Genetic interactions 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 height, DBH, leaf number and leaf breadth were free from epistatic interaction. For characters like internode length and leaf length, non-allelic interaction was manifest. The magnitude of dominant genes was high for most characters indicating the promise of heterosis breeding for these traits. Symmetrical distribution of positive and negative genes was inferred. The number of genes that control the characters was one for collar diameter and leaf length, two for height and internode length and three for leaf breadth. Narrow sense heritability was high for all the attributes, barring internode length.

Key words: Eucalyptus, GCA, genetic interactions, SCA, diallele mating, heritability

INTRODUCTION

One of the primary impediments in tree improvement programmes involving intervarietal and interspecific crosses is the choice of appropriate parental 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 (Paramathma, 2020). 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 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 by the genetical 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 hybridization 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 1,00,000 ha area under plantation. In Tamil Nadu an area of over 4,28,000 ha have been established (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 in about 50,000 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 are developed and this prompted the investigation of artificial hybridization as a means breeding fast growing with drought resistance and tolerates problems soils.

MATERIALS AND METHODS

Six species of *Eucalyptus viz., E. alba* Rein-ex., 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 dialalel 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, 300 m.a.m.s.l receiving a mean annual rainfall of 800 mm pH 7.1) during 1989-2000. Six months old progenies along with their parents were planted in a randomized with three replications (Panse and Sukhatme, 1961), at an espacement of 2x2m in single row (replication) comprising 15 plants 4 years after planting the follwoing parameters were recorded on ten randomly selected trees in each replication; (1) height; (2) dbh; (3) internode length; (4) number of leaves; (5) leaf length; and (6) leaf breadth.

Genetical analysis

The genetic analysis of diallel technique was carried out as the methodology was 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; Zucconi, 1958). The parents are maintained pure in isolation for many years and these features satisfy the above requirements for diallel analysis.

RESULTS AND DISCUSSION

Genetical 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). 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 of b from zero and unity are presented in table 2. 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) height, b) dbh, c) leaf number and d) leaf breadth (Table 1). 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 internode length and leaf length (Table 1).

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	$b \pm SE_{(b)}$	$b\text{-}o/SE_{(b)}$	$1\text{-}b/SE_{(b)}$
Height	2.20	0.648± 0.18	4.42 *	2.02
Collar diameter	2.90	0.696 ± 0.16	5.43 *	2.07
Internode Length	0.28	-0.770 ± 0.51	-0.14	2.02
Leaf number	0.83	1.780 ± 0.49	2.95 *	0.67
Leaf length	0.98	0.726 ± 0.39	1.41	-0.56
Leaf breadth	0.14	1.430 ± 0.20	9.76*	-0.29

*significant at 5% level

Estimates of genetic parameters and genetic ratios

The assumption of non-allelic interactions has been very difficult to satisfy in most of the studies involving diallel analysis (Jana, 1975). Mather (1967) has shown that with complementary interaction, and mean degree of dominance being more than unity indicted overdomiance for leaf length, and mean degree of dominance being less than unity reflect partial dominance in respect of internode length. These results, suggest that over dominance cannot be easily distinguished from non-allelic interaction (Table 3). According to Hayman (1954 a), a complementary type of gene interaction on simply correlated gene distribution will seriously inflate the dominance as apparent overdominance. For the non-interacting traits, *viz.,* height, DBH, leaf number, and leaf breadth, the mean degree of dominance ratio $(H_1/D)^{1/2}$ being more than unity indicates the presence of overdominance (Table 3). The significance of both additive and dominance components (H_1, H_2 and h^2) in respect of the following traits *viz.,* height, collar diameter, leaf number, leaf length, and leaf breadth indicates the presence of additive and dominance

genes for these traits (Table 3). The significance of GCA and SCA variance for these characters, also reflect the operation of additive-dominance gene action. Even though both additive and dominant components were present, the magnitude of dominant component was higher than that of additive for height, DBH and leaf number (Paramathma *et al.,* 1997). The reverse was true for leaf length and leaf breadth. 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 (Table 3) (Stonecypher et al., 1973). Zobel and Tablert (1984) reported that most 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 selection 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_1 component (Table 3) indicated presence of dominance component of variance alone and significant h^2 presence of dominance at all loci in respect of internode length, which is in conformity with the higher GCA:SCA variance ratio (Paramathma et al., 1996). This non-additive variation can be thus exploited by making specific cross between *E. alba* x *E. tereticornis* and mass multiplying the hybrid through vegetative propagation or by employing mass pollination between the two species (Zobel and Talbert, 1984). Significant H_2 indicated dominance with asymmetry of positive and negative effects of genes in respect of height, DBH, internode length, leaf number, and leaf breadth. In the present study, values of 0.24, 0.29 and 0.28 were obtained for height, collar diameter, and internode length respectively which has close approximations to the expected value for symmetry of genes. The asymmetrical distribution of genes indicated for the following traits *viz.,* leaf number (0.20) leaf length (0.17) leaf breadth (0.11), have possibly inflated otherwise partical 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. K_D /K_R ratio of more than unity underscores preponderance of dominant alleles over recessive alleles for the following traits *viz.,* internode length, leaf number, leaf length and leaf breadth. Earlier in the discussion, non-allelic interaction was indicated for a few of the above characters *viz.,* leaf number, leaf length and leaf breadth. That is both dominance and epistasis are indicated for these characters and it cannot be said with certainty whether dominance is due to intergenic or intragenic action. K_D /K_R ratio of less than unity indicates the frequency of recessive alleles to be in excess of dominant alleles in respect of height and collar diameter. A greater environmental influence as reflected by higher values was evident in respect of the following traits *viz.,* internode length and leaf breadth. This is further confirmed by low heritability values for these characters (Table 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, collar diameter and leaf length (Table 3). Digenic inheritance is indicated for the traits height, internode length leaf number and trigenic control in respect of leaf breadth. Tree breeders are often concerned with heritabilities, which become important when selection can be practiced as is done in advanced generation tree improvement, where selections are made from genetic tests (Zobel and Talbert, 1984). Magnitude of heritability in broad sense differed for the different characters. Traits like height, DBH, leaf number (Table 3) leaf length and leaf breadth, exhibited high heritability of more than 80% whereas low heritability (21.8%) was associated with internode length; low heritability may be due to higher environmental influence.

Table 2. Estimation of genetic parameters at the age of 8 years

Characters	D	F	H_1	H_2	h^2	E
Height	65.14**± 17.1	16.55 ± 17.20	981.2** ±189.6	1087.** ±169.3	1190.1** ±114	31.06 ±25
DBH	0.45**± .024	0.309 ±0.03	0.278**±0.040	0.496** ±0.28	0.416** ±0.07	0.086 ±0.013
Internode length	0.927 ± 0.071	0.197 ± 0.17	0.96** ± 0.207	0.98** ±0.19	1.75** ±0.121	0.198** ±0.05
Leaf number	128.4**± 24.2	58.3 ±35.8	1825.5** ± 392	1259.7** ±294	1532** ±191	48.15 ±54
Leaf length	6.50* ± 2.80	8.51 ± 8.0	25.64 ± 9.7	12.62** ±1.93	8.18 ±5.40	1.67 ±1.58
Leaf breadth	3.48** ± 0.55	-0.06 ± 0.48	3.64 ± 0.64	2.97** ±0.7	6.50** ±0.47	0.79** ±0.10

D - component of variation due to additive effect.:
F - Co-variance of additive & dominance effect.
H_1 - Component of variation due to dominance effect of gene.
H_2 - Dominance indicating asymmetry 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 at the age of 8 years

Characters	$(H_1/D)^{1/2}$	$H_2/4H_1$	K_D/K_R	h^2/H_2	heritability (%)	$r(W_r+V_r), y_r$
Height	4.23	0.26	0.73	1.12	89.6	-0.816**
DBH	3.65	0.28	1.10	0.82	89.4	0.836**
Internode length	1.00	0.30	1.21	1.09	21.8	-0.052
Leaf number	3.83	0.20	4.07	1.27	89.4	0.707
Leaf length	1.71	0.17	2.37	0.66	86.5	0.898**
Leaf breadth	1.02	0.11	1.11	2.57	83.9	0.919**

$(H_1/D)^{1/2}$ = 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) versus negative (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.
Heritability (narrow sense)

CONCLUSION

The tree breeding programmes are highly concerned with the gene action and heritablility of the trait of interest toimprove the tree species especialy in *Eucalyptus* species. This experiment we have identified the gene interaction and heritability for the important traits of *Eucalyptus* species through the diallele analysis. By analysing the gene interaction and heritablity nature of the traits can break the impediment on the tree breeding programmes apart from the post fertiliation barrier concerns.

AUTHOR CONTRIBUTIONS

The author has designed the experiment, generated data and reproduced this manuscript.

COMPETING INTERESTS

The author declares that no competing interest for this article.

ETHICS APPROVAL

Not applicable

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