Genetic interaction of physiological traits in *Eucalyptus* species

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Six species of *Eucalyptus viz., E. alba*, *E. camaldulensis*, *E. microtheca*, *E. tereticornis*, *E. polycarpa* and *E. torelliana*, were subjected to full diallel mating. The cross between *E. polycarpa* and *E. torelliana* was characterised by post-fertilization abortion. An evaluation of the remaining four parents and 12 hybrids revealed that characters like leaf temperature and diffusive resistance were free from epistatic interaction. For the characters PAR, non-allelic interaction was obserrved. Leaf temperature was shown to be under the influence of predominantly dominant gene action. Predominance of additive gene action was evident in respect of diffusive resistance and transpiration rate. The gene distribution among the parents was observed to be unequal with greater frequencies of dominant allels for PAR and diffusive resistance. The number of genes that control the characters was one for leaf temperature, PAR and transpiration rate and two for diffusive resistance. Narrow sense heritability was low for all the attributes.

Key words: diallel mating, Eucalyptus, genetic analysis, gene action, physiological traits, tree breeding

INTRODUCTION

One of the primary impediments in tree improvement programmes involving intervarietal and interspecific crosses is the choice of appropriate perental lines which when crossed would throw high proportions of desirable segregates in early segregating generations. Breeding for high biomass remains one of the objectives in tree improvement programmes. Zobel and Talbert (1984) opined that the success of any tree breeding programme depended to a great extent on the knowledge of the genetic architecture of the population handled by the breeder. The breeder needs a methodology which can provide reliable information on the nature of gene action and quantum of genetic potential available in the material handled. It is obvious that in any projected experiment the genetic variability should be of high order that will permit high selection efficiency. The diallel method of analysis was considered developed in order to give information on the genetic mechanisms controlling various traits (Jinks and Hayman, 1953; Hayman 1954, a,b; Jinks, 1954; 1955; Mather and Jinks, 1982). In the present study, the estimation of genetic parameters was done both by the genetical and graphical analysis. The genetic system of *Eucalyptus* is a classic open recombination system (Pryor, 1978) and barriers to interspecific hybridization are generally weak (Pryor and Johnson, 1971; 1981; Potts and Reid 1988). There are no studies reported which compare the relative contribution and importance and nature of gene action in interspecific hybridisation although such studies are important for a full understanding of gene flow and evolutionary consequences of hybridization in the genus (Pryor, 1976; Pryor and Johnson, 1981; Potts and Jackson, 1986) and the development of breeding strategies.

Eucalyptus tereticornis is one of the main species in pulpwood production in India and especially in Tamil Nadu 1.00.000 ha and over 4,28,000 ha have been established in India (Kondas 1986). *E. camaldulensis* is one of the main species for pulpwood production in Spain, Portugal and Morocco (Turnbull and Pryor , 1984), it has been widely planted overseas about 5,00,00 ha. (Turnbull and Pryor, 1984). *E. microtheca* tolerates heavy textured calcareous and gypseous soils (Turnbull and Pryor, 1984), soil salinity (Hart, 1972) and is drought resistant (Pryor, 1961). It will be rewarding if a hybrid with all these qualities prompted the investigation of artificial hybridization as a means breeding fast growing in problems soils with drought resistance genotypes for clonal selection and nature of action of gene in the parents.

MATERIALS AND METHODS

Six species of *Eucalyptus viz., E. alba* Reinex R., (P_1) *E. camaldulensis* Dehnh., (P_2) *E. microtheca* F.Muell (P_3)., *E.tereticornis* Sm., (P_4) *E. polycarpa* F.Muell (P_5) and *E. torelliana* F.Muell (P_6) were subjected to a full diallel mating (Jinks and Hayman, 1953; Mather and Jinks, 1971) at the Forest College and Research Institute, Mettupalayam (11° 19' and 11° 20' N latitude and 76° 56' E. longitude, 300m.a.m.s.l receiving a mean annual rainfall of 800 mm, pH 7.1) during 1989-1995. Six months old progenies along with their parents were replicated thrice using a replicated blocks design (Panse and Sukhatme, 1961). The seedlings were planted at an espacement of 2x2 m in single row (replication)

comprising 15 plants 3 ½ years after planting the follwoing parameters were recorded on ten randomly selected trees in each replication; (1) leaf temperature, (2)PAR, (3) diffusive resistance and (4) transpiration rate.

The genetic and graphical analyses of diallel technique was carried out as given by Hayman (1954 a,b) operates with the following assumptions, i) the parents are homozygous, ii) the inheritance is wholly diploid, iii) there are no maternal effects, iv) each locus is represented by not more than two alleles, v) non-correlated gene distribution and vi) absence of non-allelic interaction *viz.,* no epistasis, the chosen *Eucalyptus* spp. are diploid (2n=22; Zuccone, 1958), the parents are maintained pure in isolation for many years. These features satisfy the above requirements for diallel analysis which has been employed.

RESULTS AND DISCUSSION

Genetic analysis validity of hypothesis

The direct or reciprocal cross involving the two species of *E. polycarpa* and *E.torelliana* with others or between these failed to set seeds due possibly to species incompatibility or post-fertilization abortion (Pryor, 1978).

Table 1. Tests of goodness of fit of the data to the diallel model : t^2 value; estimates of b of W_r on V_r, standard error of b and deviation of b from zero and unity

Character	t^2 value	$b+SE_{(b)}$	$b-o/SE_{(b)}$	$1-b/SE_{(b)}$
Leaf temperature	12.230	1.60+0.23	6.68	-2.50
PAR	0.067	0.485+0.35	0.96	1.02
Diffusive resistance	0.003	0.978+0.17	5.57*	0.11
Transpiration rate	0.821	1.167+0.29	3.95*	-0.56

*significant at 5% level

of b from zero and unity are presented in table 1. All the three tests viz., i) non-significant t^2 value; (ii) the regression coefficient 'b' significantly deviating from zero; (iii) the regression coefficient not deviating from unity indicated additive-dominance genes for the following characters: a) leaf temperature, diffusive resistance and traspiration rate. Hence all the assumptions hold true for these characters. But the presence of non-allelic interaction of genes was indicated by non-significant deviation of regression either from zero or unity in respect of PAR.

Estimates of genetic parameters and genetic ratios

The assumption of non-allelic interactions has been very difficult to setisfy in most studies involving diallel analysis (Jana, 1975). the regression slope (0.093, 0.426, and the array points generation an upward concave curve indicated complementary type of interactions of genes for PAR. Mather (1967) has shown that with complementary interaction , V_r -Wr slope is positive (i.e. change in W_r is less than the change in V_r) indicated by the W_r , V_r array points lying to the right of the straight line of unity slope. Thus, complementary interaction affects the distribution pattern of array points (Coughtrey and Mather 1970). It become difficult to distinguish between the effect of dispersed gene distribution and complementary interaction on a W_r , V_r graph for these traits. Negative interception of regression lime in the W_r , V_r graph and mean degree of dominnce being more than unity (Table 2) indicted overdomiance for PAR. These results, suggest that over dominance cannot be easily distinguished from non-allelic interaction. According to Hayman (1954 a), a complementry type of gene interacion on simply correlated gene distribution will seriously inflate the dominance as apparent overdominance. For the non-interacting traits, viz., leaf temperature and diffusive resistance, the negative interception of regression on the W_r , V_r , axis for leaf temperature (1a) and the mean degree of dominance ratio $(H_1 / D)^{1/2}$ being more than unity (Table 3) indicate the presence of overdominance where as positive interaction of regression slope and mean degree of dominance $(H/D)^{1/2}$ being less than

Table 2. Estimation of genetic parameters

Characters	D	F	H_1	H_2	h^2	E
Leaf temperature	0.74**+0.20	0.88+0.53	3.01*+0.62	1.57+0.56	0.42+0.38	0.57**+0.09
PAR	4597.5**+788.4	4130.9+2625.5	6751.4**+2345.5	21782.2**+211.5	2289+1435.0	5520.5**+352.6
Diffusive resistance	2.97**+0.13	-0.31+0.35	1.52**+0.4	0.28+0.36	0.37+0.25	0.92**+0.06
Transpiration rate	0.046+**0.003	0.015+0.009	0.12+0.11	0.026*+0.01	0.0095+0.006	-0.012**+0.0017

D-component of variation due to additive effect: F-Co-variance of additive and dominance effect.
H_1 - Component of variation due to dominance effect of gene.
H_2 - Dominance indicating asymetry of positive and negative effects of genes.
h^2 - Dominance effect overall loci.: E - The expected environmental component of variance.
* - Significant at 5% level; ** - Significant at 1% level.

Table 3. Estimates of genetic ratios involving different genetic parameters

Characters	$(H_1 /D)^{1/2}$	$H_2 /4H_1$	K_D /K_R	h^2 /H_2	heritability narrow sense (%)	$r(W_r + V_r)$, y_r
Leaf temperature	1.16	0.13	3.07	0.26	20.5	-0.790**
PAR	1.46	0.80	0.46	0.11	39.7	0.842**
Diffusive resistance	0.49	0.04	0.80	1.31	67.0	0.807**
Transpiration rate	0.51	0.54	4.05	0.36	20.3	0.986**

$(H_1 /D)^{1/2}$ = Mean degree of dominance over all loci (0-1 indicates partial dominance, > 1 over dominance, 1 complete dominance
$H_2 /4H_1$ = An estimate of average frequency (uv) of positive (u) versusnegative (v) alleles in the parents when u+v=1
K_D /K_R = The ratio of total number of dominant to recessive genes in all parents.
h^2 /H_2 = an estimate of number of groups of genes which control the character and exhibit dominance to some degree.

This narrowed down the number of species to just four. The t^2 estimated were non-significant for all these characters (Table 1). The estimates of regression coefficient (b) of W_r on V_r , standard error of b and deviation

unity (Table 3) indicate the presence of partial dominance in respect of diffusive resistance and transpiration rate. The significance of both additive and dominance components (H_1 , H_2 and h^2) in respect of the

following traits leaf temperature, PAR, diffusive resistance and transpiration rate indicates the presence of additive and dominance genes for these traits. The significance of GCA and SCA varience for these characters, (Paramathma et al., 1997) also reflect the operation of additive-dominance geneaction. Even though both additive and dominant components were present, the magnitude of dominant component was higher than that of addtive for PAR. The reverse was true for diffusive resistance and transpiration rate. The response to selection of traits with considerable non-additive variance, such as growth is generally less satisfactory than for quality traits that are usually under strong additive genetic control (Stonecypher et al., 1973), Zobel and Tablert (1984) reported that most of the traits of economic importance in forest trees are under some degree of additive genetic control. This according to them was fortunate because additive variance can be successfully used in simple selecion systems. Characteristics such as wood specific gravity, bole straightness, and other quality characteristics of trees have stronger additive variance components than do growth characteristics. Although growth traits are controlled to some degree by additive genetic effects, they also have considerable non-additive variance associated with them (Zobel and Talbert 1984). Significant H_2 indicated dominance with asymmetry of positive and negative effects of genes in respect of PAR. The asymetrical distribution of genes indicated for leaf temperature (0.13), have possibly inflated otherwise partial dominance $(H_1/D)^{1/2}$ to over dominance. Hayman (1954 a) stated that a particular combination of dispersion can cause serious inflation of dominance into overdominance. The parameter $H_2/4H_1$ was more than 0.25 for PAR (0.80) and transpiration rate and these high values are considered spurious. K_D/K_R ratio of more than unity underscores preponderance of dominant alleles over receive alleles for the leaf temperature and transpiration rate (Table 2) Earlier in the discussion non-allelic interaction was indicated for the character leaf temperature. That is both dominance and epistasis are indicated for this characters and it can not be said with certainity whether dominance is due to intergenic or intragenic action. K_D/K_R ratio of less than unity, indicate the frequency of recessive alleles to be in excess of dominant alleles in respect of PAR and diffusive resistance .

A greater environmental influence as reflected by high e values was evident in respect of the following traits *viz.,* leaf temperature, PAR, transpiration rate and diffusive resistance. This is further confirmed by low heritability values for these characters (Table 2 & 3). A value lesser than unity for the ratio, h^2/H_2 indicates monogenic inheritance;A value of 1-2 digenic, 2-3 trigenic and so on and so forth, measured by this yardstick, monogenic inheritance is indicated for the characters, leaf temperature, PAR, and diffusive resistance. Digenic inheritance is indicated for the traits diffusive resistance. Tree breeders are often concerned with heritabilities, which become important when selection can be practiced as is done in advanced generation tree improvement, where selecions are made from genetic tests (Zobel and Talbert, 1984). Magnitude of heritability in broad sense differ for the different characters. The trait diffusive resistance (Table 3) exhibited moderate heritability (40 to 50) low heritability (<40%) was associated with leaf temperature, PAR, and transpiration rate. Low heritability may be due to higher environmental influence.

CONCLUSION

The tree breeders should have the perfect methodology to elucidate the information on the gene interaction in the tree species. In this analysis the dialle analysis with the six species of *Eucalyptus viz., E. alba* Reinex R., *E. camaldulensis* Dehnh., *E. microtheca* F.Muell., *E. tereticornis* Sm., *E. polycarpa* F.Muell and *E. torelliana* F. Muell., showed that *E. polycarpa* x *E. torelliana* showed the post-fertilization abortion. Additive gene action was confirmed for the diffusive resistance and transpiration

rate. Besides, the genetic interaction for the physiological characters must be clearly elucidated in with further genetic analysis with more cross combinations to attain the hybrids with highest biomass yield in *Eucalyptus* species.

AUTHOR CONTRIBUTIONS

Paramathma – designed the experiment and produced this manuscript.

COMPETING INTERESTS

The author declare that they have no competing interests.

ETHICS APPROVAL

Not applicable.

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