

KIN, M.: Rare alleles as indicators of gene flow. *Evolution* 39: 53–65 (1985). — SORK, V. L.: Examination of seed dispersal and survival in red oak, *Quercus rubra* (Fagaceae), using metal tagged acorns. *Ecology* 65: 1020–1022 (1984). — STAM, P.: The evolution of reproductive isolation in closely adjacent plant populations through differential flowering time. *Heredity* 50: 105–118 (1983). — TIGERSTEDT, P. H. A.: Study on isozyme variation in marginal and central populations of *Picea abies*. *Hereditas* 75: 47–60 (1973). — VINCENT, J. P.: Interaction entre les micromammifères et la production de semences forestières. *Ann. Sc. Forest.* 34: 77–87 (1977). — WEIR, B. S. and COCKERHAM, C. C.: Estimating F-statistics for the analysis of population structure. *Evolution* 36: 1358–1370 (1984). — WRIGHT, S.: Evolution in mendelian populations. *Genetics* 16: 97–159 (1931). — WRIGHT, S.: Isolation by distance under diverse systems of mating. *Genetics* 31: 39–59 (1946). — WRIGHT, S.: The genetical structure of populations. *Ann. Eugenics* 15: 323–354 (1951). — WRIGHT, S.: The interpretation of population structure by F-statistics with special regard to systems of mating. *Evolution* 19: 358–420 (1965). — WRIGHT, S.: Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. Univ. of Chicago Press, Chicago. 580 p. (1978).

variation has been observed in *E. grandis*, and successful selection programs have been reported (Rockwood and MESKIMEN, 1981; MESKIMEN, 1983). Limited information is available on the genetic variation for coppicing ability in *E. grandis*. Significant genetic variation in this trait has been reported by GEARY *et al.* (1983). In southern Florida, four progenies at two different sites showed no significant differences in coppicing ability (Rockwood and GEARY, 1982).

## Breeding Strategies for Coppice Production in a *Eucalyptus grandis* Base Population with Four Generations of Selection

By K. V. REDDY and D. L. ROCKWOOD

Department of Forestry, University of Florida,  
Gainesville, Florida, USA

(Received 25th July 1988)

### Summary

A genetic base population (GPOP77) of *Eucalyptus grandis* (HILL) ex MAIDEN planted in July 1977 with 529 families representing four generations of selection was partially harvested in August 1978. Regrowth through December 1983 was evaluated to assess genetic improvement potential for coppice productivity.

Four generations of selection have produced impressive genetic gains. At 64 months after harvest, first-, second-, third- and fourth generation families averaged 7.04 dm<sup>3</sup>, 21.54 dm<sup>3</sup>, 25.91 dm<sup>3</sup> and 40.16 dm<sup>3</sup> per tree, respectively. Fourth-generation families also had the best frost resilience and coppice quality. In individual tree volume, the best trees were more than three times larger than the fourth generation trees at 64 months after harvest. Provenances from Queensland, Australia, grew better than other sources studied. High individual and family tree heritabilities were observed for all growth traits at different ages.

The potential inbreeding depression resulting through mating of related families was examined. The mean inbreeding coefficients in the offspring of all possible matings of selected individuals for six different selection strategies ranged from 0 to 1%. The predicted genetic gains, adjusted for any inbreeding through relatedness and selfing, were high. The highest gain of 90% was predicted by the selection of three trees from the top 100 families.

**Key words:** *Eucalyptus grandis* (HILL) ex MAIDEN, genetic variation, frost resilience, heritabilities, inbreeding, genetic gains, provenance.

### Introduction

Although eucalypts occupy perhaps one-fifth of the world's plantations (LOGAN, 1967), only a small part of the world's tree breeding effort has been devoted to this genus. In Florida, eucalypts were first planted in 1878, and industrial plantations were first established in 1972 (GEARY *et al.*, 1983). The ability of *E. grandis* to coppice, combined with its exceptional growth rate in low quality soils, makes it an attractive species for short rotation biomass production.

*Eucalyptus grandis* has revealed significant provenance variation around the world (ASSIS and BRUNE, 1983; ADES and BURGESS, 1983; DARROW and ROEDER, 1983; KING, 1983; BORGES and BRUNE, 1983). In Florida, appreciable genetic

Due to the absence of annual resting buds in *Eucalyptus*, indeterminate shoots grow continuously year round (FAO, 1979). In the southern United States temperatures drop suddenly from well above freezing to well below (HUNT and ZOBEL, 1978). This sudden drop has a devastating impact on the survival of trees. Of all the *Eucalyptus* species examined in Florida, *E. grandis* was notably frost sensitive (HUNT and ZOBEL, 1978). MESKIMEN *et al.* (1987) found significant relationship ( $r = 0.33$ ) between tree height and frost resilience among clones of *E. grandis*.

In recent years research has been done on the pollination biology of the eucalypts. The amount of natural selfing occurring in eucalypts is higher than the 7% that is reported for most pines (WRIGHT, 1976). Published estimates for the degree of natural selfing occurring in eucalypts vary somewhat among species: 24% in *E. obliqua* L'HERIT. (BROWN *et al.*, 1975), 37% in *E. pauciflora* SIEB. ex SPRENG (PHILLIPS and BROWN, 1977), 23% in *E. delegatensis* R. T. BAK. (MORAN and BROWN, 1980) and 18% in *E. stoatei* C. A. GARDN. (HOPPER and MORAN, 1981). In *E. grandis* ELDRIDGE (1978) reported 20% to 40% selfing, and VAN WYK (1981) estimated this to average about 30%. In *E. grandis* HODGSON (1974, 1976, 1977) studied the extent of inbreeding depression for inbred individuals where he observed height of selfed progenies to be 8% to 49% less than that of out-crossed progeny.

### Materials and Methods

*Eucalyptus grandis* in Florida constitutes a landrace developed through four generations of selection and progeny testing in local environments (GEARY *et al.*, 1983) (Figure 1). GPOP77, the fourth-generation base population planted in July 1977, had a total of 529 (144 first-genera-

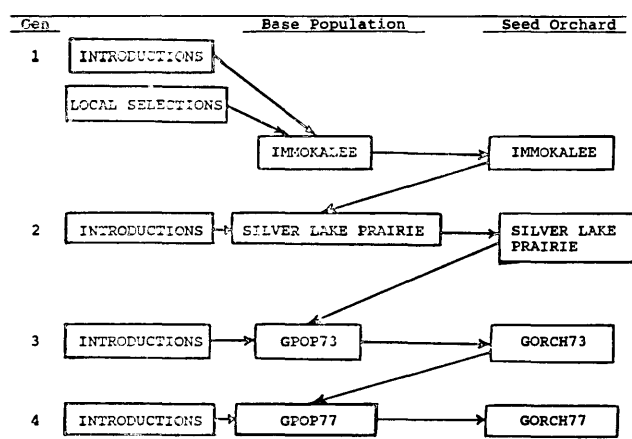


Figure 1. — Development of *Eucalyptus grandis* base population GPOP77 in southern Florida.

tion, 211 second-generation, 126 third-generation and 48 fourth-generation) open-pollinated families. Each family was represented some 60 times in a completely randomized single tree plot design on 17.3 hectares for a total of 31,725 trees. Planting density was 1,916 trees per hectare using paired planting beds with 2.3 m spacing within a pair, 3.5 m between pairs, and 1.8 m between seedlings along the beds. The southern-half of GPOP77, with 15,510 planting positions, was harvested in August 1978 to obtain coppice information. Geographically, 37% of the families trace their origins to New South Wales (NSW), 32% to Queensland (QLD), 21% originated in South Africa (SA) and 10% from other nations.

Seedling and coppice growth was evaluated through 64 months for several traits: seedling height at 7 months after initial planting (SHGT7M), coppice height (CHGT64M), DBH (CDBH64M) and volume (CVOL64M) at 64 months. The analyses of traits utilized only live trees at 64 months. Analysis of variance for all the traits used least square methods, and heritabilities were derived from the variance components estimated for half-sib families. The model used in estimating the variance components include Generation and Family within Generation. Since variation due to Origin was not included in the model, the derived individual heritabilities may be biased. However, for a selection procedure which ignores Origin, the variance estimates are approximately correct. A severe frost ( $-11^{\circ}\text{C}$ ) in January 1982 gave an opportunity to score the trees for frost resi-

lience (FR64M) and coppice quality (CQ64M). All trees were scored from 0 to 3, with the most desirable trees assigned a score of zero.

To determine the most effective method of converting GPOP77 to a seed orchard, seven different selection strategies were considered: mass selection of 200 best trees or 300 best trees, and combined selection of 10 best families (30 trees per family), 30 best families (10 trees per family), 100 best families (3 trees per family), 300 best families (1 tree per family) or 425 families (4 trees per family). All assumed that the initial introductions were not related.

Because inbreeding was possible as a consequence of some families in GPOP77 having common ancestors, genetic gains through alternative selection strategies were adjusted for inbreeding. For each selection strategy, the inbreeding coefficient (F) was calculated for all possible matings among the selected trees in 50-tree orchard. The pedigree of each mating was traced to its common ancestor, and the probabilities of relatedness at each level were computed according to Li (1976). Representative pedigrees and inbreeding coefficients in GPOP77 are shown in Figure 2.

### Results and Discussion

Four generations of selection resulted in significant genetic improvement for all coppice growth traits studied

Table 1. — *Eucalyptus grandis* generation means for individual tree performances in GPOP77 through 64 months after harvest.

Trait	Generation				
	Overall	1	2	3	4
SHGT7M (m)	1.75	1.60 <sup>a1/</sup>	1.79 <sup>b</sup>	1.81 <sup>b</sup>	1.83 <sup>b</sup>
CHGT64M (m)	7.36	5.00 <sup>a</sup>	7.75 <sup>b</sup>	8.42 <sup>c</sup>	9.39 <sup>d</sup>
CDBH64M (cm)	6.66	4.03 <sup>a</sup>	7.09 <sup>b</sup>	7.75 <sup>c</sup>	9.18 <sup>d</sup>
CVOL64M (dm <sup>3</sup> )	20.16	7.04 <sup>a</sup>	21.54 <sup>b</sup>	25.91 <sup>c</sup>	40.16 <sup>d</sup>
FR64M	1.47	1.75 <sup>a</sup>	1.39 <sup>b</sup>	1.34 <sup>b</sup>	1.25 <sup>b</sup>
CQ64M	0.54	0.77 <sup>a</sup>	0.48 <sup>b</sup>	0.41 <sup>b</sup>	0.40 <sup>b</sup>

1) Generation means not followed by the same letter are significantly different at 5%.

Table 2. — Comparison of seedling and coppice height among New South Wales (NSW), Queensland (QLD), South Africa (SA) and other origins of *Eucalyptus grandis* progenies in GPOP77.

Trait	Gen.	Origin <sup>1/</sup>			
		NSW	QLD	SA	Other
SHGT7M (m)	1	1.6bB	1.6aB	1.7aA	1.6aB
	2	1.8aA	1.8bA	1.8aA	1.8bA
	3	1.8aA	1.7bA	-	1.8bA
	4	1.8aA	1.8bA	-	-
CHGT64M (m)	1	5.2aA	4.9aA	4.9aA	5.4aA
	2	7.8bA	8.2bA	7.5bA	7.7bA
	3	8.4cB	9.8cA	-	8.4bA
	4	7.4dB	9.9cA	-	-

1) Origins within generations not sharing the same upper case letter are significantly different at 5%. Generations within origin not sharing the same lower case letter are significantly different at 5%.

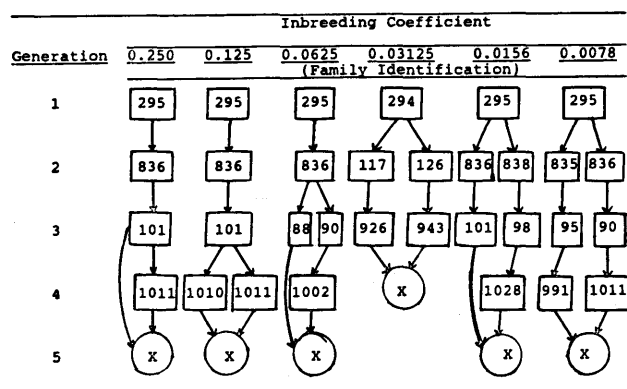


Figure 2. — Representative pedigrees and inbreeding coefficients possible in progenies (X) derived from first-generation introductions 294 and 295 in a 50-family *Eucalyptus grandis* seed orchard developed from GPOP77.

(Table 1). At 64 months after harvest first-generation trees averaged 7.04 dm<sup>3</sup> of stem wood. Second-generation trees were 206% larger, third-generation trees an additional 20% larger, and the fourth-generation trees another 55% greater. Survival at 64 months averaged 60% and was similar across generations. The low survival is a typical consequence of an August harvest (WEBLEY *et al.*, 1986).

Geographic origin increased in importance with age (Table 2). For early seedling growth, sources were generally similar in each generation. Introductions from South Africa (crosses among selected parents (VAN WYK, 1976)) were slightly taller when first grown in Florida, but were virtually the same height as other sources in the second-generation. For 64-month coppice height, QLD sources improved considerably with each generation of selection beyond the initial introductions and surpassed the third- and fourth-generation means from NSW, SA and other sources by more than one meter. These results suggest that higher gain could be achieved by concentrating future introductions in the QLD regions of Australia.

High individual and family heritabilities were observed for all traits examined (Table 3). For seedling height at 7 months, individual tree heritability was twice that of estimates reported by VAN WYK (1977). For 64-month coppice height the individual tree heritabilities ranged from 0.31 to 0.39, and the family heritabilities ranged from 0.65 to 0.75. The analyses of variance table is presented in Table 4. These heritabilities, however, may be biased due to two reasons. Firstly, the families in GPOP77 are related, since their pedigrees can be traced back to common ancestors and secondly, the bias may be introduced by excluding Origins from the model. High family heritabilities indicate the potential genetic gains through family or combined selection.

Considerable variability was observed among the four generations for frost resilience and coppice quality, with the fourth generation being the most resilient and of better coppice quality (Table 1). Geographically, sources from NSW had the highest frost resilience and coppice quality. Individual and family heritabilities for frost resilience and coppice quality were 0.29, 0.71, and 0.12, 0.45, respectively.

Table 3. — Heritabilities of *Eucalyptus grandis* traits within and over generations.

Trait	Individual heritability Generation					Family heritability Generation				
	1	2	3	4	Overall	1	2	3	4	Overall
SHGT7M					0.31					0.71
CHGT64M	0.63	0.31	0.29	0.38	0.39	0.75	0.59	0.58	0.64	0.70
CDBH64M	0.57	0.33	0.29	0.33	0.39	0.73	0.59	0.58	0.64	0.70
CVOL64M	0.37	0.27	0.25	0.25	0.31	0.63	0.56	0.54	0.54	0.59

Table 4. — Expected mean squares used for all traits and analyses of variance for 7-month seedling height (SHGT7M) and 64-month coppice height (CHGT64M) for *Eucalyptus grandis* in GPOP77.

Source	d.f.	Mean Squares		Expected Mean Squares
		SHGT7M	CHGT64M	
Generation	3	1322.7	640261.4	$V_e^{1/} + 20.15V_{f(g)} + 2121.4V_g$
Family within generation	523	98.5	3128.5	$V_e + 17.21V_{f(g)}$
Error	8555	16.7	1098.9	$V_e$
Total	9081			

1)  $V_e$  is error variance,  $V_{f(g)}$  is variance of family within generation and  $V_g$  is the variance due to generation.

Table 5. — Frequency of different degrees of relationship among trees in a 50-family subset of *Eucalyptus grandis* seed orchard in GPOP77.

Inbreeding coefficient (F)		Frequency
0.250		2
0.125		13
0.063		6
0.031		93
0.016		19
0.008		28
0.000		1064
Mean	0.005	Total 1225

High family variation for frost and coppice scores, evident from the above family heritabilities, suggests the use of family selection to obtain higher genetic gains for improvement in frost resilience and coppice quality.

Conversion of GPOP77 into a seedling seed orchard requires the use of the selection strategy that leads to maximum genetic gain in the next generation. Inbreeding coefficients of all possible crosses among selected individuals ranged from 0 to 0.25. The frequency of F values for a 50-family seed orchard is given in Table 5. The mean inbreeding coefficient for the seven selection strategies ranged from 0 to 1.5%. This was attributed to the fact that only a small percent of individuals (13% in a 50-family seed orchard) had an F greater than zero. In addition two to three generations have passed since direct relationship by common ancestry. The presence of related individuals in the GPOP77 seed orchard does not seem to affect the predicted gains appreciably through loss from inbreeding depression. This supports the results reported in *Pinus eliottii* by SQUILLACE (1973) who concluded that inclusion of small number of relatives in seed orchards will not cause appreciable loss from inbreeding and can increase overall gain. However, in this study predicted genetic gains were adjusted for potential inbreeding depression resulting from selfing, which is reported to occur at high rates in *Eucalyptus*.

In adjusting the predicted genetic gains for inbreeding from selfing, HODGSON'S (1976) and ELDRIDGE'S (1978) estimates of inbreeding depression were used. They predicted a height loss of 8% to 49% for selfed individuals (F = 0.50). Using the estimated 30% selfing reported in *E. grandis* it was deduced that 30% of the offspring from the seed orchard will have an F of 0.50 and the remaining 70% will have an estimated F (in proportion to the degree of relatedness) for a given strategy. Thus for each selection strategy the weighted mean inbreeding was calculated for both selfing and mating of related individuals. Using the conservative approach in the range of inbreeding depression reported for *E. grandis*, a 50% loss in height growth for selfed progenies (F = 0.50) amounts to 10% loss for every F of 0.10. So for a given selection strategy the predicted gains were reduced by a proportion equal to the weighted mean inbreeding coefficient.

The predicted genetic gains (adjusted for selfing) through seven different selection strategies are given in Table 6. As indicated earlier, the heritability estimates may be biased due to the exclusion of Origin from the model. Nevertheless, for the selection procedures used in this study, the variance estimates are approximately correct and the predicted genetic gains are valid. At 64-month coppice age,

Table 6. — Predicted genetic gains over population mean in 64-month coppice volume for alternative improvement strategies of *Eucalyptus grandis* in GPOP77.

Selection Strategy	Genetic gain (%)
<b>Mass Selection</b>	
200 best trees	80
300 best trees	69
<b>Combined Selection</b>	
10 top families (30 trees per family)	41
30 top families (10 trees per family)	61
100 top families (3 trees per family)	90
300 top families (1 tree per family)	86
425 families (4 trees per family)	54

the highest gain (90%) in volume over the population mean was predicted from a combined selection of the top 100 families with three trees per family. Comparable gains were also predicted for other selection strategies: 86% for family selection of top 300 families; 80% for mass selection of the best 200 trees. In February 1986, GPOP77 was converted into a seedling seed orchard (GORCH77) by retaining over 1700 selected individuals from 425 families (REDDY *et al.*, 1986).

### Conclusions

Considerable genetic gains have been achieved through four generations of selection in *E. grandis* for increased coppice stem size, frost resilience and coppice quality. Genetic variation in the base population still seems to be high enough to expect further gains in biomass productivity through continued selection. Differences in productivity between geographic sources suggest that sources from Queensland should be favored in future introductions. Genetic variation was also observed for frost resilience and coppice quality, for which sources from New South Wales exhibited the most resilience.

Potential inbreeding depression resulting from mating of related individuals in GPOP77 was negligible, hence there was no effect on the predicted genetic gains. Nevertheless, the predicted genetic gains were adjusted for relatedness among selected individuals and selfing. A 90% gain in coppice volume at 64 months is predicted for a combined selection of the top 100 families with three trees per family. Some other strategies predicted comparable genetic gains.

### Acknowledgements

Journal series paper no. 8237 of the Florida Agricultural Experiment Station. This study was supported in part under Subcontract no. 19X-09050C with Oak Ridge National Laboratory under Martin Marietta Energy Systems, Inc., contract DE-AC05-84OR21400 with the U.S. Department of Energy and by a cooperative program between the Institute of Food and Agricultural Sciences of the University of Florida and the Gas Research Institute entitled "Methane from Biomass and Waste". The assistance of G. F. MES-

KIMEN, formerly of the Southeastern Forest Experiment Station, U.S. Forest Service at Lehigh Acres, Florida, is gratefully acknowledged.

### Literature Cited

- ADES, P. K. and BURGESS, I. P.: Provenance trials of *Eucalyptus grandis* in northern New South Wales. *Silvicultura* 8 (31): 396–397 (1983). — ASSIS, T. F. D. and BRUNE, A.: Heritabilities and correlations in progenies of *Eucalyptus grandis* from Australia, South Africa and Brazil. *Silvicultura* 8 (31): 524–525 (1983). — BORGES, R. C. G. and BRUNS, A.: Heritability estimates and correlations between characters in *Eucalyptus grandis*. *Silvicultura* 8 (31): 525–527 (1983). — BROWN, A. H. D., MATHESON, A. C. and ELDRIDGE, K. G.: Estimates of the mating system of *Eucalyptus obliqua* using allozyme polymorphisms. *Aust. J. Bot.* 23: 931–949 (1975). — DARROW, K. W. and ROEDER, K. R.: Provenance studies of *Eucalyptus grandis* (HILL) ex. MAIDEN in South Africa. *Silvicultura* 8 (31): 402–406 (1983). — EARL, D. E.: Forest Energy and Economic Development. Clarendon press, Oxford (1975). — ELDRIDGE, K. G.: Genetic improvement of eucalypts. *Silv. Gen.* 27: 205–109 (1978). — FAO: Food and Agricultural Organization of the United Nations. Eucalypts for planting. FAO Forestry series no. 11, FAO, Rome, Italy. (1979). — GEARY, T. F., MESKIMEN, G. F. and FRANKLIN, E. C.: Growing *Eucalyptus* for industrial wood production. *Gen. Tech. Rep. SE-23. USDA For. Serv., Southeast. For. Exp. Sta.*, 43 p. (1983). — HODGSON, L. M.: Breeding of eucalypts in South Africa. *S. Afr. For. J.* 89: 13–15 (1974). — HODGSON, L. M.: Some aspects of flowering and reproductive behavior in *Eucalyptus grandis* (HILL) ex. MAIDEN at J. D. M. Keet For. Res. Sta. S. A. For. J. 97: 18–28 (1976). — HODGSON, L. M.: Methods of seed orchard management for seed production and ease of seed reaping in *Eucalyptus grandis*. S. A. For. J. 100: 38–42 (1977). — HOPPER, S. D. and MORAN, G. F.: Bird pollination and the mating system of *Eucalyptus stoatetii*. *Aust. J. Bot.* 29: 625–638 (1981). — HUNT, R. and ZOBEL, B.: Frost hardy eucalypts grow well in the Southeast. S. J. Appl. For. 2 (1): 6–10 (1978). — KING, J. P.: Selection of *Eucalyptus* species for northern California. *Silvicultura* 8 (31): 453–455 (1983). — LI, C. C.: First course in population genetics. Boxwood Press, Pacific Grove, CA. 594 p. (1976). — LOGAN, W. E. M.: Policy. *Unasylva* 21 (3/4): 8–22 (1967). — MESKIMEN, G. F.: Realized gain from breeding *Eucalyptus grandis* in Florida. *Gen. Tech. Pap. Pac. Southwest For. and Range Exp. Sta., USDA For. Serv., PSW-69*, pp. 121–128. (1983). — MESKIMEN, G. F., ROCKWOOD, D. L. and REDDY, K. V.: Development of *Eucalyptus* clones for a summer rainfall environment with periodic severe frosts. *New Forests* 3: 197–205 (1987). — MORAN, G. F. and BROWN, A. H. D.: Temporal heterogeneity of outcrossing rates in alpine ash (*Eucalyptus delegatensis*). *Theor. Appl. Gen.* 57: 101–105 (1980). — PHILLIPS, M. A. and BROWN, A. H. D.: Mating system and hybridity in *Eucalyptus pauciflora*. *Aust. J. Biol. Sci.* 30: 337–344 (1977). — REDDY, K. V., ROCKWOOD, D. L. and MESKIMEN, G. F.: A strategy for conversion of an *Eucalyptus grandis* base population into a seedling seed orchard. *Proc. IUFRO Conf. on Breeding Theory, Progeny Testing, and Seed Orchards*. pp. 613–621 (1986). — ROCKWOOD, D. L. and GEARY, T. F.: Genetic variation in biomass productivity and coppicing of intensively grown *Eucalyptus grandis* in southern Florida. *Proc. 7th N. Amer. For. Biol. Wrkshp.* pp. 400–405 (1982). — ROCKWOOD, D. L. and MESKIMEN, G. F.: Genetic, spacing and genetic × spacing interaction influences on growth of *Eucalyptus grandis* in southern Florida. *Proc. 16th For. Tree Improv. Conf.* pp. 77–85 (1981). — SQUILLACE, A. E.: Comparison of some alternative second-generation breeding plans for slash pine. *Proc. 12th So. For. Tree Imp. Conf.*, pp. 2–13 (1973). — VAN WYK, G.: Early growth results in a diallel progeny test of *Eucalyptus grandis* (HILL) MAIDEN. *Silv. Gen.* 25: 126–132 (1976). — VAN WYK, G.: Progress with the *Eucalyptus grandis* breeding program in the Republic of South Africa. *Proc. 3rd World Consul. For. Tree. Breeding, Canberra, Australia*. pp. 639–643 (1977). — VAN WYK, G.: Inbreeding effects in *Eucalyptus grandis* in relation to the degree of relatedness. S. A. For. J. 116: 60–63 (1981). — WEBLEY, O. J., GEARY, T. F., ROCKWOOD, D. L., COMER, C. W. and MESKIMEN, G. F.: Seasonal coppicing variation for three eucalypts in southern Florida. *Aust. For. Res.* 16: 181–190 (1986). — WRIGHT, J. W.: Introduction to forest genetics. Academic press, NY. 463 p. (1976).