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Reciprocal and Maternal Effects on Growth and Form Traits in Radiata Pine in New Zealand

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Abstract

The information from two experiments was used to study reciprocal and maternal effects on several growth and form traits in *Pinus radiata.* In *Experiment 1*, 10 families and their reciprocals obtained from a 5 x 5 diallel experiment were planted across three sites. In *Experiment 2*, 17 parents were used in a partial diallel design and all available crosses were planted at a single site. All three sites for *Experiment 1* were assessed at 9 years of age. The site for *Experiment 2* was assessed at the age of 6-years. Four growth and form traits, namely diameter at breast height (DBH), straightness (STR), branching (BR) and malformation (MAL) were measured in both experiments while needle retention (NRA) was assessed only in *Experiment 1.*

General combining ability (GCA) effects, in *Experiment 1*, were found to be significant for all traits. The overall reciprocal effects were, in general, found insignificant at all three sites. Further partitioning of the reciprocal effect revealed that maternal effect was non-significant for all traits at all three sites and non-maternal (or residual reciprocal) effect was significant only for BR at Site 1 and for NRA at Site 2. The interaction of reciprocal by site effect was found non-significant for all traits. Analysis of *Experiment 2* revealed significant overall reciprocal effects for all traits. Further partitioning of reciprocal effects revealed that maternal effect was significant for all traits except STR, but non-maternal effects were significant for STR and BR only. This study showed that existence of maternal and non-maternal effects could vary considerably for different sets of parents. Estimated correlation between parental GCA estimates obtained with-and-without taking into account reciprocal effects were 0.99 for all growth and form traits considered in this study.

Key words: Reciprocal effect, maternal effect, radiata pine, general and specific combining abilities.

Introduction

In monoecious tree species, like *Pinus radiata*, it is possible to use the same tree both as a male and a female parent in controlled crossing. Assuming normal diploid chromosomal inheritance, each parent contributes genes equally to the offspring. Thus, the progeny of m_i x f_j (i^{th} tree as male and j^{th} tree as female) are expected to be, on the average, genetically similar to those of m_j x f_i (i^{th} tree as female and j^{th} tree as male). The difference in the performance of a full-sib family when a parent is functioning as the mother or the father is termed as reciprocal effect. Reciprocal crosses may not perform the same owing to early phenotypic differences between them in the size and vitality of the embryos, associated with respective peculiarities

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in the maternal tissues of the seed (SWEET and WAREING, 1966; WILCOX, 1983).

WILCOX (1983) reported significant reciprocal cross effects on the early seedling growth in radiata pine. Ignorance of reciprocal effects when they are present might result in incorrect selection of candidates and thus resulting in loss of genetic gain (WILCOX, 1983; WU and MATHESON, 2001). The obvious questions arise about how large and persistent are these reciprocal effects at the time of selection age in radiata pine? Can these reciprocal effects be interpreted as maternal effects? Do they cause any significant mistakes in the estimation of breeding values of parents? Recently, WU and MATHESON (2001) evaluated reciprocal effects in a 6 x 6 diallel experiment at four Australian sites. The objective of this study is to test whether such effects exist in radiata pine breeding population in New Zealand conditions. In tree breeding programs, diallel mating designs are commonly used to obtain estimates of general combining ability (GCA) and specific combining ability (SCA) effects (VAN BUIJTENEN, 1976). The present study was conducted to investigate the existence of reciprocal effects, by using information from two diallel experiments, at the selection age for growth and form traits in radiata pine.

Materials and Methods

The information from two separate experiments was used in this study. The details of the mating design and the field design for these experiments are given below.

Experiment 1

A series of trial was planted at 11 locations in 1975 for the purpose of evaluating genotype by environment interaction. Six block replicates of each of the five sets of 5 x 5 half-diallel were planted at each site. Within each block replicate, each diallel was randomly assigned to one of the sub-blocks. Five trees from each full-sib cross per diallel were randomised as single-tree plots within that diallel's sub-block. Full details of these experiments are given in CARSON (1991). Reciprocal crosses obtained from only one set of 5 x 5 half-diallel mating were included in this experiment to study the importance of the various reciprocal effects on various economic traits. Self-families of the parents involved were not obtained. A 5 x 5 half-diallel mating design resulted in 10 full-sib families and there were a total of 20 crosses when reciprocals were also obtained for each family. These reciprocal crosses were planted at three sites only. For simplicity, these sites will be called as Site 1, Site 2 and Site 3 in the following text.

Experiment 2

The partial-diallel mating structure involving 17 parents is shown in *Appendix 1*. Out of a total of 71 crosses made in this experiment, reciprocals were successfully created only for 26 crosses. Among 17 parents, there were 5 parents (1, 2, 4, 5 and 10) that are currently being used as female testers for estimation of breeding values of pollen parents in the New Zealand radiata pine breeding programme. Thirty-two replicates of single-tree plots of all available crosses were planted at one site only.

Assessment Details and Statistical Analysis

Various growth and form traits at all three sites (Site 1, Site 2 and Site 3) of *Experiment 1* were measured at the age of 9 years. Full assessment details of *Experiment 1* are given in CARSON (1991). The single site for *Experiment 2* was assessed at 6 years of age. The traits measured and the assessment criteria are given in *Table 1*. The locations of the various trials are shown in *Table 2*.

Appendix 1. – Mating structure among 17 parents involved in Experiment 2. No crosses were made corresponding to the blank cells.

	Male																
Female	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1						x	x	x	x								
2						x	x	x									
3								x	x								
4						x	x	x	x				x	x	x	x	x
5						x	x	x	x				x	x	x	x	x
6	x	x	x	x	x												
7	x	x	x														
8			x														
9	x	x	x	x	x												
10													x	x	x	x	x
11													x	x	x	x	x
12													x	x	x	x	x
13				x	x					x	x	x					
14				x							x	x					
15											x	x					
16											x	x					
17					x						x	x					

Table 1. – Assessment criteria for various growth and form traits.

Trait (code)	**Units**	**Description**
Diameter (DBH)	millimeters	Measured at breast-height at age 6 (DBH06) and 9 (DBH09) years.
Straightness (STR)	1 to 9 visual scale	1 = most crooked, 9 = very straight. Measured at age 6 (STR06) and 9 (STR09) years.
Branch Habit (BR)	1 to 9 visual scale	1 = fewest branch clusters, 9 = most clusters. Measured at age 6 (BR06) and 9 (BR09) years.
Malformation (MAL)	1 to 9 visual scale	1 = multiple forking, 9 = no forks. Measured at age 6 (MAL06) and 9 (MAL09) years.
Needle Retention (NRA)	1 to 6 visual scale	1 = about half of first-year needles retained, 6 = all first-, second-, and third-year needles retained. Measured at age 9 years (NRA09).

Table 2. – Site latitude, altitude (m), mean-annual rainfall (mm), the year of planting and assessment for *Experiment 1* and *Experiment 2*.

Experiment	Site	Latitude	Altitude	Rainfall	Planting	Assessment
1	1. Maramarua	$37^{0}15'$	107	1263	1975	1984
	2. Golden Downs	$41^{0}43'$	670	1307	1975	1984
	3. Kaingaroa Cpt. 327	$38^{0}30'$	580	1483	1975	1984
2	1. Tarawera	$38^{0}7'$	60	1397	1994	2000

As the main objective of this study was to test whether the performance of a full-sib family is dependent on which of the parents is functioning as a female or male parent, the model given below should be satisfactory for testing whether or not such reciprocal effect occurs (e.g., LINDGREN and WANG, 1986; DORMLING and JOHNSON, 1992) at each site:

$$y_{jklm} = \mu + b_j + f_k + r_l(f_k) + e_{jklm} \tag{1}$$

where y_{jklm} is the individual observation, μ is the general mean, b_j is the effect of j^{th} block, f_k is the aggregate ($m_i \times f_j$ and $m_j \times f_i$) effect of full-sib family k, $r_l(f_k)$ is the effect of reciprocal l within family k, e_{jklm} is the residual. Family x block interaction effects (applicable only for *Experiment 1*) were not included in this model because they were found insignificant in preliminary analysis. This model was implemented using SAS PROC GLM (SAS INSTITUTE, 1989).

When the reciprocal effects prove significant in *Model 1*, they can be partitioned into maternal and non-maternal (or residual reciprocals) effects. The family effects in *Model 1* were also further partitioned into GCA and SCA effects. For this purpose, the following model (COCKERHAM and WEIR, 1977), which is the expanded version of *Model 1*, was used at each site:

$$y_{ijk} = \mu + b_k + g_i + g_j + s_{ij} + m_i + m_j + r_{ij} + e_{ijk} \qquad (2)$$

where b_k is the effect of k^{th} block (or replicate), g_i and g_j is the additive contributions (GCA) of parents i and j; s_{ij} is non-additive interaction (SCA); m_i and m_j is the maternal effects of parents i and j; r_{ij} is the difference caused by the direction of the cross between parents i and j; e_{ijk} is the residual. It is assumed that the variance of the additive effects through mothers and fathers are identical, $s_{ij} = s_{ji}$ and $r_{ij} = -r_{ji}$. *Model 2* was used for partitioning the overall reciprocal effects into maternal and residual reciprocal (or non-maternal) effects at each site of both experiments. *Model 2* was implemented using computer programme DIALL based on generalised least-squares (GLS) analysis (SCHAFFER and USANIS, 1969).

For across-site analysis of the reciprocal effects in *Experiment 1*, the following model was used:

$$y_{ijklm} = \mu + s_i + b_j(s_i) + f_k + r_l(f_k) + s_i \times f_k + r_l(f_k) \times s_i + e_{ijklm} \quad (3)$$

where s_i is the effect of i^{th} site, $b_j\,(s_i)$ is the effect of j^{th} block within the i^{th} site, f_k is the aggregate effect of full-sib family k, $r_l(f_k)$ is the effect of reciprocal l within family k, $s_i \times f_k$ is the interaction between k^{th} cross and the i^{th} site, $r_l(f_k) \times s_i$ is the interaction between the reciprocal and site effects. When the family by site interaction effect is significant, *Model 3* can be expanded to study the interaction of GCA and SCA effects with the environment. Similarly, when the overall reciprocal by site interaction is significant, the interaction of maternal and non-maternal effects with the environment can be studied. All effects in *Model 1–3* were assumed fixed in this study.

If reciprocal effects are significant, it could bias estimates of parental breeding values especially if there is imbalance in the mating scheme. When reciprocal effects were found significant in this study, parental GCA estimates were obtained with-and-without accounting for reciprocal effects. Estimates of correlation between these two estimates of parental GCA were obtained to study what the impact the exclusion of reciprocal effects would have on parental GCA (or their ranking). This analysis was implemented using model developed by WU and MATHESON (2001).

Results and Discussion

Experiment 1

Individual-Site Analysis

Analysis of variance (*Model 1*) of *Experiment 1* revealed that the family effect was significant for DBH09 and NRA09 at Site 1 and for all traits except STR09 at Site 2 (*Table 3*). The results of the partitioning (using *Model 2*) of the family effects into GCA and SCA effects are also shown in *Table 3*. GCA effects were found significant ($P < 0.05$) for all traits except STR09 and MAL09 at Site 1 and STR09 at Site 2. SCA effects were non-significant for all traits at Site 2, but significant only for NRA09 at Site 1. At Site 3, SCA was significant in three (DBH09, MAL09 and NRA09) of the five traits. The general pattern of non-significant SCA revealed that GCA was the main contributor to the family effects. CARSON (1991) using data from 11 sites (including three sites considered in *Experiment 1*) showed that relative importance of SCA component was 22, 8, 3, 0 and 4 percent for DBH09, STR09, BR09, MAL09, NRA09 respectively. WU and MATHESON (2001) also reported non-significance of SCA effects for various growth and form traits in a 10.5 year old 6 x 6 diallel experiment.

Table 3. – The mean sums-of-squares and the corresponding significance level (*p*-values in parenthesis) for various traits in *Experiment 1.* All traits were assessed at age 9 years. DBH09: diameter; STR09: straightness; BR09: branching; MAL09: malformation; NRA09: needle retention. * ResReci = Residual Reciprocal.

Source	DF	DBH09	STR09	BR09	MAL09	NRA09
Site 1						
Replication	5	16599 (0.001)	8.3 (0.016)	10.6 (0.003)	5.3 (0.011)	27.0 (0.001)
Family	9	5879 (0.001)	3.8 (0.249)	5.4 (0.056)	1.8 (0.431)	5.5 (0.001)
GCA	4	9515 (0.000)	6.8 (0.058)	9.1 (0.015)	3.3 (0.111)	8.6 (0.001)
SCA	5	2969 (0.072)	1.3 (0.813)	2.5 (0.511)	0.5 (0.909)	2.9 (0.003)
Reciprocals	10	407 (0.985)	2.6 (0.566)	5.9 (0.030)	1.4 (0.615)	0.6 (0.628)
Maternal	4	249 (0.953)	3.5 (0.312)	3.1 (0.381)	0.7 (0.811)	0.1 (0.967)
ResReci*	6	513 (0.909)	1.9 (0.694)	7.8 (0.015)	1.9 (0.367)	1.0 (0.284)
Error	410	1457	2.9	2.9	1.8	0.80
Site 2						
Replication	5	7157 (0.001)	56.1 (0.001)	30.2 (0.001)	0.8 (0.912)	8.5 (0.001)
Family	9	1544 (0.042)	1.1 (0.862)	9.1 (0.001)	5.8 (0.032)	3.0 (0.001)
GCA	4	2592 (0.011)	1.4 (0.608)	16.5 (0.001)	9.6 (0.009)	5.1 (0.001)
SCA	5	707 (0.482)	0.8 (0.857)	3.3 (0.486)	2.7 (0.436)	1.3 (0.085)
Reciprocals	10	1464 (0.049)	3.1 (0.137)	5.9 (0.107)	2.3 (0.604	1.7 (0.004)
Maternal	4	1416 (0.128)	1.9 (0.446)	5.6 (0.200)	3.0 (0.366)	0.8 (0.281)
ResReci*	6	1496 (0.079)	3.9 (0.084)	6.1 (0.132)	1.8 (0.684)	2.3 (0.002)
Error	446	787	2.1	3.7	2.8	0.67
Site 3						
Replication	5	1909 (0.030)	19.3 (0.001)	28.7 (0.001)	0.89 (0.953)	48.9 (0.001)
Family	9	9121 (0.001)	9.1 (0.001)	32.5 (0.001)	11.6 (0.002)	6.7 (0.001)
GCA	4	16035 (0.001)	18.2 (0.001)	69.5 (0.001)	11.9 (0.019)	12.9 (0.001)
SCA	5	3589 (0.001)	1.8 (0.665)	3.0 (0.534)	11.3 (0.016)	1.8 (0.002)
Reciprocals	10	1289 (0.081)	2.1 (0.687)	2.6 (0.701)	1.8 (0.923)	0.3 (0.823)
Maternal	4	1134 (0.206)	1.8 (0.634)	3.1 (0.489)	2.0 (0.745)	0.3 (0.669)
ResReci*	6	1393 (0.093)	2.3 (0.565)	2.3 (0.700)	1.7 (0.867)	0.3 (0.740)
Error	529	766	2.8	3.6	4.0	0.46

While the overall reciprocal effect was non-significant for all traits at Site 3, it was significant ($P < 0.05$) for BR09 at Site 1, and for DBH09 and NRA09 at Site 2 (*Table 3*). The partitioning (using *Model 2*) of the overall reciprocal effects into the maternal and non-maternal (or residual reciprocal) effects revealed that the maternal effects were non-significant for all traits at all three sites of *Experiment 1*. The non-maternal (or residual reciprocal) effects were also non-significant for all traits except BR09 at Site 1 and for NRA09 at Site 2 (*Table 3*). WU and MATHESON (2001), using a 6 x 6 diallel, also reported non-significant overall reciprocal effects for various growth and form traits including diameter, branching and straightness.

Across-Site Analysis

The results of analysis of variance (*Model 3*) to study the significance of reciprocal x site interaction effects in *Experiment 1* are presented in *Table 4*. While the family effect was found significant, the overall reciprocal effects were non-significant for all traits except needle retention (NRA09). This is similar to results obtained from analysing each site separately (*Table 3*). The family x site interaction effect was significant for all traits except BR09 and STR09. Further partitioning into the GCA x site and the SCA x site interaction effects revealed that while the former was significant but the latter was non-significant for all traits (results not shown). CARSON (1991) and WU and MATHESON (2001) also reported that the interactions between family and site were mainly due to site x GCA effects.

In general, overall reciprocal effects in *Experiment 1* of this study and also in WU and MATHESON study were non-significant, but the interaction of reciprocal x site effect was significant only in WU and MATHESON study. Genotype x site interaction is generally not important in radiata pine in New Zealand (SHELBOURNE, 1972; CARSON, 1991). Results from this study (*Table 4*) indicate that similar conclusion could be drawn for reciprocal x site interaction. As the overall reciprocal x site interaction effect was non-significant (*Table 4*), no attempt was made to test the significance of the interaction of the maternal and non-maternal effects with the environment.

Experiment 2

GCA effects were found significant ($P < 0.05$) for all traits while SCA effects were non-significant only for the DBH06