

RECIPROCAL, MATERNAL AND NON-MATERNAL EFFECTS IN RADIATA PINE DIALLEL MATING EXPERIMENT ON FOUR AUSTRALIA SITES

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ABSTRACT

To investigate the importance of the reciprocal effect in a series of Australia-wide radiata pine 6 × 6 half-diallel matings, one diallel mating set was deliberately mated to include reciprocal crosses. At age ten and a half, five traits (DBH, stem straightness, branch angle, branch size and cluster whorl number) were assessed at four sites, and the reciprocal effects were estimated and partitioned into the maternal and non-maternal components.

General combined ability was significant ($P < 0.001$) for DBH, stem straightness, branch angle, and branch size while specific combined ability was significant ($P < 0.039$) for stem straightness, branch angle, and cluster number. The overall reciprocal effect was significant for branch angle only; however, there were reciprocal effects in individual pair-crosses for DBH, branch size and cluster number. A partitioning of these significant reciprocal effects suggests either maternal (e.g. cytoplasmic DNA effect) and non-maternal effects (e.g. interaction effect between nuclear and cytoplasmic DNA) or purely non-maternal interaction may be the causes of the reciprocal effects. The observed overall weak reciprocal effect in this experiment indicates that (1) reciprocal mating could be used if it is easier or cheaper to use a particular parent as female for commercial production in radiata pine, and (2) half-diallel mating is suitable for the mating design to estimate genetic parameters and variance components, and pooling reciprocal crosses into a half-diallel mating structure should be acceptable for the standard half-diallel genetic analysis.

Keywords: diallel cross, GCA, SCA, reciprocal difference, maternal effect, non-maternal effect, *Pinus radiata*

INTRODUCTION

Mating designs are an integral factor of any tree breeding program. As such, they constrain, and are constrained by the choice of breeding strategy and the management of co-ancestry. Crucial to designing a tree breeding strategy is to choose mating designs to accomplish the estimates of parental breeding values and genetic parameters (BRIDGWATER 1992). Half-diallel and balanced factorial mating designs are two popular mating designs in tree breeding programs, because they can provide for excellent estimates of general combining ability (GCA) and specific combining ability (SCA) effects and good management of coancestry (VAN BUIJTENEN 1976; STONECYPHER *et al.* 1996). Since there can be two mating arrangements for each pair-cross in monoecious species in the factorial and half-diallel mating designs (parents can serve as either males and females), one important concern in using factorial and half-diallel mating designs is the possibility of reciprocal effects. The reciprocal effect, if significant, may create operational difficulty in arranging controlled pollination for seed production (i.e. male and female are not inter-changeable in the mating) and in genetic analysis if it was not accounted for.

Trees do not always have equal ability to produce similar amounts of male or female flowers, and they vary in their production of viable seeds. For example, in the plus trees in the Australia radiata pine breeding program, one clone with excellent growth (clone registration 12038) produces very little or no seeds if it is mated as female at early ages. Therefore, this clone is preferred as a male in practical mating designs and in controlled pollination for producing commercial seeds. If there are reciprocal (or rather, favourable maternal) effects for crosses involving this particular clone, these effects cannot be readily used because the clone is best used as a male. Also, in some large factorial or disconnected half-diallel experiments, there are always some prescribed crosses that cannot be made or are very difficult to make owing to unavailability of mature ramets, insufficient flowers, poor pollen viability or poor mating success. To overcome these problems, it is not uncommon for the reciprocals to be used for the most desirable crosses to complete the mating design. This is the case in 21 sets of a 6 × 6 half-diallel mating scheme for radiata pine Australia-wide in the early 1980s. All 21 sets involved reciprocal crosses in the order to make up the desired half-diallel design. If reciprocal effects were considerable in such a design, it would

bias estimates of parental breeding values, genetic parameters, and genetic gain predictions in the usual standard half-diallel genetic analysis. Thus, one needs to examine whether reciprocal effects are important enough to warrant partitioning in the experiments, and to investigate the possible causes of the reciprocal effects. If reciprocal effects are not important, then the half-diallel without self-pollination (method 4 according to Griffing's classification) (GRIFFING 1956) mating design is most suitable for the diallel mating design because it needs relatively few crosses (BRIDGWATER 1992). On the other hand, if there are considerable reciprocal effects, the number of crosses may need to be substantially increased in order to partition reciprocal effects from GCA and SCA effects.

According to COCKERHAM and WEIR (1977), reciprocal effects can be further partitioned into maternal (general reciprocal) and non-maternal (specific reciprocal) effects. This further partition may allow the genetic causes of the reciprocal effects to be inferred: e.g. whether it is a true maternal effect caused by cytoplasmic DNA or due to an interaction between nuclear and cytoplasmic DNA or due to purely environmental effects associated with the particular parent or crosses. If true genetic maternal effects cause the reciprocal effect, it may persist with the age and may be exploited in the production population. If it is due to environment and interaction between environment and genetic factors, it would increase the bias of the genetic analysis if they were not separable, as in the Griffing's number 4 half-diallel mating design.

To our knowledge, no reports could be found of partitioning reciprocal effects into maternal and non maternal effects in tree species although reciprocal effects were tested and estimated in many diallel matings of species, such as *Pseudotsuga menziesii* (CAMPBELL 1971), *Picea sitchensis* (SAMUEL *et al.* 1972), *Pinus strobus* (KRIEBEL *et al.* 1972), *Pinus patula* (BARNES & SCHWEPPENHAUSER 1979), *Pinus elliotti* (PERRY & HAFLEY 1981), *Cunninghamia lanceolata* (YE *et al.* 1981), *Pinus virginiana* (BRAMLETT *et al.* 1983), *Cryptomeria japonica* (SAITO & KAWASAKI 1984), *Pinus taeda* (FOSTER & BRIDGWATER 1986), *Eucalyptus grandis* (WYK & VAN WYK 1990), and *Picea abies* (SKRØPPA 1994). This report presents a method for partitioning the reciprocal effects in an unbalanced half-diallel mating design (with missing crosses) and the results from a radiata pine diallel mating.

MATERIAL AND METHODS

As an integral part of 21 sets of radiata pine 6 × 6 half-diallel mating scheme made in Australia, one set was

deliberately mated to include reciprocal crosses so that the importance of the various reciprocal effects could be investigated. Among 30 possible crosses in the full 6 × 6 diallel mating (excluding selfs), 24 matings were made as illustrated below.

		Male parent					
		1	2	3	4	5	6
Female parent	1			x	x		x
	2	x		x	x	x	x
	3	x	x		x	x	x
	4	x					x
	5	x	x		x		x
	6	x	x	x	x	x	

The progeny from the 24 crosses were planted in July and August of 1987 at four sites across Australian (two in Victoria, one each in South Australia and Western Australia). The seedlings were raised in a Mount Gambier nursery along with other 15 sets of half-diallel. Seedlings were pooled together from several nursery replicates before allocating into different sites, therefore there is no separable effects of nursery bed into different sites and replicates. The original field designs are 12 rows by 18 columns incomplete block design within each replicates for adjusting row and column effects (seedling lots within each row and column were randomized). However, in the implication process, the row and column was not exactly followed due to various topography of each site. Therefore, analyses can only be done as a fully randomized complete block design. Seedlings were planted in three replicates of four-tree row-plots at each site. At the beginning of 1998 seven traits were assessed for each tree, including: DBH – diameter over bark at breast height (1.3 m above ground) to nearest mm; FORK – the number of forks on main bole; STEM – stem straightness, a subjective rating of straightness of stem between 1 and 10 meters above ground with a 6-point scale: 1 = most crooked and twisted trees in the trial, 6 = straightest trees in the trial; BRA – branching angle, a subjective 6-point rating with 1 indicating the worst (steepest) angle and 6 the best (flattest) angle; BRS – branching size, a subjective 6-point rating with 1 the worst (largest) branches and 6 the best (smallest) branches of the trial; RAM – the number of ramicornes from 1 to 10 meters of the bole above ground; CLUST – the cluster number between 1 and 6 meters of the main bole for each tree. After preliminary analyses, it was found that only DBH, STEM, BRA, BRS, and

CLUST had normal distributions, therefore only analyses for these five traits are presented in this report. The following three linear models were used for the analyses. The first model is a family effect model as

$$Y_{lmijk} = \mu + l_i + r_{m(l)} + f_{ij} + lf_{ij} + rf_{mij(l)} + e_{lmijk} \quad [1]$$

where Y_{lmijk} is the individual observation, μ is the grand mean, l_i is the i^{th} site, $r_{m(l)}$ is the m^{th} replicate at the i^{th} site, f_{ij} is the ij^{th} family effect, lf_{ij} is the interaction between the i^{th} site and the ij^{th} family, $rf_{mij(l)}$ is the interaction between the m^{th} replicate at the i^{th} site and the ij^{th} family, and e_{lmijk} is the residual. The second model partitions the family effect into GCA (g_i or g_j), SCA (s_{ij}) and reciprocal (rec_{ij}) effects and the family by site interaction effects into the interactions of GCA by site ($lg_{ii} + lg_{ij}$), SCA by site (ls_{ij}) and reciprocal by site ($lrec_{ij}$):

$$Y_{lmijk} = \mu + l_i + r_{m(l)} + g_i + g_j + s_{ij} + rec_{ij} + lg_{ii} + lg_{ij} + ls_{ij} + lrec_{ij} + e_{lmijk} \quad [2]$$

The third model partitions the reciprocal effect into maternal (m_i) and non-maternal (nm_{ij}) effects, and the reciprocal by site interaction effects ($lrec_{ij}$) into maternal by site ($lm_{ii} + lm_{ij}$) and non-maternal by site (lnm_{ij}) interactions:

$$Y_{lmijk} = \mu + l_i + r_{m(l)} + g_i + g_j + s_{ij} + m_i + m_j + nm_{ij} + lg_{ii} + lg_{ij} + ls_{ij} + lm_{ii} + lm_{ij} + lnm_{ij} + e_{lmijk} \quad [3]$$

Family \times within-site replicate effects were not further partitioned into GCA, SCA, and reciprocal by replicate effects because the complexity of the model and less interest for these effects. All effects are assumed fixed in this analysis in order to estimate effects of single parents, therefore, following restrictions are imposed in order to estimate GCA, SCA, reciprocal, maternal and

non-maternal effects: e.g. $\sum g_i = 0$, $\sum s_{ij} = 0$ for each j with $s_{ij} = s_{ji}$, $rec_{ij} = -rec_{ji}$, $\sum m_i = 0$, $\sum nm_{ij} = \sum nm_{ji} = 0$ with $nm_{ij} = -nm_{ji}$. The formulae for mean of squares and estimated effects (GCA, SCA, reciprocal, maternal and non-maternal effects) have been worked out for balanced design (no missing crosses) (GRIFFING 1956, COCKERHAM & WEIR 1977) and have been incorporated into a computer program (ZHANG & KANG 1997). However, for designs with missing crosses such as our experiment with radiata pine, these formulae are not directly useful for the analysis. Estimates of reciprocal and maternal effects have been estimated by using DIALL program (a Fortran program) when there are missing crosses (SCHAFER & USANIS 1969), but estimation of non-maternal effect was not implemented in the program. Derivation of the appropriate design matrix for the reciprocal effect, maternal effect and non-maternal effects for the mating design is required. This is derived for this particular mating pattern as in Appendix 1. This customised design matrix is incorporated into SAS GLM (Type III) and IML procedures (SAS Institute Inc. 1989) for hypothesis testing and estimating model effects.

RESULTS AND DISCUSSION

Analysis of variance by family effect model (model 1) indicates that all effects (site, replicate, family, site by family, family by replicate interactions) are significant ($P < 0.01$ or $P < 0.05$) for the traits DBH, and CLUST (Table 1). Except for family by replicate interaction effect, all effects are significant for STEM. Similarly, all other effects in the model 1 are significant except for replicate for BRA and BRS, and interaction between replicate and family for BRA. The significant family- and family \times site interaction effects suggest further partitioning of these effects into GCA, and SCA and their interactions with site are meaningful and necessary for the complete genetic analysis.

The partitioning of family effects (Table 2) reveals

Table 1. Analysis of variance of 24 radiata crosses for five traits^a at age 10.5 from planting.

Sources of variation	DF	DBH		STEM ^a		BRA		BRS		CLUST	
		MS	Pr > F	MS	Pr > F	MS	Pr > F	MS	Pr > F	MS	Pr > F
Site	3	22648	0.001	3.426	0.007	4.734	0.002	3.863	0.007	46.02	0.001
Rep(site)	7	4	0.010	1.998	0.020	1.354	0.194	1.600	0.104	6.484	0.013
Family	23	2138	0.001	2.356	0.001	3.294	0.001	2.110	0.001	5.596	0.001
Site*family	67	3212	0.001	1.589	0.001	1.683	0.001	1.952	0.001	5.628	0.001
Rep*family(site)	153	1439	0.001	0.894	0.291	1.134	0.079	1.415	0.001	3.117	0.047
Error	608	1277		0.836		0.952		0.936		2.533	
Total	861	801									

^a STEM - stem straightness, BRA - branching angle, BRS - branching size, CLUST - whorl cluster number.

Table 2. Analysis of variance for the radiata pine 6 × 6 diallel mating design at age 10.5 from planting (partitioning reciprocal effects into maternal and non-maternal effects for five traits).

Source ^a	DF	DBH		STEM		BRA		BRS		CLUST	
		MS	Pr > F	MS	Pr > F	MS	Pr > F	MS	Pr > F	MS	Pr > F
Site	3	128708	0.001	1.906	0.082	5.300	0.001	2.168	0.099	24.977	0.001
Rep site)	7	1857	0.045	2.141	0.014	1.194	0.295	1.974	0.065	5.547	0.043
Gca	5	7516	0.001	2.602	0.009	6.568	0.001	2.747	0.020	2.258	0.516
Sca	9	774	0.561	2.512	0.001	1.954	0.039	0.941	0.517	8.076	0.001
Rec	9	1459	0.107	0.642	0.656	2.833	0.003	1.126	0.369	4.166	0.120
Mat	5	445	0.781	0.442	0.761	3.630	0.002	1.268	0.288	4.892	0.103
Nmat	4	2723	0.017	0.941	0.352	1.823	0.118	1.058	0.395	3.285	0.295
Gca*site	15	1726	0.018	2.609	0.001	2.126	0.007	2.716	0.001	5.544	0.009
Sca*site	24	1241	0.107	1.116	0.145	0.942	0.527	1.776	0.018	5.193	0.004
Rec*site	27	784	0.660	1.842	0.001	2.009	0.002	1.646	0.030	5.231	0.002
Mat*site	15	920	0.429	1.953	0.003	2.273	0.003	2.195	0.008	7.105	0.001
Nmat*site	12	718	0.653	1.574	0.037	1.693	0.059	0.906	0.574	2.553	0.488
Error	762	901		0.850		0.987		1.036		2.667	
Total	861										

^a Rec - reciprocal effect, Mat - maternal effect, Nmat - non maternal effect.

that GCA is generally the main contributor to the family effects among the five traits. This is because GCA is significant in four (DBH, STEM, BRA, and BRS) of the five traits ($P \leq 0.02$), while SCA is significant only in STEM, BRA and CLUST ($P \leq 0.04$, Table 2). The overall reciprocal effect was only significant ($P \leq 0.04$) for one trait (BRA) although $P \leq 0.10$ for DBH and $P \leq 0.12$ for CLUST. Similarly, the interactions between family and site are mainly due to site × GCA effects: site by GCA interactions are all significant for the five traits, while only BRS and CLUST have significant SCA × site interactions. Reciprocal × site interactions are also significant for STEM, BRA, BRS and CLUST.

Partitioning of reciprocal effects into maternal and non-maternal effects for DBH and BRA shows a significant non-maternal effect ($P < 0.02$) for DBH, and a significant maternal effect ($P < 0.01$) for BRA. The non-maternal effect in BRA is significant at $P \leq 0.12$, and maternal effect in CLUST is significant at $P \leq 0.10$. Similarly, further partitioning of significant reciprocal × site interactions for STEM, BRA, BRS and CLUST indicates that the interactions are mainly due to significant maternal by site interaction. This is because non-maternal by site interaction is significant only for

STEM ($P < 0.01$) while for all four maternal × site interactions ($P < 0.05$).

Detailed examination of reciprocal effects and their partition into maternal and non-maternal effects in Table 3 reveals:

1. The reciprocal effect for the pair-wise mating between parents 2 and 5 (R25) is significant for DBH ($P < 0.02$). None of the six maternal reciprocal effects are significant for DBH, however, non-maternal effect of parents 2 and 5 (N25) and parents 5 and 6 (N56) are highly significant ($P < 0.001$). This indicates the non-maternal reciprocal effects for N25 and N56 are the contributors to the reciprocal effect involving parents 2 and 5 (R25).

2. The reciprocal effects for two mating pairs (parents 1 and 4, and parents 2 and 6) are significant for BRA ($P < 0.02$ and $P < 0.002$, respectively). The significant reciprocal effect between parents 2 and 6 is associated with the maternal effect of parent 6 (M6) and the non-maternal reciprocal effect between parents 2 and 6 (N26) because M6 and N26 are highly significant ($P < 0.003$ and $P < 0.007$, respectively).

3. The reciprocal effect for the mating pair of parents 4 and 6 is highly significant for CLUST ($P < 0.001$). This may be due to the significant maternal

Table 3. Estimated GCA (G), SCA (S), reciprocal (R), maternaô (M). And non-maternal (N) effects for the radiata pine 6 × 6 diallele mating design at age 10.5.

Parameter	DBH	STEM	BRA	BRS	CLUST
G1	-2.499	-0.090	0.255***	0.069	-0.085
G2	-4.601*	-0.045	-0.209**	0.013	-0.103
G3	3.862	0.229**	-0.248**	-0.017	0.292*
G4	-3.812	-0.100	0.163	0.092	-0.094
G5	-5.860*	-0.126	-0.022	0.103	-0.011
G6	12.911***	0.134*	0.060	-0.261***	0.001
S12	-2.860	-0.001	0.109	-0.045	0.030
S13	-3.271	0.193	0.108	0.242*	0.484**
S14	1.488	0.069	-0.134	-0.050	-0.134
S15	7.418	-0.104	0.125	-0.174	-0.148
S16	-2.775	-0.157	-0.208	0.027	-0.231
S23	4.913	-0.213	-0.217	-0.133	-0.512**
S24	-0.277	0.369**	-0.003	0.047	0.093
S25	-3.660	0.230**	0.221	0.179	0.487**
S34	2.195	-0.443***	0.287*	-0.001	0.032
S35	-3.003	0.478*	-0.257	-0.117	0.107
S45	-2.942	-0.117	-0.239	0.052	-0.440
S26	1.884	0.075	-0.110	-0.048	-0.099
S36	-0.834	-0.014	0.079	0.009	-0.112
S46	-0.463	0.122	0.090	-0.047	0.449*
S56	2.187	-0.025	0.149	0.058	-0.005
R13	-2.069	-0.139	0.119	-0.008	-0.301
R14	5.278	0.004	0.264*	-0.199	-0.023
R16	-0.178	0.213	0.007	-0.076	0.103
R23	-4.438	-0.053	0.180	0.301*	0.012
R25	7.834*	0.034	0.185	-0.091	0.132
R26	-4.854	0.058	-0.357**	0.026	0.142
R36	-0.421	0.009	-0.133	-0.001	0.029
R46	-0.075	-0.126	-0.221	-0.004	-0.637***
R56	6.294	0.006	-0.088	-0.059	-0.088
M1	1.053	0.016	0.114	-0.106	-0.107
M2	-0.140	0.025	0.003	0.074	0.183
M3	2.391	0.069	-0.060	-0.105	0.150
M4	-2.110	-0.073	-0.119	0.051	-0.327*
M5	-1.073	-0.01	-0.066	0.067	0.027
M6	-0.121	-0.027	0.132**	0.018	0.073
N13	-0.735	-0.085	-0.055	-0.007	-0.042
N14	2.084	-0.084	0.030	-0.041	-0.242*
N16	-1.349	0.169*	0.025	0.048	0.284
N23	-2.188	-0.001	0.115	0.130	-0.003
N25	7.017***	-0.003	0.112	-0.100	-0.028
N26	-4.828	0.005	-0.227**	-0.029	0.032
N36	-2.923	-0.087	0.059	0.122	-0.045
N46	2.084	-0.084	0.030	-0.041	-0.242*
N56	7.017***	-0.003	0.112	-0.100	-0.028

*, **, and *** represent significant level at 5%, 1%, and 0.1% probability, respectively.

effect of parent 4 (M4, $P < 0.01$) and/or the significant non-maternal reciprocal effects between parents 1 and 4 (N14, $P < 0.05$), and between parents 4 and 6 (N46, $P < 0.05$).

It is commonly believed that maternal effects are due to epigenetic effects (such as cytoplasmic genetic

factors or environmental preconditioning) of the mother tree, while non-maternal reciprocal effects are due to interaction between nuclear and cytoplasmic genetic factors or interaction between the environment of the mother tree with nuclear genetic factors (BORGES 1987). A number of possible extra-nuclear maternal

effects, dependent upon the tree under consideration, have been recognised, including seed weight, seed coat thickness, polyembryony, time of seed collection, seed stratification, etc. (CANNELL *et al.* 1978, ROBINSON & VAN BUIJTENEN 1979, PERRY & HAFLEY 1981, DUNLAP & BARNETT 1983, SORENSON & CAMPBELL 1993). A number of authors have reported significant reciprocal or maternal effect in progeny trials involving diallel crosses, (*Pseudotsuga menziesii*, CAMPBELL 1971; *Pinus strobus*, KRIEBEL *et al.* 1972; *Picea sitchensis*, SAMUEL *et al.* 1972; *Pinus elliotii*, PERRY & HAFLEY 1981; *Cunninghamia lanceolata*, YE *et al.* 1981; *Pinus virginiana*, BRAMLETT *et al.* 1983; *Picea abies*, SKRØPPA 1994), while others found reciprocal and maternal effects were trivial (*Pinus patula*, BARNES & SCHWEPPEHAUSER 1979; *Cryptomeria japonica*, SAITO & KAWASAKI 1984; *Pinus taeda*, FOSTER & BRIDGWATER 1986; *Eucalyptus grandis*, WYK & VAN WYK 1990). In radiata pine, seed size effect was observed up to 32 weeks after sowing in seedlings (GRIFFIN 1981), and initial differences in height growth between reciprocal families was related to seed size, however, the influence of reciprocal differences in seed size on height growth had reduced after two years' growth in the field (WILCOX 1983).

The effect of environmental preconditioning of mother tree may disappear after a period of seedling growth, but its existence in the first few years complicates effective early selection (WU *et al.* 1995). Similarly, the non-maternal reciprocal effect: e.g. the interaction between mother tree environment and nuclear genetic factors of the father tree may disappear later on. However, the effect of mother tree cytoplasmic genetic factors or the interaction between cytoplasmic genetic factors of mother tree and nuclear genetic factors of father tree may persist as the tree grows.

At age ten and half years, the preconditioning effect of mother tree environment may not be important anymore even if it existed at earlier ages. However, canopy closes usually at ages 5 and 6 for these trials. If maternal effect does not disappear at these ages, they may reinforce by competition. In this radiata pine experiment, we observed that overall reciprocal effect was not an important feature since only BRA had a significant reciprocal effect. There are, however, some individual significant reciprocal and maternal or non-maternal effects. These significant maternal and non-maternal effects at this late age may be due purely to cytoplasmic genetic factors and their interaction with nuclear genetic factors. The significant reciprocal effect between parents 2 and 6 (R26), coupled with the significant maternal effect for parent 6 (M6) and non-maternal effect between parents 2 and 6 (N26) for BRA, suggest that this reciprocal effect is caused by

cytoplasmic DNA or by the interaction between nuclear and cytoplasmic DNA. This may explain the significant reciprocal effect between parents 4 and 6 (R46) for CLUST since there is a significant maternal effect from parent 4 (M4) and non-maternal effect between parents 4 and 6 (N46) for CLUST.

The significant reciprocal effect, caused purely by non-maternal interaction, such as the effect between parents 2 and 5 (R25) for DBH, (i.e. insignificant M2 and M5 effects, but significant N25 effect), may indicate that there is interaction between nuclear and cytoplasmic DNA for parents 2 and 5.

The implications of our observations in this radiata pine diallel experiment are:

1. Half-diallel mating is thus confirmed as suitable for the mating design to estimate genetic parameters and variance components. Pooling reciprocal crosses into a half-diallel mating structure should be acceptable for standard half-diallel genetic analyses.

2. Reciprocal mating could be used if it is operationally easier and cheaper to use a particular parent as female for commercial production and mating design in radiata pine.

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REFERENCES

- BARNES, R. D. & SCHWEPPEHAUSER, M. A. 1979: Genetic control of 1,5-year-old traits in *Pinus patula* Schiede et Deppe and a comparison of progeny test methods. *Silvae Genet.* **28**:156–167.
- BORGES, O. L. F. 1987: Diallel analysis of maize resistance to sorghum downy mildew. *Crop Sci.* **27**:178–180.
- BRAMLETT, D. L., DELL, T. R. & PEPPER, W. D. 1983: Genetic and maternal influences on Virginia pine seed germination. *Silvae Genet.* **32**:1–4.
- BRIDGWATER F. E. 1992: Mating designs. In: Handbook of quantitative forest genetics. Edited by Fins, L., Friedman, S.T., Brotschol, J.V., Pp.69–95. Kluwer Academic Publishers.
- CAMPBELL, R. K. 1971: Genetic variability in juvenile height growth of Douglas-fir. *Silvae Genet.* **21**:126–129.
- COCKERHAM, C. C. & WEIR, B. S. 1977: Quadratic analyses of reciprocal crosses. *Biometrics* **33**:187–203.
- CANNELL, M. G. R., BRIDGWATER, F. E. & GREENWOOD, M. S. 1978: Seedling growth rates, water stress responses and root-shoot relationships related to eight-year volumes among families of *Pinus taeda* L. *Silvae Genet.* **27**: 237–247.
- DUNLAP, J. R. & BARNETT, J. P. 1983: Influence of seed size on germination and early development of loblolly pine

- (*Pinus taeda* L.) germinates. *Can. J. For. Res.* **13**:40–44.
- FOSTER, G. S. & BRIDGWATER, F. E. 1986: Genetic analysis of fifth-year data from a seventeen parent partial diallel of loblolly pine. *Silvae Genet.* **35**:118–122.
- GRIFFIN, A. R. 1981: The effects of seed size, germination time and sowing density on seedling development in radiata pine. *Aust. For. Res.* **5**:25–28.
- GRIFFING, B. 1956: Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* **9**:463–493.
- KRIEBEL, H. B., ROBERDS, J. H. & COX, R. V. 1972: Genetic variation in vigor in a white pine incomplete diallel cross experiment at age 6. In: Proc. Eighth Central State Forest Tree Improvement Conference, School of For., Univ. of Missouri. Pp.40–42.
- PERRY, T. O. & HAFLEY, W. L. 1981: Variation in seedling growth rates: their genetic and physiological bases. In: Proc. South Forest Tree Improvement 16th Conference, Blacksburg, Virginia. Pp. 288–301.
- ROBINSON, J. F. & VAN BUIJTENEN, J. P. 1979: Correlation of seed weight and nurserybed test with 5-, 10-, 15-year progeny test results. *For. Sci.* **25**:591–596.
- SAMUEL, C. J. A., JOHNSTONE, R. C. B. & FLETCHER, A. M. 1972: A diallel cross in Sitka spruce: assessment of first year characters in an early glasshouse test. *Theor. Appl. Genet.* **42**:53–61.
- SAS Institute Inc. 1989. SAS/STAT User's Guide, Version 6, Fourth Edition, Volume 1&2, Cary, NC. SAS Institute INC. 943pp, 846 pp.
- SAITO, T. & KAWASAKI, H. 1984: Studies on flowering characteristics and their heredity in *Cryptomeria japonica* D. Don. Bulletin of Japanese Forestry and Forest Products Research Institute. Pp. 17–41.
- SCHAFFER, H. E. & USANIS, R. A. 1969: General least squares analysis of diallel experiments. North Carolina State University, Genetics Department Research Report Number 1. 61 pp.
- SKRØPPA, T. 1994: Growth rhythm and hardiness of *Picea abies* progenies of high altitude parents from seed produced at low elevations. *Silvae Genet.* **43**:95–100.
- SORENSEN, F. C. & CAMPBELL, R. K. 1993: Seed weight – seedling size correlation in coastal Douglas-fir: genetic and environmental components. *Can. J. For. Res.* **23**:275–285.
- STONECYPHER, R. W., PIESCH, R. F., HELLAND, G. G., CHAPMAN, J. G. & RENO, H. J. 1996: Results from genetic tests of selected parents of Douglas-fir (*Pseudotsuga menziesii* [Mirb] Franco) in an applied tree improvement program. *For. Sci.* **42**(2) Monograph 32.
- VAN BUIJTENEN, J. P. 1976: Mating Designs. In: Proc. of the IUFRO Joint Meeting of Genetic Working Parties on Advanced Generation Breeding. Bordeaux, pp.11–27.
- WILCOX, M. D. 1983: Reciprocal cross effects in *Pinus radiata*. *N. Z. J. For. Sci.* **13**: 37–45.
- WU, H. X., YEH, F. C., DANCİK, B. P., PHARIS, R. P., DHIR, N. K. & ISRAEL, B. J. 1995: Genetic parameters of greenhouse growth and performance of 2-year *Pinus contorta* subsp. *latifolia*. *Scand. J. For. Res.* **10**:12–21.
- WYK, G. & VAN WYK, G. 1990: Genetic improvement of timber yield and wood quality in *Eucalyptus grandis* (Hill) Maiden. Part 1. Genetic parameters of growth characteristics. *South African Forestry Journal* **153**:1–11.
- YE, P. H., CHEN, Y. W., LIU, D. L., RUAN, Y. C., CHEN, S. B., GUO, M. C., LIN, Q. Y., ZHENG, Y. H. & ZHOU, C. G. 1981: Application of the analysis of the combining ability of the quantitative genetics study of Chinese fir. *Journal of Nanjing Technological College of Forest Products* **3**:1–21.
- ZHANG, Y. & KANG, M. S. 1997: Diallel-SAS: A SAS program for Griffing's diallel analyses. *Agron. J.* **89**:176–182.

Appendix 1. Design matrix for estimating reciprocal, maternal and non-maternal effects for the 6 × 6 diallel of radiata pine (F and M are indexed for female and male parents, and R, M, and N, are indexed for reciprocal, maternal and non-maternal effects).

F	M	R13	R14	R16	R23	R25	R26	R36	R46	R56	M1	M2	M3	M4	M5	N13	N14	N23	N24	N25	N34	N35
1	3	1	0	0	0	0	0	0	0	0	1	0	-1	0	0	1	0	0	0	0	0	0
1	4	0	1	0	0	0	0	0	0	0	1	0	0	-1	0	0	1	0	0	0	0	0
1	6	0	0	1	0	0	0	0	0	0	2	1	1	1	1	-1	-1	0	0	0	0	0
2	1	0	0	0	0	0	0	0	0	0	-1	1	0	0	0	0	0	0	0	0	0	0
2	3	0	0	0	1	0	0	0	0	0	0	1	-1	0	0	0	0	1	0	0	0	0
2	4	0	0	0	0	0	0	0	0	0	0	1	0	-1	0	0	0	0	1	0	0	0
2	5	0	0	0	0	1	0	0	0	0	0	1	0	0	-1	0	0	0	0	1	0	0
2	6	0	0	0	0	0	1	0	0	0	1	2	1	1	1	0	0	-1	-1	-1	0	0
3	1	-1	0	0	0	0	0	0	0	0	-1	0	1	0	0	-1	0	0	0	0	0	0
3	2	0	0	0	-1	0	0	0	0	0	0	-1	1	0	0	0	0	-1	0	0	0	0
3	4	0	0	0	0	0	0	0	0	0	0	0	1	-1	0	0	0	0	0	1	0	0
3	5	0	0	0	0	0	0	0	0	0	0	0	1	0	-1	0	0	0	0	0	0	1
3	6	0	0	0	0	0	0	1	0	0	1	1	2	1	1	1	0	1	0	0	-1	-1
4	1	0	-1	0	0	0	0	0	0	0	-1	0	0	1	0	0	-1	0	0	0	0	0
4	6	0	0	0	0	0	0	0	1	0	1	1	1	2	1	0	1	0	1	0	1	0
5	1	0	0	0	0	0	0	0	0	0	-1	0	0	0	1	0	0	0	0	0	0	0
5	2	0	0	0	0	-1	0	0	0	0	0	-1	0	0	1	0	0	0	0	-1	0	0
5	4	0	0	0	0	0	0	0	0	0	0	0	0	-1	1	0	0	0	0	0	0	0
5	6	0	0	0	0	0	0	0	0	1	1	1	1	1	2	0	0	0	0	1	0	1
6	1	0	0	0	-1	0	0	0	0	0	-2	-1	-1	-1	-1	1	1	0	0	0	0	0
6	2	0	0	0	0	0	-1	0	0	0	-1	-2	-1	-1	-1	0	0	1	1	1	0	0
6	3	0	0	0	0	0	0	-1	0	0	-1	-1	-2	-1	-1	-1	0	-1	0	0	1	1
6	4	0	0	0	0	0	0	0	-1	0	-1	-1	-1	-2	-1	0	-1	0	-1	0	-1	0
6	5	0	0	0	0	0	0	0	0	-1	-1	-1	-1	-1	-2	0	0	0	0	-1	0	-1