). The juvenile pattern of variation among the provenances has therefore been confirmed. This suggests the existence of strong juvenile-mature correlation with respect to growth characteristics in this species. Thus early results from a

Table 6. — Range and mean values of height and girth-at-breast height (GBH) of 13-year-old trees of sixteen provenances of *Eucalyptus camaldulensis* tested at Afaka.

PROVENANCE	HEIGHT (m)		GBH (cm)	
	RANGE	MEAN	RANGE	MEAN
Petford, Q.	13-37	26.4(5.3) ^a	31-109	69.5(16.6)
Bullock Creek, Q.	13-31	22.0(7.1)	24-100	66.9(14.8)
Katherine, N.T.	13-30	21.6(3.9)	36-92	65.6(12.4)
Eulo, Q.	11-33	20.0(5.7)	27-96	57.5(15.5)
Mundiwindi, W.A.	9-27	18.5(4.1)	35-85	56.7(12.1)
Willuna, W.A.	8-28	17.7(4.6)	17-93	56.0(14.9)
Tennant Creek, N.T.	10-26	17.7(3.2)	31-85	56.8(12.3)
Newcastle Waters, N.T.	9-26	17.5(3.4)	27-95	56.4(13.4)
Darlington Point, N.S.W.	9-25	16.7(3.6)	25-76	45.3(12.1)
Alice Springs, N.T.	8-27	16.5(3.9)	33-87	53.3(13.3)
Bourke, N.S.W.	7-26	16.4(3.8)	22-76	45.4(12.1)
Walpole, N.S.W.	7-23	14.3(3.8)	23-85	41.9(13.2)
Silverton, N.S.W.	6-25	14.2(7.1)	24-91	50.7(15.1)
Lake Albacutya, V.	6-23	13.7(3.3)	26-69	46.7(9.1)
Wohlpooer, V.	6-19	12.9(3.1)	18-63	40.6(9.4)
Mengers Hill, S.A.	7-24	12.4(3.5)	24-89	43.8(12.7)

^aStandard deviation in parenthesis.

provenance trial can be used to predict relative performance at later ages.

Based on the first analysis involving fourteen provenances, it was found that variation among the provenances contributed about 28.3 per cent while differences among trees contributed about 58.0 per cent to the observed variation in height growth. For girth growth, provenance variation accounted for about 27.5 per cent while variation among trees accounted for about 65.6 per cent of the observed variation.

Differences among the provenances were more expressed in girth than in height growth. Genetic variance (σ^2_p) in girth was more than eight times greater than that of height growth. The variance among trees was also greater in girth than in height growth. This shows that in a genetic improvement programme involving growth characteristics, more gain will be expected in girth than in height.

Implications to Genetic Improvement of *Eucalyptus camaldulensis* in the Savanna Region of Nigeria

The results obtained indicate that great genetic differences exist among the provenances of *Eucalyptus camaldulensis* tested for height and girth growth. It has also been reported that variation in stem form exists among provenances of the species (JACKSON and OJO, 1973; KEMP, 1970). All these show that genetic gain in volume production and form is possible through proper provenance selection. A high degree of variation among trees within provenance was also obtained. For height growth, variation among trees contributed about 58.0 per cent to the observed variation while about 65.6 per cent of the observed variation in girth was accounted for by variation among trees. In each case the value was more than double that of provenance variation. Although no formal assessment was made of stem form and crown characteristics it was observed that there was some degree of variation among individual trees within provenance for these characteristics. The existence of these variations among trees offers a great opportunity for further improvement of the species following a careful provenance selection.

Since evidence of strong juvenile-mature correlation with respect to growth of *Eucalyptus camaldulensis* has been established for the Afaka site, recommendations based on 5-year growth of the provenances (JACKSON and OJO, 1973) can still be said to be valid at age 13 years. Thus provenances recommended for planting in the different savanna zones are as follows:

- (a) Sudan zone — Katherine provenance.
- (b) Northern Guinea Zone — Petford followed by Katherine provenance.
- (c) Jos Plateau — (Petford), Katherine provenance.
- (d) Lake Chad Basin (where the experiment was conducted under irrigation because of the arid condition there) — Mundiwindi followed by Wohlpooper provenance.

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Nutrient Use Efficiency of Clones of *Picea sitchensis* and *Pinus contorta*

By L. J. SHEPPARD and M. G. R. CANNELL

Institute of Terrestrial Ecology, Bush Estate,
Penicuik, Midlothian, EH26 OQB, Scotland

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Summary

The total nutrient uptake of 8-year-old clones of *Picea sitchensis* and *Pinus contorta* were determined from the nutrient concentrations and dry weights of all above-ground parts, plus fallen needles. Seven clones (raised from cuttings) were harvested of each species at a lowland fertile site, and needle samples were analysed from the same clones growing at an upland peaty-gley site.

P. sitchensis had a relatively high demand for Ca, K and P compared with *P. contorta* and *P. contorta* had a high demand for Mg. N concentrations were similar in both species.

Clonal differences of 10–30% were found in 'nutrient use efficiencies' defined as the amounts of dry matter produced over the 8 years per unit of nutrient taken up (omitting roots). These differences were related to three tree characteristics. (a) Clones with inherently low needle nutrient concentrations had high efficiencies, because the needles took over 50% of most of the nutrients absorbed. (Clonal differences in needle nutrient concentrations were consistent between sites). (b) Clones which partitioned a large proportion of dry matter to stems (i.e. were sparsely branched) had high nutrient use efficiencies, because the nutrient requirement for a unit increment in stem dry weight was usually less than half of that for a unit increment of branches, and only about 5–15% of that for a