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Impact of mating design on selection response in *Brassica rapa* L.

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Abstract The impact of four mating designs on selection response for leaf area was assessed at four different population sizes, using fast-cycling *Brassica rapa* L. Mating designs were either balanced (partial diallel or pair mating) or unbalanced (factorial mating designs with either one or two testers). When balanced, the mating designs required different numbers of crossings for the same number of parents: the partial diallel design, in the configuration retained here, required three times as many crossings as pair mating. Population sizes were 4, 8, 16, and 32. The percentage of selected individuals was kept constant at 25%. Despite an average estimated heritability around 0.4, the overall response to selection after five generations was fairly weak in all three replicates. For a given population size, selection response was larger under balanced mating designs than under unbalanced ones. There was no difference among balanced mating designs. Both results indicate that effective population size is more important than population size or the number of crossings in maintaining genetic gain.

Key words Mating design · Effective population size
Brassica rapa L.

Introduction

Mating designs are “rules” for arranging controlled crossings. These rules were initially derived to allow the estimation of additive and dominance genetic variances (Cockerham 1963); indeed, in most breeding programs, mating designs are used with no other aim than estimating genetic parameters. Consequently, the efficiency of various mating designs in estimating genetic parameters has been thoroughly investigated and is now well known. In general, for a given number of parents, the sampling variance of the estimates decreases as the number of crossings increases (Klein et al. 1973; Namkoong and Roberds 1974; Pepper 1983). In other selection schemes, mating designs are used simultaneously to estimate genetic parameters and to create the next generation (Squillace 1973; Gallais 1990 p. 289–294). In conservation programs or long-term breeding (Kang and Nienstaedt 1987), mating designs may primarily be used for the latter. Mating designs, as “rules” to create the next generation, will then be judged on their impact on future genetic gain and on their cost, the latter of which depends largely on the number of controlled crossings involved.

For a given number of parents, theoretical work indicates that the balance of mating designs, so that “all parents have equal probability of passing the same number of alleles to the progeny gene pool” (Kang 1991), is of prime importance in minimizing the loss of alleles and hence in permitting the maintenance of genetic variation (Kang and Namkoong 1980). Among balanced mating designs, pair mating is certainly the most economic: for n parents, the number of crossings is $n/2$. Partial diallels with a number of crossings of $ns/2$, where s is a number greater or equal to two (Kempthorne and Curnow 1961; Fyfe and Gilbert 1963), are generally considered a good compromise between low-cost pair matings and expensive matings such as full-diallels, which require n^2 crossings. Under mass selection, simulation studies showed that there are little differences among balanced mating designs with respect to the probability of allele fixation and the time to fixation

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(Kang and Namkoong 1979, 1980), but that response during early generations was greater with a pair mating than with partial diallel (Kang 1991). Under family selection, pair mating led to a lower probability of allele fixation and a longer time to fixation than in the case of a partial diallel (Kang 1983).

In this paper, we will compare the impact on selection response of four mating designs; two balanced (pair mating and partial diallel) and two unbalanced (factorial mating design with either one or two testers) for different levels of population size. Two questions will be investigated in turn: (1) do balanced and unbalanced mating designs have significantly different impacts on selection response?, and (2) when mating designs are balanced, does the number of crossings matter?

Results from a five-generation recurrent selection experiment for leaf area in *Brassica rapa* L. are used to address these two questions. Because we have few generations, effects of mutations may be ignored. Migration was prevented and the same proportion was selected in all populations. Therefore, we actually investigate the impact of genetic drift on the genetic changes of the experimental population.

Materials and methods

Three separate experimental sets (replicates) were carried out over five generations according to the same general procedure. Set 2 was initiated 4 weeks after the beginning of Set 1, and Set 3 was initiated 4 weeks after the beginning of Set 2. This permitted a reduction in the load of technical work at any given time.

Material

Seeds of rapid-cycling *B. rapa* were obtained from the Crucifer Genetics Cooperative, Department of Plant Pathology, University of Wisconsin-Madison (Brassica CRCG stock #1, Aaa, Williams 1985). Rapid-cycling *B. rapa* has a short generation turnover period of 6–8 weeks. It germinates as early as 48 h from sowing, flowers around 16 days after sowing, and the seeds mature after approximately 20–30 days after pollination (Williams and Hill 1986). Selection for short stature and the number of basal leaves was carried out over one generation in two populations derived from the rapid-cycling stock of *B. rapa*. In the first population 32 plants were selected out of 288 while in the second 33 were selected out of 348. The two groups of plants thus obtained were open-pollinated using bee sticks; each flower received a mixture of pollen collected on “randomly-picked” plants of the parental group. We assume that this method leads to families consisting mostly of half-sibs. Seeds were harvested from 18 plants in the first group and from 14 plants in the second. These plants were chosen for their large number of seeds. Our initial population was therefore made of 32 half-sib seedlots. Seeds for the three experimental sets were independently sampled at different times from the initial 32 half-sib seedlots according to the same sampling method. In each experimental set, there were ten combinations of mating designs and population size. The overall number of plants for each combination was 128; these 128 plants were obtained by randomly sampling four seeds out of each of the 32 half-sib seedlots.

Treatments

For each combination of population size and mating design – and over the five generations – the proportion selected was kept constant

		Mating design			
		Pair mating	Partial diallel	Factorial-1	Factorial-2
N	4	4	4		
	8	8	8		
	16	16	16	4	
	32	32		4	8

a

		Mating design			
		Pair mating	Partial diallel	Factorial-1	Factorial-2
N	4	2	6		
	8	4	12		
	16	8	24	15	
	32	16		31	60

b

Fig. 1a, b Experimental layout used for comparisons. Factorial-1 has one tester, while factorial-2 has two testers. **a** Effective population size. **b** Number of crossings

at 25%. There were four population sizes, 4, 8, 16, and 32. Accordingly, the populations at generation 0 were divided into a number of separated sublimes when necessary. For instance, the 128 plants were divided into eight sublimes of 16 plants for $N=4$, four sublimes of 32 plants for $N=8$, and two sublimes of 64 plants for $N=16$. The sublimes were kept separated during the experiment. In generations 3, 4, and 5 there was a control population of plants from generation 0 that had been randomly selected and crossed.

There were four types of mating designs: pair mating, partial diallel, and factorial mating with either one or two testers (Fig. 1). Both pair mating and partial diallel are balanced mating designs. For these designs the effective population size (N_e) is equal to the population size (N). The effective population size represents, “the number in an idealized population in which each individual has an equal number of expected progeny” (Kimura and Crow 1963). The effective population sizes given in Fig. 1 are the variance effective population sizes (see below). Values have been approximated to the closest integer value. The factorial mating designs used here are unbalanced, and consequently their effective population size is much smaller than their corresponding population size (Fig. 1 a). For a given number of selected parents, mating designs also differ in the number of crossings needed (Fig. 1 b). For instance, a partial diallel requires three times as many crossings as pair mating.

Growing conditions and planting design

All three experimental sets were initiated at the Department of Forestry, University of Wisconsin-Madison. The fourth generation of Set 3 and the fifth generation of all three sets were carried out at the Department of Forest Genetics, Swedish University of Agricultural Sciences, Uppsala. The growing conditions in both places were made as similar as possible.

The seeds were sown one or two per pot in Peat-Lite, a standard mix of sphagnum peat moss, perlite, and vermiculite (Sunshine mix). A different growing media (“Plant-jord” Hasselfors Garden AB) was used in Uppsala. Each plant received five pellets of Osmocote, a balanced slow release fertilizer of 14:14:14 (N:P:K). The seeds that failed to germinate and the seedlings that died within 4 days were replaced with new seeds. The plants were grown in plastic multi-pots with six plant cells per unit (each cell: 1.5 inches×1.5 inches×1.5 inches). One plant was kept per cell. The plants were watered using a wick-system, developed by the Crucifer Genetics Cooperative (Williams 1985). The multi-pots rested on a Plexiglas plate, six multi-pots’ units per plate, with a mat to draw up water from a reservoir below. Each plant cell contained a wick that was in contact with the mat. The reservoir was refilled two to three times a week. The plants were grown on 6-foot-high plant-growing carts with four chrome-plated shelves (24 by 48 inches) and equipped with eight 40 W cool-white fluorescent bulbs suspended from each of the three upper shelves. In Uppsala five chrome-plated shelves were attached to the wall in a room smaller than the laboratory in Madison. In both loca-

tions, the plants were continuously illuminated; the light intensity was about 300 einstein $s^{-1} m^{-2}$ at the bulb level. The room temperature was maintained between 20°C and 25°C. Each shelf could hold 288 plants. Plants were completely randomized in generations 0 to 4. In generation 5 a random complete block design with eight blocks was used to take account of the light heterogeneity in the growth chamber. Sixteen days after planting, the area of the second true leaf was measured with an electronic planimeter (LI-3100 Areameter) on all plants. Within each subline, leaf areas were ranked in decreasing order, and the top 25% of plants were selected as parents for the following generation (mass selection). The selected individuals were crossed according to one of the mating designs previously described. The plants to be crossed were randomly chosen among the selected individuals. Bud pollination was conducted without emasculation and without bagging. Newly-dehiscent anthers were removed from the male plant with a pair of tweezers, and brushed against the stigma of an open bud of the female plant until pollen deposition was easily visible to the naked eye. Tweezers and fingers were carefully disinfected with 70% ethanol before each pollination. The selected plants were pollinated to produce at least eight seeds per crossing during a period of about 2 weeks. Some of the selected individuals could not be successfully crossed and had to be replaced. Once the desired number of pollinations had been done, the tops of the plants were cut off to prevent the plants from touching the light bulbs. The plants senesced after 7 weeks of growth. Plants were allowed to dry for 20–28 days from the last pollination by withholding watering. Pods were harvested at maturity and stored at room temperature before seed extraction.

Statistical analysis and mathematical definitions

All statistical analyses were performed using the Statistical Analysis System (SAS 1988). Depending on the comparisons, different linear models were used, including:

$$z_{ijk} = m_{dj} + N_j + (md \times N)_{ij} + \varepsilon_{ijk} \quad (\text{Table 3})$$

$$z_{ijk} = m_i + \varepsilon_{ij} \quad (\text{Tables 4, 6, 8}),$$

where z represents the individual score,
 md represents mating design,
 N represents population size, and
 ε represents error.

In generation 5, the block effect was removed before further analysis (by using the residuals of a model in which block is the only independent factor). A Tukey test at $P=0.05$ was used to compare group means. For the sake of clarity, actual means in generation 5 are given although the test was done on data adjusted to the block effect. However, adjusted and non-adjusted data generally led to the same results. All models were evaluated using Procedure GLM of SAS.

Heritability was estimated by using the pooled data from four combinations (mating design-population size) per set at generation 0, and was defined as,

$$h^2 = \frac{4\sigma_{fam}^2}{\sigma_{fam}^2 + \sigma_{fam \times comb}^2 + \sigma_{\varepsilon}^2},$$

where, fam represents family, $comb$ represents combinations, and ε represents error.

The variance components were estimated by using Procedure VARCOMP of SAS. The families were assumed to be half-sibs, but were likely to include some full-sibs. Therefore, the coefficient, 4, in the numerator is likely to have led to overestimation of the heritability in all three sets.

The standard error of family variance is estimated by using the relations (Becker 1975),

$$Var(\sigma_{fam}^2) = \frac{2}{m^2} \left(\frac{MS_{fam}^2}{df_{fam} + 2} + \frac{MS_{fam \times comb}^2}{df_{fam \times comb} + 2} \right),$$

$$se(h^2) = \sqrt{\frac{4^2 Var(\sigma_{fam}^2)}{\sigma_{fam}^2 + \sigma_{fam \times comb}^2 + \sigma_{\varepsilon}^2}},$$

where m represents the coefficient of family variance component, MS represents the mean square, and df represents the degree of freedom.

The estimation of the standard error assumes the presence of a balanced data set. The data at generation 1 were nearly balanced.

The realized heritability was estimated by dividing the response to selection (R) at generation 5 by the accumulated selection differential (S) (Falconer 1989):

$$h^2 = \frac{R}{S} = \frac{\frac{z_s - z_c}{4}}{\sum_{i=1}^4 (x_i - z_i)},$$

where z represents the mean of the unselected population,
 x represents the mean of the selected population,
 c represents the control population, and
 i represents the i th generation.

The variance effective population sizes of the different mating designs were determined using Robertson's (1961) definition:

$$N_e = \frac{\left(\sum_{i=1}^N u_i \right)^2}{\sum_{i=1}^N u_i^2}$$

where u_i represents the expected contribution of the i th individual and N is the number of parents.

Results

Expected and realized heritabilities

The estimated heritability at generation 0 and the realized heritabilities estimated at generations 4 and 5 for a pair mating and a partial diallel design are shown in Table 1. Means of the realized heritabilities for each mating design are substantially smaller than the corresponding estimated heritabilities. In general, smaller populations tend to have lower heritabilities. This trend is clearer in generation 5 than in generation 4 (Table 1). In all three sets, the average realized gain was much smaller than the corresponding expected gain (Table 2). Altogether the response to selection was fairly weak (Figs. 2 and 3). Selection of the top 25% generally led us to pick a few individuals in each family. This phenomenon was also accentuated by the episodic replacement of plants pertaining to the top 25% for leaf area but showing defects such as poor flowering, or by a reduced number of families. For example, in Generation 0 of Pair Mating 32, Set 1, mass selection led us to pick up individuals in most families; because each family was represented by four individuals, the selected sample should contain a minimum of eight families: 22 families were indeed represented in the selected sample. The same was also true in later generations.

Comparison of balanced mating designs

When the different population size levels are combined, the partial diallel design does not significantly differ from

Table 1 Estimated heritabilities (narrow-sense) at generation 0 and realized heritabilities at generation 4 and 5, for each set. The realized heritabilities were computed for each combination of mating design and population size (N). Pair is pair mating and partial is partial diallel

Mating design		Group	Set 1	Set 2	Set 3
Estimated h^2			0.37	0.48	0.43
se (h^2)			0.16	0.18	0.17
Realized h^2 generation 4	Mean		0.06	0.14	0.12
	sd		0.08	0.10	0.12
	Pair	N32	0.09	0.19	0.30
	Pair	N16	0.12	0.05	0.09
	Pair	N8	0.07	0.21	0.08
	Pair	N4	0.01	0.17	0.28
	Partial	N16	0.19	0.29	0.07
	Partial	N8	-0.03	0.05	-0.01
Realized h^2 generation 5	Mean		0.11	0.19	0.06
	sd		0.08	0.10	0.03
	Pair	N32	0.16	0.34	0.07
	Pair	N16	0.18	0.24	0.07
	Pair	N8	0.17	0.12	0.06
	Pair	N4	-0.04	0.19	-0.002
	Partial	N16	0.14	0.25	0.08
	Partial	N8	0.03	0.20	0.07
Partial	N4	0.11	0.03	0.07	

Table 2 Realized and expected gains at generation 4 and 5. Realized gain corresponds to the mean of the response to selection. Expected gain is estimated using h^2 from generation 1

Item	Set 1	Set 2	Set 3
σ_p	447	378	453
Estimated h^2	0.37	0.48	0.43
se (h^2)	0.16	0.18	0.17
Realized gain (4)	198	284	201
Expected gain	834	915	983
Difference	-636	-631	-782
Realized gain (5)	245	452	197
Expected gain	1051	1153	1237
Difference	-806	-701	-1040

pair mating in either Set 1 or Set 2. Mating designs differ significantly in Set 3, although the level of significance is not very high. The analysis of variance in Table 3, however, indicates a significant interaction between mating design and population size, in both Set 1 and Set 2. Therefore, we also compared mating designs at each population size level in the different sets. Table 4 shows that the impact of balanced mating designs on selection response was not substantially different, except for N=8 and N=4 in Set 1, and N=4 in Set 3. The comparison of group means indicates that no mating design was clearly superior over the others (Table 5). In five cases out of nine, there were no differences among means; and in the four cases where

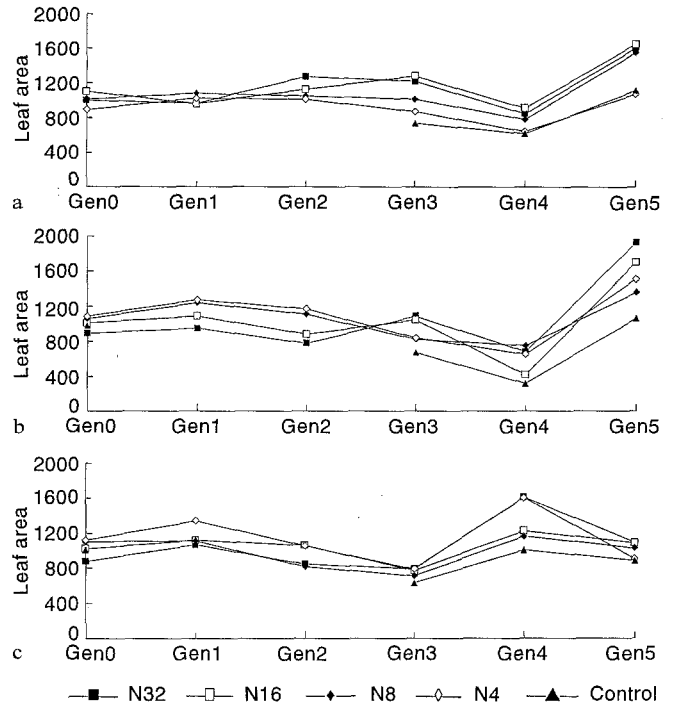


Fig. 2a-c Leaf area mean over generations when the mating design is pair mating. *N* gives the population size. Where there is more than one subline, the mean given is the mean of the sublines. **a** Set 1, **b** Set 2 and **c** Set 3. Leaf area is in mm²

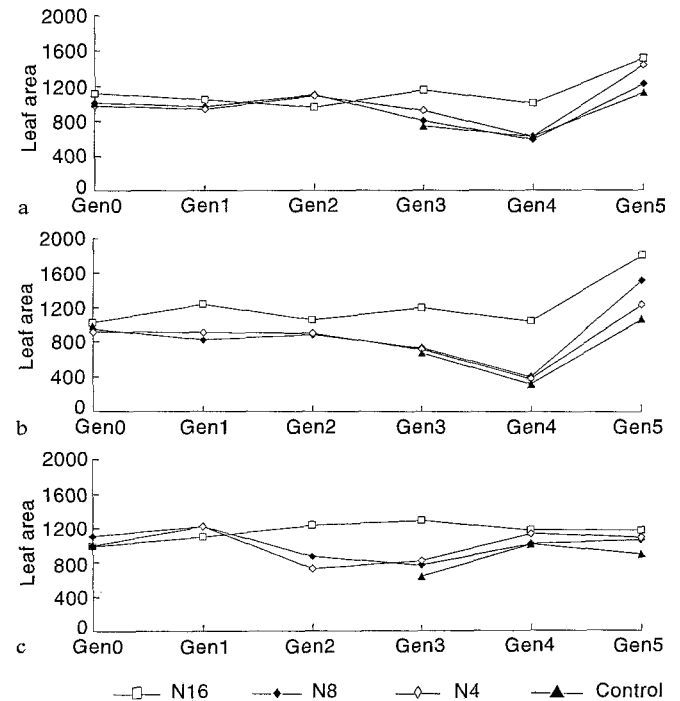


Fig. 3a-c Leaf area mean over generations when the mating design is partial diallel. *N* gives the population size. Where there is more than one subline, the mean given is the mean of the sublines. **a** Set 1, **b** Set 2 and **c** Set 3. Leaf area is in mm²

means differed significantly, two were in favor of partial diallel and two were in favor of pair mating. This result is most remarkable when we remember the difference in the number of crossings between the two mating designs (Fig. 1 b).

Table 3 Comparison of balanced mating designs (pair mating and partial diallel, md). Result from analysis of variance. The dependent variable is leaf area at generation 5. The data were first adjusted to the block effect

Source		df	Mean square	F	Pr>F
Set 1	md	1	328 352.90	0.99	0.3199
	N	3	4 617 133.62	13.93	0.0001
	md×N	2	5 462 768.10	16.48	0.0001
	Error	758	331 451.16		
Set 2	md	1	54.08	0.00	0.9915
	N	3	9 566 724.18	20.27	0.0001
	md×N	2	1 647 647.27	3.49	0.0310
	Error	711	471 978.99		
Set 3	md	1	1 097 617.93	6.73	0.0096
	N	3	939 648.47	5.77	0.0007
	md×N	2	209 518.96	1.29	0.2771
	Error	725	162 984.08		

Table 4 Comparison of balanced mating designs (md) at each population size (N). Results from analysis of variance at generation 5. Data were first adjusted to the block effect

Source		df	Mean square	F	Pr>F
Set 1	N16	md	1 152 780.453	3.72	0.0551
		Error	242 310 288.585		
	N8	md	6 014 326.868	18.56	0.0001
		Error	222 324 035.023		
	N4	md	4 717 943.663	16.52	0.0001
		Error	172 285 643.223		
Set 2	N16	md	8656 63.381	1.83	0.1775
		Error	237 473 292.898		
	N8	md	1125 043.117	2.22	0.1375
		Error	216 506 307.707		
	N4	md	1 740 975.369	4.29	0.0403
		Error	134 406 113.989		
Set 3	N16	md	386 326.770	2.29	0.1315
		Error	231 168 672.718		
	N8	md	20 410.893	0.13	0.7171
		Error	202 154 999.728		
	N4	md	1 086 042.657	6.87	0.0095
		Error	179 157 972.268		

Table 5 Comparison of balanced mating designs at each population size (N). Tukey's test at generation 5. Means with the same letter are not significantly different. $\alpha=0.05$

N	Mating design	Set 1	Set 2	Set 3
N=16	Pair mating	1658 A	1701 A	1085 A
	Partial diallel	1509 A	1810 A	1231 A
N=8	Pair mating	1558 A	1359 A	1028 A
	Partial diallel	1219 B	1515 A	1083 A
N=4	Pair mating	1078 B	1510 A	907 B
	Partial diallel	1433 A	1235 B	1053 A

Balanced vs unbalanced mating designs

Constant population size but different effective population size (see Fig. 1 a). Two different contrasts were made: (1) the impact of balanced and unbalanced mating designs when the population size was set at 16; and (2) the impact of balanced and unbalanced mating designs when the population size was set at 32. When N=16, the response was significantly greater under balanced mating designs than under unbalanced ones in all three sets (Tables 6 and 7). When N=32, the pattern is not as clear as when N=16. Yet, in both Set 1 and Set 2, response under balanced mating designs was significantly larger than under either unbalanced ones. Note that the average response in Set 3 was much smaller than in either Set 1 or Set 2.

Constant effective population size but different population size (see Fig. 1 a). Two different contrasts were made: (1) the impact of balanced and unbalanced mating designs when the effective population size was 4; and (2) the impact of balanced and unbalanced mating designs when the population size was 8 (Tables 8 and 9). When $N_e=4$, the difference between balanced and unbalanced mating designs was significant only in Set 2 and Set 3. But the means differed only in Set 2, and the ranking did not follow the population size. When $N_e=8$, means only differed in Set 3, but the difference, although significant, was very small.

Table 6 Comparison of balanced and unbalanced mating designs (md) for population sizes, N, of 16 and 32. Results from analysis of variance at generation 5. Data were first adjusted to the block effect

N	Source	df	Mean square	F	Pr>F
N=16	Set 1	md	1 8243 828.43	27.25	0.0001
		Error	358 302 555.22		
	Set 2	md	1 27 678 945.99	59.56	0.0001
		Error	337 464 726.72		
	Set 3	md	1 386.97	0.00	0.9672
		Error	352 228 631.67		
N=32	Set 1	md	2 5846 349.89	17.00	0.0001
		Error	356 343 846.14		
	Set 2	md	2 7048 757.12	17.48	0.0001
		Error	365 403 191.73		
	Set 3	md	2 124 300.41	0.62	0.5364
		Error	296 199 128.16		

Table 7 Comparisons of balanced and unbalanced mating designs for population sizes, N, of 16 and 32. Tukey's test at generation 5. Means with the same letter are not significantly different. $\alpha=0.05$

N	Mating design	Set 1	Set 2	Set 3
N=16	PM+PD	1585 A	1754 A	1160 A
	Fact-1	1265 B	1140 B	1129 A
N=32	PM	1609 A	1925 A	1093 A
	Fact-2	1277 B	1445 C	1167 A
	Fact-1	1197 B	1663 B	1136 A

Table 8 Comparison of balanced and unbalanced mating designs (md) with the same effective population size (N_e). Results from analysis of variance at generation 5. Data were first adjusted to the block effect

N_e	Source	<i>df</i>	Mean square	F	Pr>F	
$N_e=4$	Set 1	md	2	178 175.0732	0.62	0.5390
		Error	397	287 866.3577		
	Set 2	md	2	7932 301.40	17.94	0.0001
		Error	358	442 246.66		
	Set 3	md	2	923 654.381	4.04	0.0183
		Error	370	228 528.204		
$N_e=8$	Set 1	md	1	1 409 489.833	4.11	0.0433
		Error	348	342 685.403		
	Set 2	md	1	829.251	0.00	0.9657
		Error	334	446 546.950		
	Set 3	md	1	1 316 853.181	7.91	0.0052
		Error	316	166 394.629		

Table 9 Comparisons of balanced and unbalanced mating designs with the same effective population size (N_e) but different population size (N). Tukey's test at generation 5. Means with the same letter are not significantly different. $\alpha=0.05$

N_e	N	Set 1	Set 2	Set 3
$N_e=4$	Fact-1(32)	1197 A	1663 A	1136 A
	Fact-1(16)	1265 A	1140 C	1129 A
	PM(4)	1254 A	1444 B	994 A
$N_e=8$	Fact-2(32)	1277 A	1445 A	1167 A
	PM+PD(8)	1399 A	1446 A	1040 B

Discussion

In the introduction we raised two questions: (1) do balanced and unbalanced mating designs have significantly different impacts on selection response?, and (2) when mating designs are balanced, does the number of crossings matter? Our study clearly shows that a higher selection response was indeed obtained under balanced mating designs than under unbalanced ones and that pair mating and a partial diallel have the same impact on selection response over the first generations of selection. Our results might have been even more striking had the selection response been higher. For instance, the lack of difference between balanced and unbalanced mating designs observed in Set 3, but not in Sets 1 and 2 where the response to selection was substantially higher, might have simply resulted from the weakness of the selection response. Because of its bearing on the results, we shall first discuss the possible causes of the lack of selection response.

Selection response

Despite fairly-high estimated heritabilities in generation 0 in all three sets, both realized heritabilities and responses were low and erratic, indicating that non-selective forces, e.g., random drift, inbreeding, and environment, may ex-

plain most of the observed changes in leaf area over generations. Disagreement between predicted and realized values is commonly found in selection experiments when more than one generation is considered (Sheridan 1988; James 1990; Hill and Caballero 1992). In our experiment, the departure between predicted and realized values may have at least two sources:

Selecting the top 25% consistently led us to sample a few individuals in almost every family rather than many individuals in a few families.

The relative decrease of the between-family variance is accompanied by a steep increase of the within-family variance between generations 3 and 5. Obviously, we have underestimated the sensitivity of leaf area to variation in environmental conditions. Yet, environmental factors do not seem to be solely responsible for the observed increase in within-family variance because adjustment of the data to the block effect in generation 5 did not seriously alter its value.

Hence the lack of response seems to primarily follow from the inaccuracy of the selection process. This can be checked, at least in part, by repeating the experiment under more controlled environmental conditions. Notably, light intensity and temperature will have to be carefully monitored because leaf size and morphology seem very sensitive to both factors (Gurevitch 1992).

Impact of mating design on selection response and its causes

In our study, differences between mating designs for selection response could be assigned to three causes: difference in population size (number of parents), difference in number of crossings, and difference in effective population size. The various contrasts we were able to build show that effective population size is undoubtedly the most important of these three possible factors.

First, for a given effective population size, there were no differences between balanced mating designs with respect to selection response. Given that there were three times as many crossings in a partial diallel than in pair mating, and given that the population size is equal to the effective population size for balanced matings, it implies that the number of crossings does not influence the response to selection. This result generally agrees with theoretical predictions and simulations (Kang 1991). If confirmed by a larger-scale experiment, it also indicates that the slight advantage of pair mating over the partial diallel in early generations that was found in simulations studies (Kang 1991) may not be large enough to be detected under actual conditions.

Second, no clear pattern emerged when balanced and unbalanced mating designs were compared for a given effective population size, ruling out any difference in population size as a possible cause of the difference in selection response between mating designs.

Finally, comparison between balanced and unbalanced mating designs for a given population size confirmed that

effective population size was the main cause of the different impact of mating designs on selection response: the larger the effective population size, the larger the selection response.

The theory of limits to artificial selection explicitly relates selection response to effective population size (Robertson 1960). This theory stems from the expression of the ultimate probability of fixation of a favorable allele in a finite population (Kimura 1957):

$$u(q) = \frac{\int_0^q G(x) dx}{\int_0^1 G(x) dx}$$

where $G(x) = \exp[-2N_e s(2h-1)x(1-x) - 2N_e s x]$, q represents the initial allele frequency, N_e represents the variance effective population size, h represents the degree of dominance, and s represents the selection coefficient.

A series of experiments (Jones et al. 1968) indeed confirmed the importance of effective population size on long-term response to selection. Our observations show that effective population size might even have an effect on selection response as early as the fifth generation of selection.

Practical implications

Our results indicate that balanced mating designs should be favored over unbalanced ones in long-term breeding programs. Given that the number of crossings does not influence the selection response, breeders may use the simplest balanced mating design that fits their requirements.

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