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Age Trends in the Genetic Control of Stem Diameter of Eucalyptus Tereticornis and the Implication for Selection

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(Received 17th July 1990)

Abstract

The trend in the genetic control of diameter at breast height of *Eucalyptus tereticornis* SM. was investigated using growth data at ages three, five and six years. The analysis showed that variance component estimates changed with age. Both absolute values of genetic variance and their relative sizes compared with environmental source of error variance increased with age. Error variance also increased with age. However the ratio of the sum of the environmental components ($\sigma^2_e + \sigma^2_r$) to the total variance decreased with age.

Stem diameter of *Eucalyptus tereticornis* was found to be under genetic control, the degree of which increased with age. Selection for diameter growth should therefore be more efficient when older trees are used in the selection process. Adaptive growth differences existed among the provenances examined, the intensity of which increased with age. The Laura, Queensland provenance was the best adapted while the Mysore landrace and the Port Moresby provenance were least adapted.

Key words: *Eucalyptus tereticornis*, provenances, diameter at breast height, ages, variance components, heritability.

Introduction

The provenance trial involving 11 provenances of *E. tereticornis* SM. established at Afaka in 1969 revealed that provenance differences exist in the growth rate of the species (OTEGBEYE, 1990). It has also been shown in another paper (OTEGBEYE, 1988a) that the pattern of genetic control on height growth of the species varies with age. The aims of the current paper are to show (i) the degree of genetic control on diameter at breast height (dbh); (ii) the pattern of the genetic control over ages three, five and six years. Stem diameter is a very important tree characteristic since it is a very important component of yield of forest tree species. In fact, in pure mathematical terms, a 10% increase in diameter will give approximately a 20% increase in basal area, hence in volume (LAURIDSEN *et al.*, 1987). Like tree height, stem diameter is therefore a very important component of commercial growth as well as fitness.

Materials and Methods

Eleven provenances of *Eucalyptus tereticornis* were used for a provenance study involving the species in 1969. The descriptions of these provenances and the establishment conditions for the trial have been given in an earlier paper (OTEGBEYE, 1990). Each provenance was composed of seed from a small number of trees, in some cases only two trees.

The seedlings were planted at Afaka (lat. 10°37'N, long. 7°17'E) in July, 1969. The experimental design used was randomized blocks with four replications.

Although, 11 provenances were involved in the original provenance study, only nine were considered for the purpose of the present paper since the other two provenances (Kennedy River, Northern Queensland and an unidentified source from Papua New Guinea) were not replicated and therefore could not be involved in the analysis of variance. The nine provenances considered include seven from Queensland Australia namely North Laura, Mt. Garnet, Conjuboy, Laura and three different seedlots from Cooktown, one from Papua New Guinea — Port Moresby and a landrace from India — Mysore.

Total heights and dbh of 16 inner trees per plot were measured in 1972, 1974 and 1975, that is when trees were three, five and six years old respectively. However, only dbh data were analysed for the purpose of this paper, the data on total height having earlier been similarly treated (OTEGBEYE, 1988a). Analysis of variance was carried out on plot means for each of the three ages examined.

Variance components and broad sense heritability (h^2) at each age were estimated. Heritability was estimated using the relationship;

$$h^2 = \frac{\sigma^2_p}{\sigma^2_p + \sigma^2_{e/r}}$$ (BURLEY and WOOD, 1976; WELLENDORF *et al.*, 1986).

where:

$\sigma^2_p = V_G$ = Genetic variance of provenance means

$\sigma^2_{e/r} = V_E$ = Environmental variance of provenance means

r = number of replications

$\sigma^2_p + \sigma^2_{e/r} = V_P = V_G + V_E$ = Phenotypic variance among provenance means.

Broad sense heritability can be used to predict gain in first generation from provenance selection (NANSON, 1968).

Results and Discussion

The form of the analysis of variance used is presented in *table 1*. The individual analysis showed that variance component estimates changed with age (*Table 2*). Similar results have been reported for height growth of the species (OTEGBEYE, 1988a), Douglas-fir (NAMKOONG et al., 1972)

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Table 1. — Form of analysis of variance for diameter at breast height of nine provenances of *Eucalyptus* tereticornis.

Sources of variance	df	Expected mean Square		
Replication	3	σ^2_e	+	$p\sigma^2_r$
Provenance	8	σ^2_e	+	$p\sigma^2_p$
Residual	24	σ^2_e		

Table 2. — Variance component and heritability estimates for diameter at breast height of nine provenances of *Eucalyptus tereticornis* grown at Afaka[a]).

Components of source of variance	Age (years) 3	5	6
σ^2_r	0.0400	-0.3200	-0.1550
σ^2_p	0.2625	0.4850*	1.7000***
σ^2_e	0.9900	1.7700	2.5400
h^2	0.51	0.52	0.73
σ^2_p / σ^2_e	0.2652	0.2740	0.6693
Mean dbh (cm)	5.93	7.11	10.00
$C.V. = \frac{\sqrt{\sigma^2_e}}{\text{Mean dbh}}$	0.1678	0.1871	0.1594

a) * Statistically significant at 10% level of probability.
*** Statistically significant at 1% level of probability.

and ponderosa pine (Namkoong and Conkle, 1976). The components of variance attributable to replication was 0.04 representing about 3.09% of the total variance at age three years, -0.32 and -0.155 (which were assumed to be zero) at ages five and six years respectively, representing 0.00% of the total variance at each of the two ages. It is therefore clear that the contribution of replication to the observed variation in dbh among the provenances was quite minimal at age three years while it virtually contributed nothing to the variation at ages five and six years.

The genetic variance among provenances was not significant at age three years, just detectable at the 10% level of probability at age five years and highly significant (at the 1% level of probability) at age six years (*Table 2*). Absolute value of genetic variance increased with age. Similar results have been reported for the height growth of the species (Otegbeye, 1988a) and other species (Namkoong *et al.*, 1972; Namkoong and Conkle, 1976). Just like in height growth, dbh increased with age. Genetic variance should therefore be expected to increase. The relative size of genetic variance versus environmental source of error variance was 0.2652, 0.2740 and 0.6693 at ages three, five and six years respectively, showing an increasing trend, at least up to age six years. A similar trend has been reported for the height growth of the species (Otegbeye, 1988a). This shows that differences in dbh observed among the provenances became more genetically controlled as the trees advanced in age. There was, however, no striking difference in the ratio between ages three and five years. Genetic variance component accounted for 21.31%, 21.51% and 40.09% of the total variance at ages three, five and six years respectively.

There was increase in the absolute value of error variance through the three ages examined. The value obtained was 0.99, 1.77 and 2.54 at ages three, five and six years respectively. Like in height growth, diameter growth is cumulative and therefore diameter measurements normally include previous diameter growth. Therefore, except where there were strong negative relationships between different ages, the absolute value of error variance should not decrease with age (Namkoong *et al.*, 1972).

The relative size of the sum of the environmental components ($\sigma^2_e + \sigma^2_r$) was 0.797, 0.785 and 0.595 at ages three, five and six years respectively. This shows that the relative size of the environmental components decreased with age. A similar pattern has been reported for the height growth of this species (Otegbeye, 1988a) and Douglas-fir (Namkoong *et al.*, 1972). The decrease in the relative size of the environmental components of variance of dbh was more or less confirmed by the coefficient of variation which although increased from about 0.168 at age three years to about 0.187 at age five, decreased to about 0.159 at age six years, a figure that was below that recorded at age three years.

Stem diameter growth in *Eucalyptus tereticornis* was found to be under genetic control, although less so than the height growth of the species, the former having recorded lower heritability estimates at the three ages than values that have been reported for the latter (Otegbeye, 1988a). In other tree species, height growth has also been found to be more strongly genetically controlled than diameter growth (Zobel, 1971 and 1977; Otegbeye, 1988b). Heritability estimate obtained for dbh in the present study was 0.51, 0.52 and 0.73 at ages three, five and six years respectively. The provenances therefore showed dbh dif-

Table 3. — Mean diameter at breast height (cm) of nine provenances of *Eucalyptus tereticornis* grown at Afaka.

Provenance	Latitude °S	Number of seed trees	Seedlot No	Age (years) 3	5	6
N. Laura, QLD.	15°31'	2	S8211	7.28	8.38	11.75
Cooktown, North QLD.	15°40'	?	S8202	6.05	7.65	11.70
Cooktown, North QLD.	16°10'	?	S8214	6.10	8.25	11.20
Mt. Garnet, QLD.	18°00'	?	S8490	6.60	7.85	10.97
Conjuboy, QLD.	17°50'	5	S8297	5.48	6.53	9.22
Cooktown, North QLD.	16°20'	1	S8215	5.80	6.67	10.10
Laura, QLD.	15°45'	2	S8199	5.95	6.93	9.40
Mysore, India	—	?	—	4.85	6.05	7.78
Port Moresby, P.N.G.	9°25'	?	S8866	5.30	5.70	7.90
Mean				5.93	7.11	10.00

ferences which were genetically controlled and the degree of the genetic control increased with age. Thus diameter growth patterns and variations expressed at any particular growth stage of this species should be under genetic control. The closeness in the estimates obtained at ages three and five years showed that there was no dramatic change in the relative performance of the provenances over the two ages (HANOVER and BARNES, 1969). The trend in the heritability estimate tends to confirm the trend in the relative size of genetic variance versus environmental source of error variance. Since heritability increased with age, selection for dbh at more advanced ages will result in increased genetic gain.

While the relative size of the environmental components decreased with age, the genetic variance among provenances increased with age. This shows that, like the height growth, means and variances in dbh are selectively adaptive features in *Eucalyptus tereticornis* since dbh is an important component of fitness of forest tree species.

The North Laura, Queensland provenance of *E. tereticornis* exhibited the largest dbh among the provenances examined while the Mysore and Port Moresby provenances were least adapted (*Table 3*).

Conclusion

Diameter at breast height is under genetic control in *Eucalyptus tereticornis*. It is therefore possible to improve this characteristic through selection. Since heritability of dbh increased with age, selection for this characteristic at older ages will lead to higher genetic advance than that made at younger ages.

The north Queensland provenances from the Laura region (15$^1/_2$^{0}S) are the best materials for both afforestation and genetic improvement programmes involving *Eucalyptus tereticornis* in the Northern Guinea Savanna Zone of Nigeria.

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Buchbesprechungen

Genetic variation in functional and structural productivity determinants in poplar. By R. CEULEMANS. 1990. Thesis Publishers, Amsterdam. University of Antwerp. 100 pages. Dfl. 35,—/ $ 22,—.

Despite the efforts that have been put into tree breeding, selection of the desired genotypes is still done more or less retrospectively because a tree breeder is hardly able to predict which genotype will outperform some other genotype in a certain environment. To be able to do this, specific reliable selection criteria are prerequisite and would facilitate breeding programs immensely. The small monograph of REINHART CEULEMANS is a step into this direction.

Summarizing numerous publications of studies performed at Antwerp and Seattle he has given an overview of how different physiological, morphological and anatomical growth and productivity determinants vary between a certain numher of widely used *Populus* clones which represent one species or species hybrids within or between the sections Aigeiros and Tacamahaca. Thus the variation recorded is in no way representative in the sense of populations. Also only approved clones were studied which of course have passed many preselections. This is also the reason why all hybrid clones were performing much better than parental clones throughout all experiments. The studies were performed on three organizational levels, the individual leaf, the branch and the whole tree.

At the leaf level parameters such as leaf growth and size that ultimately add to a large whole tree leaf area were found to correspond to high production. Furthermore, stomatal conductance and responsiveness as well as internal leaf structure give indications about growth performance. Superior hybrid clones were found to have a better leaf orientation leading to a more efficient light interception. Finally, correlations were found between photosynthetic capacity and growth. Many of the leaf structure and other characters are known to be under strong genetic control. Therefore there seem to be many promising aspects at the leaf level.

At the branch level the following characters are recommended: acute branch angles, low biomass, and high leaf area density per unit of branch length. This is of course only applicable to biomass production models in short rotation plantations which served as basis for these studies. Furthermore the type of branch, sylleptic or proleptic, and the carbon allocation to these might have some influence on total performance.

At the tree level the optimal light interception and the conversion efficiency of the intercepted light into photosynthetic products was found to be important to maximize the CO_2 fixation per unit of land area. Connected with this the whole tree leaf area which was found to be much larger on well performing trees. Among the phenological characters duration of leaf exposition is closely related to productivity.

The author concludes that "Data on these physiological and tree level show that differences in clonal productivity are well structural growth determinants at the leaf, branch and whole related to the ideotype concept . . . " and continues further on: "These ideotypes . . . may have great potential as early predictors . . . ". Not much has to be added, except that he has given convincing examples to suprort this conclusion.

Another conclusion is worth mentioning: "In trees, more than in crops or other species, a 'snowball effect' accumulates and integrates small improvements in specific traits to large differences. . . . for example a slight superior leaf area . . . might, when integrated over space and time, result in considerable growth differences . . . ". This indicates the complexity of the