

Table 9. — Summary of analysis of variance and variance components for individual chromosome for Limones and Guanaja.

Chromosome No.	Entry No.	Sources of variation	d.f.	Test against entry	Short arm			Long arm		
					MS	F	CV (%)	MS	F	CV (%)
1		Provenances (P)	1	2	39.50	*	23.97			
5	2	Trees (T) in (P)	8	3	5.43	NS	4.78			
	3	Error	40		4.06		71.25			
1		Provenances (P)	1	2				65.42	*	20.66
11	2	Trees (T) in (P)	8	3				7.47	NS	0.00
	3	Error	40					8.74		79.34

MS= Mean square  
F = Variance ratio  
CV= Variance component

\* = Significant at P < 0.05 of probability  
NS = Not significant at P < 0.05 of probability

NOTE: This table is a summary of only those variables that present significant differences.

In *P. caribaea* var. *hondurensis* as in other pine species, it was found that the mitotic chromosomes are too long and of simple morphology. The similarity between chromosome pairs in terms of relative length, principally from chromosome 2 to 9, is such that misclassification can easily take place. The phenomenon of inversion with respect to arm a or b can occur, because 11 of the 12 chromosomes are metacentrics.

The differences detected in this study may not be conclusive for the above mentioned difficulties. A more detailed analysis is necessary to confirm these findings.

The use of haploid tissue, such as female gametophyte tissue, is recommended because the chromosomes are not excessively compressed and their morphological details can be easily analysed in this material.

If differences at chromosome level are not detectable in this variety of *Pinus*, the phenotypic differences already observed between provenances in other studies (BARNES *et al.*, 1980; SALAZAR, 1981), could be the result of changes at the gene level.

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## Limits of Artificial Selection under Balanced Mating Systems with Family Selection

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### Abstract

Two mating systems, pair mating and partial diallel mating, were evaluated with respect to three parameters single generation gene frequency advance ( $\Delta q$ ), ultimate probability of allele fixation (u), and the time required to fix or lose an allele (t). These three parameters are useful in developing long-term breeding strategies. For a given population size the pair mating showed higher values of  $\Delta q$ , lower values of u, and shorter t than partial diallel mating. However, when the number of families was fixed, u of pair mating was greater than that of partial diallel mating. The impact of the results on tree breeding is discussed.

**Key words:** Selection limit, gene frequency, probability of allele fixation, pair mating, partial diallel mating.

### Zusammenfassung

Zwei Paarungssysteme, die paarweise Kreuzung und das unvollständige diallele Kreuzungssystem, wurden bezüglich dreier Parameter: Änderung der Genhäufigkeit in einer Generation ( $\Delta q$ ), Wahrscheinlichkeit der Fixierung eines Allels (u) und Zeit, die benötigt wird, um ein Allel zu fixieren oder zu verlieren (t), untersucht. Diese drei Parameter sind bei der Entwicklung von Langzeitzüchtungsstrategien von Nutzen. Für eine gegebene Populationsgröße zeigte die paarweise Kreuzung höhere  $\Delta q$

und niedrigere u-Werte und ein kürzeres t als das unvollständige Diallel. Wenn allerdings die Anzahl der Familien fest war, war das u bei paarweiser Kreuzung größer, als das beim unvollständigen Diallel. Die Auswirkungen der Ergebnisse auf die Waldbaumzuchtung werden diskutiert.

### Introduction

Traditionally mating systems have been used to estimate population parameters such as genetic variance components. The variance component estimates enable tree breeders to predict genetic gain in the following generation. The prediction, however, usually assumes that the population used to estimate the parameters, or populations that have similar breeding histories, will undergo subsequent selection and mating. Consequently the population generated to estimate genetic variance components under a mating system frequently serves as the base population for selection. In some situations, however, mating systems are used primarily to create breeding populations. In such cases genetic variance components of the breeding populations may or may not be estimated. Therefore to compare the effectiveness of mating systems, both the selection efficiency as well as efficiency for estimation of genetic variance component must be evaluated.

The reliability of a mating system in predicting genetic gain is evaluated based on the magnitude of sampling errors of the genetic variance component estimates the system generates (NAMKOONG and ROBERDS, 1974). The selection efficiency of a mating system is evaluated based on the advance of single generation allele frequencies ( $\Delta q$ ), the ultimate probability of allele fixation ( $u$  ( $\pi$ ) or  $u$ ), and the time required to fix or lose alleles ( $t$  ( $\pi$ ) or  $t$ ) (ROBERTSON, 1960) where  $\pi$  represents an initial parental genotype combination. Single generation gene frequency advance may be viewed as the genetic gain realized in a single generation. The  $\Delta q$  obtained in the present study is different from the one that assumes random mating and mass selection shown by FALCONER (1960, p. 206) But the two  $\Delta q$ 's have essentially the same meaning. The ultimate probability of gene fixation,  $u$ , may be viewed as the level at which the population reached the selection limit. Greater values of  $u$  may result in a higher level. ROBERTSON (1960) discussed the interpretation of  $u$  more rigorously. The time,  $t$ , applies for both fixing and losing an allele. Therefore the interpretation and application of  $t$  must be evaluated separately for each situation. However, the  $t$  is useful for understanding the causes that influence the changes in  $u$ . In this study the three parameters,  $\Delta q$ ,  $u$ , and  $t$ , represent model populations but not actual breeding populations. Therefore the values of the parameters obtained are primarily useful for comparing different mating systems.

KANG and NAMKOONG (1979, 1980) found that as long as matings were balanced — all the parents were equally represented in the progeny populations — no significant differences existed among mating systems in respect to  $u$ . They showed that factorial mating designs with unequal number of male and female parents generated lower fixation probability.

KANG and NAMKOONG's conclusions were made with the assumption that phenotypic truncation selection (mass selection) was applied on a large one-locus model population. In tree breeding, however, many of the traits to be improved have low heritability, and some forms of family selection are frequently used. In this paper, I will examine

the influence of two mating systems, pair mating and partial diallel mating, on single generation allele frequency advance, ultimate probability of allele fixation and time required to fix or lose an allele when family selections are made.

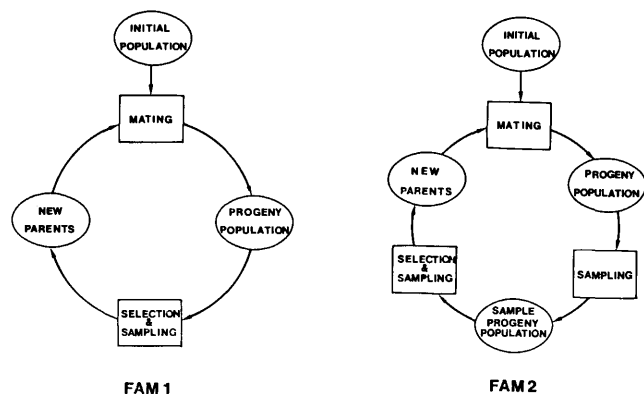
### The Models

#### Selection and Mating Schemes

I considered two selection schemes, FAM1 and FAM2 (Figure 1). In FAM1, family selection is performed based on the family averages obtained from a large number of individuals in each family (Figure 1). After the families are selected, parents for the next generation are randomly sampled from the pool of individuals in the selected families. This situation is most likely to occur in tree breeding. In FAM2, a small number of individuals (less than 10) are sampled from each family. The selection is based on the small sample family averages. After the selection, new parents are sampled from the pool of selected family samples. FAM2 is possible in animal breeding but is unlikely to occur in tree breeding. However, FAM2 uses one less assumption than FAM1 and is useful for checking the results of FAM1. The selected individuals from both FAM1 or FAM2 are mated using two mating schemes; pair mating and partial diallel mating (Figure 2). The progenies from these matings form the bases for selecting the next generation. This process of selection and mating continues until the locus of interest is fixed with an allele. The population size ( $N$ ) is assumed to be constant.

#### Transition Probability

Three possible genotypes, AA, Aa, and aa, are possible in a single locus two allele model. These three types will be represented by subscripts 1, 2, and 3 respectively. When



Figures 1. — Diagram of FAM1 and FAM2 selection models.

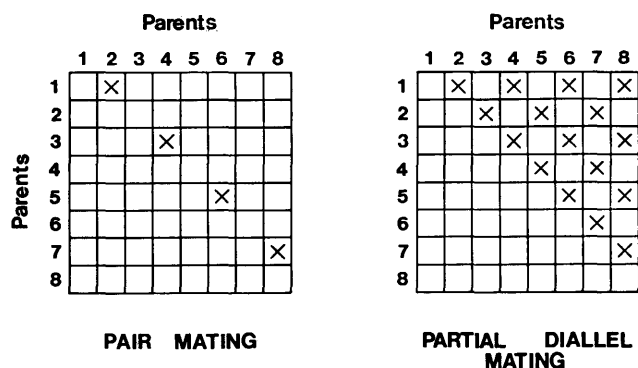


Figure 2. — Examples of two mating systems -- pair and partial diallel ( $N = 8$ ). X represents a crossing.

a set of parents are crossed, six crossing types are possible; AA × AA, AA × Aa, AA × aa, Aa × Aa, Aa × aa, and aa × aa. Subscripts 1 through 6 will be used to represent the crossing types. The six different crossing types will generate corresponding progeny families, and their expected genotype frequency distributions are (1, 0, 0), (.5, .5, 0), (0, 1, 0), (.25, .5, .25), (0, .5, .5), and (0, 0, 1). Different mating systems generate different number of families, but all the families of any mating system can be classified into the six parental crossing types with  $M_1, M_2, \dots, M_6$  families for the corresponding mating types, where  $M = M_1 + M_2 + \dots + M_6$ , and  $M$  is the total number of families generated by the mating system.

In partial diallel mating a particular combination of families,  $\underline{M}_i^T = (M_1, M_2, \dots, M_6)_i$  is uniquely determined by the parental genotype combinations  $\tau_r^T = (N_1, N_2, N_3)_r$  and the number of samples obtained from each of the genotype classes  $\underline{n}_i^T = (n_1, n_2, n_3)$ , where  $T$  represents a transposition. From KANG and NAMKOONG (1979);

$M_i^T = (n_1 v_1, n_1 v_2 + n_2 v_1, n_1 v_3 + n_2 v_2 + n_3 v_1, n_2 v_2, n_2 v_3 + n_3 v_2, n_3 v_3)$ , where  $v_h = N_h - n_h$ , and  $h = 1, 2, \text{ and } 3$ .

Let  $\theta_{it}^r$  represent the probability that  $M_i^T$  will be obtained given  $\tau_r^T$  and  $\underline{n}_i^T$ , then

$$\theta_{it}^r = \binom{N}{\underline{n}_i^T}^{-1} \prod_{h=1}^3 \frac{N_h!}{n_h!(N_h - n_h)!}$$

In pair mating  $\underline{M}_i^T$  is determined by 1) number of different genotypes assigned to different blocks,  $\underline{N}_{hj}^* = (N_1^*, N_2^*, N_3^*)_i$  where  $j$  represents the block number, and 2) number of samples obtained from each genotype class of the block,  $\underline{n}_{hj}^* = (n_1^*, n_2^*, n_3^*)_i$ . From KANG and NAMKOONG (1979);

$$\underline{n}_i^T = \frac{1}{2} \sum_{k=1}^b [2n_1(n_1 - 1), 2n_1n_2, 2n_1n_3, n_2(n_2 - 1), 2n_2n_3, n_3(n_3 - 1)]_k$$

where  $b$  represents the number of blocks.

The probability;

$$\theta_{it}^r = \binom{N}{\underline{n}_i^T}^{-1} \prod_{j=1}^b \prod_{h=1}^3 \frac{N_{hj}^*!}{n_{hj}^*!(N_{hj}^* - n_{hj}^*)!}$$

The above probabilities are the same for both FAM1 and FAM2. In the subsequent steps, however, it is necessary to separate FAM1 and FAM2. I will discuss FAM2 first.

FAM2: In FAM2, individuals are sampled from the progeny family before selection. Let  $f_{ji}$  represent  $j$ th family of  $i$ th mating outcome. When  $m$  individuals are randomly sampled within  $j$ th family, the probability of obtaining  $k$ th genotype combination  $(\underline{m}_k^T = (m_1, m_2, m_3)_k$ , where  $m = m_1 + m_2 + m_3$ ) is:

$$\theta_{kjl}^* = Pr(\underline{m}_k^T | f_j, i) = \frac{m!}{\prod_{h=1}^3 m_{jh}!} \prod_{h=1}^3 q_{jh}^{m_{jh}}$$

where

$$\begin{aligned} \underline{q}_{ji}^T &= (q_1, q_2, q_3)_{ji} \\ &= \text{expected genotype frequency distribution of } \\ &\quad j\text{th family of } i\text{th mating outcome,} \\ k &= 1, 2, \dots, K, \text{ and} \\ K &= [(m + 1)(m + 2)]/2. \end{aligned}$$

Similar sampling is made on all  $J$  families.  $L = K$  different ways are possible of combining different families to form the basis of family selection. The probability of sampling any particular combination of families,  $\theta_{li}$  is:

$$\theta_{li}^* = \left( \prod_{j=1}^J \theta_{kjl}^* \right)$$

When selection is made on the combination based on sample averages, the probability that the  $i$  combination of families will be selected is (Appendix A):

$$\Psi_{i^*} = Pr(\{f_1, \dots, f_{NS}\} | i^*) = \frac{\int_{-\infty}^{\infty} P(x) \left[ \prod_{j=1}^M r_j(x) \right]_{i^*} dx}{\sum_{i^*} \int_{-\infty}^{\infty} P(x) \left[ \prod_{j=1}^M r_j(x) \right]_{i^*} dx}$$

where

$$P(x) = \prod_j F_j(x),$$

$$r_j(x) = [1 - F_j(x)] / F_j(x),$$

$F_j(x)$  = distribution function of  $j$ th family average (in this study  $F(x)$  is considered to be standard normal),

$NS$  = number of families to be selected, and  $i^*$  indexes a particular combination of  $NS$  families that are jointly selected.

Any set of selected families has  $w = Mm$  individuals, with genotype distribution of  $w_1, w_2$ , and  $w_3$ , where  $w = w_1 + w_2 + w_3$ . When we sample  $N$  individuals from the pool of selected families, the probability that the  $\tau$ th combination of parents for the next generation,  $(N_1, N_2, N_3)_\tau$ , will be obtained is:

$$\theta_{\tau i^*} = \left[ \frac{N!(w - N)!}{w!} \prod_{h=1}^3 \frac{w_{h\tau}!}{N_{h\tau}!(w_{h\tau} - N_{h\tau})!} \right]$$

By summing the crossproduct of  $\Psi_{i^*}$  and  $\theta_{\tau i^*}$  over  $i^*$ , we get

$$\Psi_{\tau i} = \sum \Psi_{i^*} \theta_{\tau i^*}$$

By summing the crossproduct of  $\Psi_{\tau i}$  and  $\theta_{\tau i}^r$  over  $\tau$  we get

$$\Psi_{ji} = Pr(N_1, N_2, N_3 | i, \tau) = \sum_{\tau} \Psi_{\tau i} \theta_{\tau i}^r$$

Finally, the transition probability is

$$\begin{aligned} q_{ji} &= \sum_{\tau} \Psi_{\tau i} \theta_{\tau i}^r \\ &= \sum_{\tau} \sum_{i^*} \Psi_{i^*} \theta_{\tau i^*} \theta_{\tau i}^r \end{aligned}$$

where

$$\begin{aligned} \Psi_{i^*} &\text{ is as in eq 4,} \\ \theta_{\tau i^*} &\text{ is as in eq 5,} \\ \theta_{\tau i}^r &\text{ is as in eq 3, and} \\ \theta_{\tau i}^r &\text{ is as in eq 1} \end{aligned}$$

FAM1: In FAM1 selection is based on family averages computed from a large number of individuals within each family. To facilitate computation, we assume that genotype frequency of each family closely approximates the expected genotype frequency.

The expression for the probability that  $i$  combination of families to be selected is identical to eq. 4 with the change of notation such that,

$$\Psi_{i^*} = Pr(\{f_1, \dots, f_{NS}\} | i)$$

$N$  individuals are randomly sampled from the pool of selected families, and the probability that  $j$ th combination of parents for the next generation,  $(N_1, N_2, N_3)_\tau$ , would be obtained is:

$$\theta_{ji}^* = \frac{N!}{\prod_{h=1}^3 N_{hj}^*!} \prod_{h=1}^3 q_{hj}^{*N_h}$$

where

$\underline{q}^T = (q_1^*, q_2^*, q_3^*)$  = genotype frequency distribution of the pooled selected families

By summing the crossproduct of  $\psi_{i^*i}$  and  $\theta_{ji}^*$  over  $i^*$ , we get

$$\Psi_{ji} = \sum_{i^*} \psi_{i^*i} \theta_{ji}^*$$

The transition probability is:

$$q_{ji} = \sum_{i^*} \Psi_{ji} \theta_{i^*i}''$$

where

$\psi_{i^*i}$  is as in eq. 6,

$\theta_{ji}^*$  is as in eq. 7, and

$\theta_{i^*i}''$  is as in eq. 1

### Ultimate Probability of Gene Fixation and Time Required to Fix or Loss an allele.

Because the generations are discrete, transition probabilities are independent of time  $t$ , and the selection criteria do not change, recurrent selection follows a Markov process. The vector of ultimate probabilities of fixing an allele is obtained by (CARR and NASSAR (1970a):

$$\underline{u}(\pi) = (I - P)^{-1} \underline{r}$$

where  $I$  is a  $(H-2) \times (H-2)$  identity matrix,  $P$  is a  $(H-2) \times (H-2)$  matrix of transient states,  $\underline{r}$  is a  $(H-2) \times 1$  vector of transition probabilities from transient states to the fixation state,  $\pi$  is the initial parental genotype combination, and  $H$  is the total number of possible genotype combination  $N$ .

The time required to fix or lose an allele is obtained by (CARR and NASSAR 1970b):

$$\underline{t}(\pi) = (I - P)^{-1} \underline{1}$$

where  $\underline{1}$  is a  $(H-2) \times 1$  vector of 1's.

## Results and Discussion

The notations used in this section are described in Table 1. The choice of mating system will depend on the population size ( $N$ ) and the number of families ( $M$ ) generated by the system. For a given  $N$ , the partial diallel mating generates more families than the pair mating. But for a given  $M$ , the pair mating is capable of including a larger  $N$ . Therefore, I will compare the mating designs for both a given  $N$  with variable  $M$  and a given  $M$  with variable  $N$ .

Different mating systems have different structural organizations that are used to determine the pairs of parents to be crossed. The mating systems also generate a combination of  $N$  and  $M$ . Therefore, differences between mating systems could come from different structural organizations of crosses, the different combinations of  $N$  and  $M$ , or both. We will ask whether the structural organization of a mating design matters with respect to the parameters  $\Delta q$ ,  $u$ , and  $t$ . If the structural organization of a mating system

Table 1. — Glossary of notations used in Results and Discussion.

Symbol	Meaning
$\pi$	parental genotype combination.
$q$	gene frequency of progeny population before selection.
$q'$	average gene frequency of progeny population after selection.
$\Delta q$	$q' - q$ ; because mating systems are compared for given $q$ , $\Delta q$ and $q'$ will be used interchangeably.
$s(q')$	standard deviation of gene frequency after selection and sampling.
$s$	average of $s(q')$ [ = $\frac{1}{y} \sum_{i=1}^y s(q'_i)$ , where $y = \frac{(N+1)(M+2)}{2} - 2$ ].
$u(\pi)$ or $u$	ultimate probability of allele fixation.
$T(\pi)$ or $t$	time required for fixation or loss of an allele.
$\alpha$	standardized distance between homozygote genotypes.
$d$	degree of dominance.
PM	pair mating with additive gene action.
PD	partial diallele with additive gene action.
PDI	partial diallele with complete dominance.
$N$	population size.
$M$	number of families generated by a mating system.
$NS$	number of families selected.
$P$	proportion of selection (=NS/M).
$R(.)$	ratio of two average absolute differences between mating systems in respect to the parameter indicated in the parenthesis [examples: $R(q')$ , $R(u)$ , $R(t)$ ].

is not important, a breeder could custom design a system that would produce the desired combination of  $N$  and  $M$ .

Before comparing the mating designs we will examine the difference between the two selection models; FAM1 and FAM2. Because models do not exactly describe actual breeding populations, it is desirable to compare different model populations and look for consistency between them.

Allele frequency change per generation ( $\Delta q$ ), ultimate probability of gene fixation ( $u$ ) and time required for allele fixation ( $t$ ) differ greatly between FAM1 and FAM2. For given  $\alpha$  values, FAM2 generated larger  $\Delta q$  and  $u$  and smaller  $t$  than FAM1. In reality, however, the opposite is true. Because FAM1 has a larger number of individuals per family it will have smaller errors associated with family means than FAM2. Smaller error implies that the value of FAM1 always will be greater than that of FAM2. Therefore, FAM1 will generally have higher values of  $\Delta q$  and  $u$  than FAM2 in actual breeding situations.

Despite differences in absolute values of parameters between the two models, they behave essentially the same way under different mating systems and gene action models. We will primarily use the results of FAM1 and the results of FAM2 only as needed. We chose to use FAM1 because it accommodated a population size of 8. The PDP 11/34 computer used was not capable of handling FAM2 with  $N = 8$ . FAM1 is also more likely to occur in tree breeding than FAM2. In the following discussion FAM1 is used except where specified that FAM2 was used.

### 1. Comparison of mating systems for a given population size

In all our experiments, pair mating showed larger  $\Delta q$  and  $s$  than partial diallel mating ( $s$  represents the average standard deviation of gene frequencies after one generation) of selection (Table 1). When  $N = 4$  with additive gene action, the average difference between pair mating and partial diallel mating in respect to  $q'$ ,  $(PM-PD)q'$ , is .0046 (Table 2). The advantage of PM is reduced in respect to  $u$ ,  $(PM-PD)u = .0021$  (Table 3).

Although these differences (.0046 and .0021) seem to be trivial, the relative values of such differences are sub-

Table 2. — Comparison of mating systems in respect to single generation gene frequency advance. N = 4;  $\alpha$  (Gene effect = .2; (proportion selected) = .5; Selection Model: FAM1.

$\pi$	q	PD		PM		PDI		Difference in q'			
		q'	s(q')	q'	s(q')	q'	s(q')	PM-PD	%	PDI-PD	%
310	.8750	.8785	.124	.8805	.152	.8750	.125	0.0020	0.2	-0.0035	0.4
220	.7500	.7547	.160	.7574	.190	.7523	.161	0.0027	0.4	-0.0024	0.3
130	.6250	.6285	.176	.6305	.197	.6285	.176	0.0020	0.3	0.0000	0.0
040	.5000	.5000	.177	.5000	.177	.5000	.177	0.0000	0.0	0.0000	0.0
301	.7500	.7640	.177	.7721	.249	.7500	.177	0.0081	1.1	-0.0140	1.8
211	.6250	.6378	.191	.6452	.254	.6320	.190	0.0074	1.2	-0.0058	0.9
121	.5000	.5093	.191	.5147	.239	.5093	.190	0.0054	1.1	0.0000	0.0
031	.3750	.3785	.177	.3805	.198	.3785	.177	0.0020	0.5	0.0000	0.0
202	.5000	.5186	.204	.5292	.287	.5185	.200	0.0106	2.0	-0.0001	0.0
112	.3750	.3878	.191	.3952	.255	.3937	.190	0.0074	1.9	0.0059	1.5
022	.2500	.2547	.162	.2574	.192	.2570	.162	0.0027	1.1	0.0023	0.9
103	.2500	.2640	.177	.2721	.249	.2781	.176	0.0081	3.1	0.0141	5.3
013	.1250	.1285	.126	.1305	.154	.1320	.127	0.0020	1.6	0.0035	2.7
Average			.172		.215		.171	0.0046	1.1	0.0000	0.5
Ave. (Abs. Value)			.172		.215		.171	0.0046	1.1	0.0040	1.1

<sup>1)</sup> See Table 1 for notation glossary.

stantial when they are compared to parameter differences between partial diallel mating with complete dominance (PDI) and partial diallel mating with additive gene action (PD) (Tables 2 and 3). Dominance models, when compared to corresponding additive models, retard the allele frequency advance when the initial allele frequency is high, while they accelerate allele frequency advance when the initial allele frequency is low. Therefore the sign of difference between PDI and PD changes depending on the initial allele frequencies. The sign does not change in PM-PD. The average values of the parameter differences of PDI-PD cannot be used to evaluate the significance of the difference between pair mating and partial diallel mating. Therefore we will use the average of absolute differences of several parameters,  $|PDI-PD|$ . We will primarily use the ratio  $R(.) = |PM-PD|/|PDI-PD|$ , where “.” represents a parameter.

In the models shown in Tables 2 and 3,  $R(q')$  is 1.15 and  $R(u)$  is .3 (Table 4). This strongly suggests that differences such as .0046 and .0021 are not negligible values. As the population size increases,  $R(u)$  also tends to increase. For example a model under  $N = 8$  shows that  $R(u)$  is .98, which suggests that the difference in ultimate probability between mating systems, PM vs PD, is as great as that between additive and complete dominance models of the

Table 3. — Comparison of mating systems in respect to ultimate probability of gene fixation. N = 4;  $\alpha = .2$ ; P = .5; Selection Model; FAM1.

$\pi$	q	$u(\pi)$			Difference in $u(\pi)$			
		PD	PM	PDI	PM-PD	%	PDI-PD	%
310	.8750	.8950	.8959	.8883	0.0009	0.1	-0.0067	-0.7
220	.7500	.7839	.7855	.7776	0.0016	0.2	-0.0063	-0.8
130	.6250	.6663	.6684	.6639	0.0021	0.3	-0.0024	-0.4
40	.5000	.5419	.5441	.5429	0.0022	0.4	0.0010	0.2
301	.7500	.7902	.7922	.7745	0.0020	0.3	-0.0157	-2.0
211	.6250	.6730	.6754	.6656	0.0024	0.4	-0.0074	-1.1
121	.5000	.5489	.5515	.5497	0.0026	0.5	0.0008	0.1
31	.3750	.4176	.4199	.4218	0.0023	0.6	0.0042	1.0
202	.5000	.5558	.5587	.5564	0.0029	0.5	0.0006	0.1
112	.3750	.4248	.4275	.4342	0.0027	0.6	0.0094	2.2
22	.2500	.2861	.2881	.2946	0.0020	0.7	0.0085	3.0
103	.2500	.2937	.2961	.3133	0.0024	0.8	0.0196	6.7
13	.1250	.1470	.1483	.1562	0.0013	0.9	0.0092	6.3
Average					0.0021	0.5	0.0011	1.1
Ave. (Abs. Value)					0.0021	0.5	0.0071	1.9

<sup>1)</sup> See Table 1 for notation glossary.

partial diallel mating. Furthermore, the difference between PM and PD in respect to  $t$  is usually much greater than that of PDI and PD. The largest and smallest  $R(t)$  observed were 116 and 1.61, respectively (Table 4). However,  $R(t)$  will become smaller as  $\alpha$  increases.

The difference in  $u$  between PM and PD is even greater under FAM2 (Table 4). For example, for the combinations shown in Tables 2 and 3, FAM2 showed that  $(PM-PD)q' = .0048$  but  $(PM-PD)u = -.0063$ . The negative value in  $(PM-PD)u$  seems to be due to larger  $s$  of pair mating (Tables 2 and 5), and suggests that pair mating is not as good as partial diallel mating in long-term recurrent family selection, in spite of its superiority in single generation allele frequency advance. It is not clear why the difference in  $u$  did not have a negative value in FAM1. Both FAM1 and FAM2 have similar  $s$  values in pair mating, but FAM1 has larger  $s$  than FAM2 in partial diallel mating (Table 5). The actual difference in  $s$  between FAM1 and FAM2, however, does not seem to be large

Table 4. — Average difference between mating systems.

N	Model	Parameter	$\alpha$	F	(PM-PD)	(PDI-PD)	(PDI-PDI)	R*	
4	FAM1	q'	.01	.5	.0002	0	.0002	1	
			.2	.5	.0046	0	.004	1.15	
			.8	.5	.0163	-.0006	.0159	1.03	
		u	.01	.5	.0001	0	.0003	.33	
			.2	.5	.0021	.0011	.0071	.3	
			.8	.5	.0065	.0145	.0281	.34	
	t	.01	.5	-2.32	.02	.02	116		
		.2	.5	-2.31	.34	.34	6.79		
		.8	.5	-2.14	1.33	1.33	1.61		
	4	FAM2	q'	.01	.5	.0002	0	.0062	1
				.2	.5	.0048	0	.0047	1.02
				.8	.5	.0163	-.0008	.0188	.867
u			.01	.5	-.0003	0	.0005	.6	
			.2	.5	-.0063	.0028	.0103	.61	
			.8	.5	-.0193	.0303	.0401	.48	
t		.01	.5	-2.86	.03	.03	95.3		
		.2	.5	-2.82	.59	.59	4.78		
		.8	.5	-2.39	2.12	2.12	1.13		
8	FAM1	q'	.2	.5	.0025	0	.0033	.75	
			.2	.25	.0043	-.0002	.0058	.81	
			.2	.5	-.0198	.0051	.0123	1.61	
	u	.2	.25	-.0513	.0163	.0524	.98		
		.2	.5	-6.06	1.44	1.44	4.21		
		.2	.25	-6.85	1.41	1.41	4.86		

\*  $R = IPM-PDI/IPDI-PDI$

<sup>1)</sup> See Table 1 for notation glossary.

Table 5. — Average standard deviations of gene frequencies after one generation of selection (S) under various mating systems.

N	Model	$\alpha^{1/}$	F	PD	PM	PD1
4	FAM1	.01	.5	.172	.215	.172
		.2	.5	.172	.217	.171
		.8	.5	.17	.208	.168
4	FAM2	.01	.5	.164	.215	.164
		.2	.5	.164	.217	.164
		.8	.5	.162	.207	.16
8	FAM1	.2	.5	.119	.158	.118
		.2	.25	.138	.226	.139
		.2	.125	.174	--	.172
		.2	.0625	.226	--	.223

<sup>1)</sup> See Table 1 for notation glossary.

enough to account for the sign reversal in (PM-PD) u between the two models.

When  $N = 8$ , FAM1 also shows negative values in (PM-PD) u (Table 4). Under the additive gene action model with  $\alpha = .2$ , (PM-PD)  $q' = .0025$  but (PM-PD)  $u = -.0198$ . When compared to the equivalent values under  $N = 4$  (.0046 and .0021), the difference between mating systems in respect to  $q'$  decreased while that in respect to  $u$  increased and changed sign. The reduction in (PM-PD)  $q'$  at  $N = 8$  is difficult to explain, but when the population is larger the increase in the difference in  $u$  and the change of the sign seem to be due to the greater imbalance in family numbers (M) and number of families selected (NS) between the mating systems. Pair mating generates  $N/2$  families while partial diallel mating generates  $(N/2) **2$ . The ratio between family numbers of pair mating and partial diallel mating is  $2/N$ , and the ratio decreases as the population size increases. For a given selection proportion ( $P = NS/M$ ), the ratio between the two mating systems in respect to the number of families selected behave the same as M. Therefore, it is most likely that the sign reversal between (PM-PD)  $q'$  and (PM-PD)  $u$  will continue to exist for  $N < 8$ , and the disadvantage of PM in respect to  $u$  will become greater as N increases.

The influence of s in long-term recurrent selection is most dramatically demonstrated in fixation time, t. In general PM has smaller t than PD, and PD1 has larger t than PD (Table 6). The difference between PM and PD in respect to t is almost constant for different  $\alpha$  values (Table 4). Table 5 also shows that for given mating system s is almost constant for different  $\alpha$  values. However, the difference between PD1 and PD increased as the  $\alpha$  increased. Therefore, the difference in t between mating systems is primarily influenced by s, or sampling effect, while that between gene action models for a given mating system depends on the magnitude of  $\alpha$ , or selection effect.

## 2. Comparison of mating systems for a given number of families

The number of families generated by a mating system seems to have a tremendous impact on the success in long-term recurrent family selection. However, the variations in M among mating systems were generated under the assumption that the population size, N, is fixed. The natural question that follows is: which has greater impact, different M or different N? An associated question is: what happens of M is fixed and N is not? In fact, in many practical breeding situations M is the factor that determines the amount of work associated with crossing.

In all the observations made so far, we have found nothing to indicate that the impact of M on u is greater

than that of N. In no case was u of the largest M at the lower N greater than that of the smallest M at higher N. Regardless of the size of N, PM produces higher  $\Delta q$  than PD. Therefore if M is fixed, pair mating is not necessarily inferior to partial diallel mating. For example, if M is fixed at 4, the corresponding N values are 4 and 8 for PD and PM, respectively. Under  $F = .5$  and  $\alpha = .2$  (PM8-PD4) $q' = .0023$  and (PM8-PD4) $u = .0328$ , where PM8 and PD4 represent PM with  $N = 8$  and PD with  $N = 4$ , respectively. When  $F = .25$  and  $\alpha = .2$ , (PM8-PD4) $q' = .0037$  and (PM8-PD4) $u = .016$ . Therefore, for a given M, pair mating is a competitive mating system; it is a good system that can handle a large breeding population. As M increases, the ratio between the mating systems in respect to corresponding N increases rapidly. For example, when M is 100, PD and PM correspond to population sizes 20 and 200 respectively a tenfold difference in population size. Undoubtedly the use of pair mating with  $N = 200$  would be better than the use of partial diallel mating with  $N = 20$  in this particular example.

## 3. How important is the structural organization of a mating system?

This question cannot be examined rigorously because the mating systems and the number of families generated by them are confounded. We will take an indirect approach, which will not help explain the differences between mating systems in respect to  $q'$  but will help in understanding potential causes of the differences in u.

When  $N = 8$ , we can change the selection proportion (P). P is a function of both the number of families selected (NS) and M. By changing P for a given mating system we can observe the changes of u and determine the causes of such changes. If the most likely cause of such changes happened to be s, as was the case when comparing mating systems, we can strengthen our intuition that: 1) s is the major factor influencing the magnitude of u, and 2) s is primarily influenced by the factors related to the various sample sizes N, M, and NS, rather than to structural differences between mating systems. Note also that the examination of the behaviour of u under varying selection proportion itself generates important information.

Let  $f1 = .5$  and  $f2 = .25$ , where f represents a fixed level of selection proportion. In pair mating  $(f2-f1)q' = .0075$  and  $(f2-f1)u = -.0114$ . In PM with  $N = 8$ , therefore, a

Table 6. — Comparison of mating systems in respect to time for fixation.  $N = 4$ ;  $\alpha = .2$ ;  $P = .5$ ; Selection Model: FAM1.

$\alpha^{1/}$	q	t( $\kappa$ )					Difference in t( $\kappa$ )		
		PD	PM	PD1	PM-PD	·%	PD1-PD	·%	
310	.8750	4.45	3.15	4.71	-1.30	-29.2	0.26	5.8	
220	.7500	6.82	4.83	7.12	-1.99	-29.2	0.30	4.4	
130	.6250	8.25	5.96	8.56	-2.29	-27.8	0.31	3.8	
040	.5000	8.82	6.47	9.14	-2.35	-26.6	0.32	3.6	
301	.7500	6.41	3.95	6.89	-2.46	-38.4	0.48	7.5	
211	.6250	8.01	5.31	8.36	-2.70	-33.7	0.35	4.4	
121	.5000	8.69	6.06	9.00	-2.63	-30.3	0.31	3.6	
031	.3750	8.47	6.12	8.78	-2.35	-27.7	0.31	3.7	
202	.5000	8.50	5.32	8.85	-3.18	-37.4	0.35	4.1	
112	.3750	8.35	5.61	8.71	-2.74	-32.8	0.36	4.3	
022	.2500	7.23	5.15	7.54	-2.08	-28.8	0.31	4.3	
103	.2500	7.11	4.52	7.59	-2.59	-36.4	0.48	6.8	
013	.1250	4.86	3.47	5.14	-1.39	-28.6	0.28	5.8	
Average					-2.31	-31.3	0.34	4.8	
Ave. (Abs. Value)					2.31	31.3	0.34	4.8	

<sup>1)</sup> See Table 1 for notation glossary.

smaller selection proportion is useful for single-generation but not for long-term recurrent family selection. The reversal of sign associated with different selection proportion in PM is related to the number of families actually selected (NS). In pair mating NS are 2 and 1 when P are .5 and .25, respectively. The change from two families to one family in pair mating might be more significant than that from 8 families to 4 families in partial diallel mating. Under the same change in the selection proportion (i.e., P = .5 to P = .25) PD did not decrease u and  $(f_2-f_1)u = .0179$ . However, similar reduction of u occurs in PD when the selection proportion is further decreased (Figure 3). The reduction in u occurs for all initial parental genotypic combinations ( $\pi$ ) when P is decreased from .25 to .125 or .0625. When P equals .25, .125, and .0625, NS equals 4, 2, and 1 respectively. The u ( $\pi$ ) s when P = .0625 are even smaller than those of pair mating with P = .5. At these P values, (PM-PD)u = .0008. The q' however continues to increase as P decreases. For the given model of diallel mating system u is maximum when P = .25.

As expected the reduction in u is associated with the increase in s (Table 5). Therefore, it is not difficult to see that changes in NS influence u through s. Therefore the result is consistent with our first intuition. The main idea that supports the second intuition comes from the fact that parents are randomly assigned to the row and column headings of the crossing tables and are equally represented in the mating systems. It is reasonable to suspect that there are no inherent properties of mating systems other than generating different combinations of N and M.

#### Application to Tree Breeding

Under mass selection little difference is found among balanced mating systems (KANG and NAMKOONG, 1979). Under family selection, however, substantial differences exist between mating systems. In long-term breeding partial diallel mating is better than pair mating for a given population size (N). If the number of families (M) is fixed, pair mating is more desirable. The advantage of pair mating

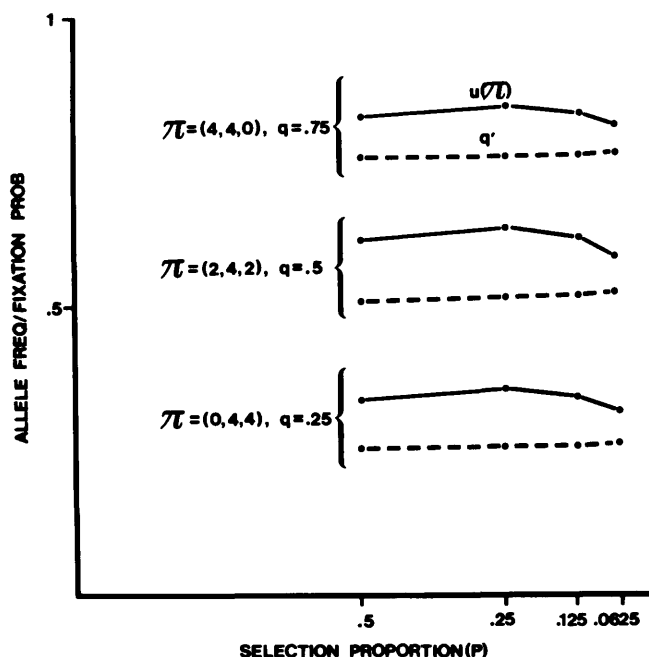


Figure 3. — Changes in gene frequency and fixation probability for various selection proportions (N = 8, a = 2, partial diallel mating).

with fixed M is also true under mass selection. So the choice of mating design depends on the choice of the factor (N or M) to be fixed.

Operationally M tends to be more critical than N. Because pair mating can incorporate the largest population size for a given M, it seems to be more desirable than any other balanced mating system. However, pair mating is not effective for estimating variance components, and the use of the mating system will require separating the breeding operation and the variance component estimation activities. This can be done either by augmenting pair mating with polycrosses or by sampling a smaller number of individuals from the breeding population and by making a form of diallel crossing.

If both breeding and variance component estimation must be done by using the same levels of N and M, the breeder might find any balanced mating system that meets the specifications for N and M. The results of this study suggest that the structural organization of mating designs may not be important.

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#### Appendix A. Derivation of equation 4

Let  $P_i(x) = F_i(x)$ , and  $q_i(x) = 1 - F_i(x)$ , where  $F_i(x)$  is the distribution function of  $i^{\text{th}}$  family average. The family average is obtained by  $a(p_1^* + dp_2^* - p_3^*)/2$  for FAM1, and  $a(r_1 + dr_2 - r_3)/2r$  for FAM2, where  $p_h^*$  represents  $h^{\text{th}}$  genotype frequencies in the progeny family,  $r$  represents the number of  $h^{\text{th}}$  genotypes in the family sample,  $a$  represents standardized distance between homozygotes, and  $d$  represents degree of dominance. We are interested in selecting NS families, including  $i^{\text{th}}$  family, from a total of M families. We require the average of NS-1 families and that of  $i^{\text{th}}$  family greater than  $x$ , while the averages of M-NS family should be less than or equal to  $x$ . The families can be classified into 2 groups in  $\binom{M}{NS}$  ways, selected vs unselected, and it is possible to calculate the joint probability of selecting the  $i^{\text{th}}$  combination of families for any given combination of families and  $x$  values. The probabilities are integrated over all possible values of  $x$ . After normalizing, we get the probability of selecting the  $i$  combination of families,

$$\Psi_i^* = \Pr(\{f_1, \dots, f_{NS}\}_i^* | \cdot) = \frac{\int_{-\infty}^{\infty} \left[ \prod_j q_j(x) \prod_{k \neq j}^{M-NS} p_k(x) \right]_{i^*} dx}{\sum_{i^*} \int_{-\infty}^{\infty} \left[ \prod_j q_j(x) \prod_{k \neq j}^{M-NS} p_k(x) \right]_{i^*} dx}$$

$$\text{Let } r_i(x) = \frac{q_i(x)}{p_i(x)}, \text{ and } P(x) = \prod_i p_i(x)$$

Because  $q_i(x) = r_i(x)p_i(x)$ , the numerators of (1) become,

$$\int_{-\infty}^{\infty} \left[ \prod_j^{NS} r_j(x) p_j(x) \prod_{k \neq j}^{M-NS} p_k(x) \right]_{i^*} dx$$

$$= \int_{-\infty}^{\infty} \left[ \prod_j^{NS} r_j(x) \prod_{k=1}^M p_k(x) \right]_{i^*} dx$$

Because  $P(x) = \prod_{k=1}^M p_k(x)$  is an invariant for given  $x$ , 2 can be rewritten as,

$$\int_{-\infty}^{\infty} P(x) \left[ \prod_j^{NS} r_j(x) \right]_{i^*} dx$$

Therefore (1) becomes,

$$\psi_{i^*} = \frac{\int_{-\infty}^{\infty} P(x) \left[ \prod_j^{NS} r_j(x) \right]_{i^*} dx}{\sum_i \int_{-\infty}^{\infty} P(x) \left[ \prod_j^{NS} r_j(x) \right]_{i^*} dx}$$

The numerical integration is made by using Simpson's rule between 4 standard deviations with 64 subdivisions.

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## Clonal Differences in Dry Matter Distribution, Wood Specific Gravity and Foliage „Efficiency“ in *Picea sitchensis* and *Pinus contorta*

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### Summary

Seven clones of both *Picea sitchensis* and *Pinus contorta* growing at a lowland site in Scotland were felled at age 8, and measurements were taken at each annual height level, of stem, branch and needle dry weights, foliage areas, and the specific gravities and volumes of each annual ring of stemwood.

On average, *P. sitchensis* clones had similar stem dry weights to *P. contorta* clones, but only 56 % as much branch wood and 61 % as much needle dry weight. The branch wood on *P. sitchensis* was “spread” over a long total branch length, and the needles were “spread” over a large projected needles area. At ages 6–8 *P. sitchensis* produced 44 % more stemwood per unit needle area than *P. contorta*.

Within both species, sparsely branched clones were the most efficient stemwood producers, allocating a high proportion of their dry matter to stems, and, at ages 6–8, producing 1.5 to 2.0 times as much stemwood per unit of needles as heavily branched clones. These sparsely-branched clones varied in height and total weight, indicating that large genetic gains in stemwood production per tree could be made by selecting simultaneously for rapid growth and a high harvest index. Tallness, sparse branching and, in *P. contorta*, the absence of large basal branches, were the most important characters associated with large, efficient stemwood production.

Stemwood specific gravities differed by 20–30 % between clones and between the innermost and outermost annual ring cylinders. For all clones the specific gravity of the annual cylinders of stemwood decreased linearly with  $\log_e$  cylinder volumes, and both the initial specific gravities (the intercepts) and their rates of decrease (the slopes) differed between clones (especially in *P. sitchensis*). That is, the value of juvenile stemwood specific gravities, and clonal rankings, were dependent upon volume growth rates.

**Key words:** *Picea sitchensis*, *Pinus contorta*, clones, harvest index, dry matter distribution, needle area, wood specific gravity, branching.

### Zusammenfassung

Es wurden je 7 Klone von *Picea sitchensis* und *Pinus contorta* einer Versuchsfläche auf einem Tieflandstandort in Schottland im Alter 8 gefällt und in jedem Jahrestrieb das jeweilige Trockengewicht des Stammes, der Zweige und der Nadeln, der Umfang der Benadelung und die spezifischen Gewichte und Volumina in jedem Jahrring des Stammes gemessen.

Im Durchschnitt hatten die *Picea sitchensis*-Klone ähnliche Stamm-trockengewichte wie die *Pinus contorta*-Klone, aber nur 56 % soviel Astholz und 61 % des Nadel-trockengewichtes. Bei *Picea sitchensis* waren die Astlängen in der Summe größer als bei *Pinus contorta* und die Nadeln über eine größere Zone verbreitet. Im Alter 6–8 produzierte *Picea sitchensis* 44 % mehr Stammholz pro Nadeleinheit als *Pinus contorta*. Innerhalb beider Arten produzierten Klone mit weniger Ästen effektiv mehr Stammholz, da ein hoher Anteil an Trockenmasse den Stämmen zugute kam, was im Alter 6–8 1,5 bis 2,0 mal soviel Stammholz als bei stark beasteten Klone ausmachte. Diese wenig beasteten Klone variierten in der Höhe und im Gesamt-Trockengewicht, woran zu erkennen ist, daß darin eine Möglichkeit zur Selektion von starkwüchsigen Individuen mit einem genetischen Gewinn besteht. Die wichtigsten Kriterien für eine effiziente Stammholzproduktion waren Stammstärke, spärliche Beastung und bei *Pinus contorta* das Nichtvorhandensein einer breiten basalen Verzweigung. Das spezifische Gewicht differierte zwischen 20 % und 30 % zwischen den Klone und zwischen den am weitesten innen und außen liegenden Jahrringzylindern des Stammholzes. Bei allen Klone verringerte sich die Holzdichte der Jahrringzylinder des Stammholzes mit dem  $\log_e$  Zylinder-Volumen, wobei sich die Ini-