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Estimates of gene frequencies in two heterotic maize populations

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Summary. The present study was undertaken to obtain information on average gene frequency in two heterotic populations of maize (*Zea mays* L.), Mezcla Amarillo Selection (MAS) and J607. Sixty-four male plants were taken in each of the populations and each of these were crossed to a different set of eight plants, four of which belonged to the same population and four to the other population. This resulted in two groups of intra-population (within MAS and within J607) and two groups of inter-population (MAS × J607 and J607 × MAS) progenies. Each group consisted of 256 full-sib progenies on the pattern of the North Carolina Design I mating system. The male plants were selfed to produce 64 S_1 prgenies in each population. The materials were evaluated at two diverse locations, Ludhiana and Gurdaspur, for grain yield, ear length, ear girth, number of kernel rows, plant height, ear height and days to silk. An incomplete block design with two replications were used. The plot consisted of a 5 m long row. Ratios of estimated genetic components of variance and covariance were compared with corresponding theoretical ratios computed for a single locus for various gene frequencies and levels of dominance, and approximate ranges of the gene frequencies and their relative magnitude were worked out in the two populations. The average frequency of favourable genes for plant height was estimated as 0.6 in MAS and 0.8 in J607. For grain yield the average gene frequency was 0.8 to 0.9 in MAS and 0.7 to 0.8 in J607 whereas for ear height it was 0.5 to 0.7 in MAS and 0.4 to 0.6 in J607. The gene frequency in the two populations seemed to be similar for days to silk, ear length, ear girth and kernel rows.

Key words: *Zea mays* L. – Maize – Genetic variances – Covariances – Gene frequency

Introduction

Plant breeders, in their endeavour to develop better cultivars, attempt to manipulate gene frequencies. Additive genetic and dominance variances are maximum when gene frequencies are 0.5. The change in variance is relatively small when selection is applied to the traits controlled by genes with frequencies around 0.5, whereas with higher gene frequencies, the reduction in genetic variance is larger (Eberhart 1977). The population with a relatively low frequency of favourable alleles is expected to respond to selection over a longer time span than those populations which have high gene frequencies. Estimates of gene frequency would also indicate the probability of deriving good inbred lines from a base population. Thus, information on gene frequencies in open-pollinated populations is important in assessing their suitability as base material and is helpful to the breeders in planning their programme. In the present study the frequency of genes controlling important agronomic traits was evaluated in two heterotic random mating populations.

There are few reports wherein on the basis of the study of half-sib-full-sib progenies (NCD-I) and S_1 lines, in two random mating populations, inferences have been made about average gene frequency in maize. Robinson et al. (1955) discussed the effect of gene frequency on additive (σ^2_A) and dominance (σ^2_D) variance components and explained that a σ^2_D/σ^2_A greater than unity could result even when there is no real over-dominance. Robinson et al. (1958) used the ratio of average intra-to inter-population male components of variance $(\sigma^2_{m11}+\sigma^2_{m22})/(\sigma^2_{m12}+\sigma^2_{m21})$ to make inferences about levels of dominance and gene frequency differences in two populations: 'Jarvis' and 'Indian Chief'. Compton et al. (1965) employed average intra-to-inter-population female components of variance $(\sigma_{f11}+\sigma_{f22})/(\sigma_{f12}+\sigma_{f21})$ to make average gene frequency inferences in 'Golden Republic' and 'Barber Reid'. Goodrich et al. (1975) evaluated S_1 lines developed by selfing the male parents along with the biparental progenies of NCD-I in 'Golden Jewel' and 'Osterland's Yellow Dent'. The additional ratios calculated by them were covariance of intra-to inter-population male effects in one population compared to the other population ($\sigma_{m11m12}/\sigma_{m22m21}$), S_1 progeny variance in one population compared to the other ($\sigma^2_{s1}/\sigma^2_{s2}$), covariance of S_1 and intra-population male effects to S_1 and inter-population male effects ($\sigma_{s1m11}/\sigma_{s1m12}$ and $\sigma_{s2m22}/\sigma_{s2m21}$).

In the present study, all the above mentioned ratios were used.

Materials and methods

The present investigation was based on two open pollinated populations: 'Mezcla Amarillo Selection' (MAS) and J607. MAS is an introduction from CIMMYT, Mexico. J607 is a population developed at the Punjab Agricultural University, Ludhiana, through intra-population improvement in a germplasm complex created by crossing an indigenous collection 'Bhodipur Yellow' with three hybrid introductions, two from the USA and one from Yugoslavia. In addition to the good performance of the populations, their varietal hybrids exhibited a high degree of heterosis (Anonymous 1975).

These populations were grown under staggered sowings and a North Carolina Design I mating system was followed to generate 256 full-sib progenies within 64 half-sib groups, within and between the populations. In addition, 64 S_1 progenies were produced in each population by selfing the male plants. The resulting material was as follows: (i) S_1 progenies in MAS (ii) S_1 progenies in J607 (iii) Intra-population progenies in MAS (iv) Intra-population progenies in J607 (v) inter-population progenies involving male from MAS and female from J607 and (vi) Inter-population progenies involving male from J607 and female from MAS.

The materials were evaluated at two agro-climatically diverse locations in India, Ludhiana and Gurdaspur. The experimental area was divided into 32 blocks. A set of four male groups, each having four intra-population full-sib progenies, four inter-population full-sib progenies and one S_1 progeny, was assigned at random to each block. Each progeny was replicated twice within the block. The progenies were randomized in each replication except the four S_1's which were assigned to four adjacent rows. The full-sib and S_1 progenies were separated by using two appropriate border rows. A plot consisted of a 5 m row with row-to-row and plant-to-plant spacing of 75 and 20 cm, respectively. Data were recorded from 10 randomly taken competitive plants for grain yield (g), ear length (cm), ear girth (cm), number of kernel rows, plant height (cm) and ear height (cm) and an average of 10 plants was used for statistical analysis. The number of days taken from sowing to silking of 75% plants in a plot was also recorded.

Analyses of variance were computed for males mated to the same population (intra) and to the other population (inter) and also for S_1 progenies in each population. Covariance analysis were also performed for each trait between intra-population and inter-population half-sib progenies and for S_1 progenies with both intra- and inter-population half-sib progenies performance. The male and female within male components of variance for intra- and inter-population crosses were estimated following Anderson and Bancroft (1952).

By using theoretical expressions for intra- and inter-population male and female within male components of variance (Compton et al. 1965), variance among S_1 progenies and covariance of S_1 progenies and intra- and inter-population half-sib progenies (Goodrich et al. 1975), theoretical tables, some of which have been partly published by Robinson et al. (1955); Compton et al. (1965) and Goodrich et al. (1975) were constructed for the following ratios pertaining to a single locus using several gene frequencies and levels of dominance, where 'p' is the frequency of favourable allele in MAS (population 1), 'x' is the frequency of the same allele in J607 (population 2) (as dominance has always been taken to be positive, p and x are the frequency of dominant alleles) and 'a' indicates the level of dominance.

R_1 $=\sigma^2_D/\sigma^2_A$ in terms of p (x) and a (Appendix 1)
R_2 $=(\sigma^2_{m11}+\sigma^2_{m22})/(\sigma^2_{m12}+\sigma^2_{m21})$ in terms of p, x and a (Appendix 2)
R_3 $=(\sigma^2_{f11}+\sigma^2_{f22})/(\sigma^2_{f12}+\sigma^2_{f21})$ in terms of p, x and a (Appendix 3)
R_4 $=\sigma_{m11m12}/\sigma_{m22m21}$ in terms of p and x (this ratio is independent of a) (Appendix 4)
R_5 $=\sigma^2_{s1}/\sigma^2_{s2}$ in terms of p, x and a (Appendix 5)
$R_{6(1)}=\sigma_{s1m11}/\sigma_{s1m12}$ in terms of p, x and a (Appendix 6)

The ratio $\sigma_{s2m22}/\sigma_{s2m21}$ ($R_{6(2)}$) has the same values as $\sigma_{s1m11}/\sigma_{s1m12}$ except that p and x are interchanged. Suffices 11 and 22 refer to intra-population estimates of population 1 (MAS) and population 2(J607), respectively, whereas 12 and 21 refer to inter-population estimates when males are from population 1 and females from population 2 and vice versa, respectively.

The inferences about gene frequencies were made by inspecting theoretical values to detect combinations of gene frequencies and levels of dominance which give rise to approximately the same value as the corresponding observed ratios. The method does not give exact estimates but inferences can be made about the relative magnitude of gene frequencies.

Results and discussion

The estimates of components of variance and covariances are given in Tables 1–2. Table 3 includes observed ratios of variances and covariances used to infer gene frequency.

Grain yield

Additive genetic variance was significant and greater than the dominance component in MAS (Table 1). Assuming a = 0.50 to 0.75 in this population, the observed ratio R_1 of 0.519 (Table 3) indicated a high frequency of favourable alleles, i.e. as high as 0.8 to 0.9 (p) (Appendix 1). However, in J607 a predominant role of σ^2_D was observed. Under the assumption of a = 1.25 the frequency of favourable genes in this population seemed to be 0.7 to 0.8 (x).

The observed ratio of average intra-to-inter-population female component, R_3, was 1.112. This ratio is obtainable under the above hypothesised gene frequencies (Appendix 3). The ratio of covariances of S_1 and intra-population male effects to covariance of S_1 and inter-population male effects, $R_{6(1)}$, in MAS was 1.386. This ratio indicated that x may be between 0.7 and 0.8 whereas p = 0.8 to 0.9 continued to be tenable

Table 1. Estimates of components of genetic variance

Character	MAS				J 607			
	σ^2_A	σ^2_D	σ^2_{AL}	σ^2_{DL}	σ^2_A	σ^2_D	σ^2_{AL}	σ^2_{DL}
Grain yield	97.92* ±49.71	50.78 ±79.45	– 5.11 ±38.44	15.71 ±92.45	26.68 ±44.02	153.87* ±70.84	71.99 ±45.33	–38.43 ±81.34
Ear length	1.158* ± 0.469	0.902 ± 0.588	0.120 ± 0.237	0.128 ± 0.512	0.060 ± 0.264	1.790** ± 0.480	0.270 ± 0.241	0.010 ± 0.467
Ear girth	0.292* ± 0.134	0.188 ± 0.188	0.080 ± 0.088	0.170 ± 0.180	0.222 ± 0.137	0.254 ± 0.190	0.210* ± 0.096	– 0.190 ± 0.153
Kernel rows	0.522* ± 0.225	0.778* ± 0.318	0.000 ± 0.084	0.080 ± 0.196	0.565* ± 0.259	0.925** ± 0.355	0.190 ± 0.122	0.214 ± 0.211
Plant height	121.22* ±44.84	108.24* ±54.54	27.15 ±17.41	–15.19 ±31.43	124.75* ±58.89	322.80** ±68.86	18.96 ±15.52	– 5.32 ±29.68
Ear height	128.85** ±38.38	– 0.56 ±44.28	16.33 ±11.49	3.09 ±20.97	118.00** ±38.00	75.24 ±46.32	9.32 ± 8.48	– 0.05 ±16.54
Days to silk	6.465** ± 1.817	– 4.625 ± 2.087	0.660 ± 0.812	3.532* ± 1.583	5.408** ± 1.658	– 9.778 ± 1.929	0.915 ± 0.634	3.965* ± 1.120

*, ** Significant at 5% and 1% probability levels, respectively

Table 2. Estimates of components of variance and covariance

Component	Grain yield	Ear length	Ear girth	Kernel rows	Plant height	Ear height	Days to silk
σ^2_{m11}	24.48* ±12.43	0.289* ±0.117	0.073* ±0.033	0.138* ±0.056	30.30** ±11.21	32.21** ± 9.60	1.616** ±0.454
σ^2_{f11}	37.17* ±15.50	0.515** ±0.089	0.120** ±0.033	0.333** ±0.056	53.62** ± 8.71	32.07** ± 5.52	0.460* ±0.257
σ^2_{m22}	6.67 ±11.01	0.015 ±0.066	0.056 ±0.034	0.141* ±0.065	31.19* ±14.72	29.50** ± 9.50	1.352** ±0.415
σ^2_{f22}	45.14** ±13.87	0.463** ±0.100	0.119** ±0.033	0.373** ±0.061	99.39** ±13.10	48.31** ± 6.62	1.158** ±0.247
σ^2_{m12}	19.92 ±11.52	0.242* ±0.099	0.054 ±0.029	0.174** ±0.066	24.48* ±10.14	36.97** ±10.85	0.871** ±0.308
σ^2_{f12}	17.90 ±20.70	0.490** ±0.128	0.148** ±0.034	0.398** ±0.059	76.34** ±10.87	50.31** ± 6.80	0.955** ±0.282
σ^2_{m21}	23.12 ±12.96	0.294** ±0.104	0.089** ±0.033	0.207** ±0.070	36.22** ±12.24	38.05** ±11.69	0.736** ±0.292
σ^2_{f21}	56.09** ±20.60	0.443** ±0.113	0.155** ±0.037	0.079** ±0.056	57.72** ±10.45	47.80** ± 7.17	1.333** ±0.252
σ^2_{s1}	125.41** ±47.60	1.559** ±0.422	0.258* ±0.130	0.589** ±0.198	242.11** ±56.95	69.38** ±17.23	3.888** ±1.145
σ^2_{s2}	359.14** ±86.12	1.809** ±0.496	1.129** ±0.277	1.147** ±0.316	115.13** ±29.43	117.03** ±27.54	7.227** ±1.927
σ_{m11m12}	1.98	0.161	–0.097	0.136	31.91	33.87	0.803
σ_{m22m21}	3.45	0.070	0.050	0.191	22.41	31.99	0.971
σ_{s1m11}	26.89	0.607	0.133	0.287	27.63	34.47	1.665
σ_{s1m12}	19.34	–2.017	0.067	0.272	27.09	44.96	0.483
σ_{s2m22}	– 8.69	0.152	0.111	0.194	55.88	43.26	2.462
σ_{s2m21}	27.99	0.399	0.105	0.231	75.76	65.39	1.848

*, ** Indicate significance of variance components at 5% and 1% probability levels, respectively (significance of covariance components has not been given)

Table 3. Observed ratios of Design I variance components, S_1 progeny variances and some covariances used in making gene frequency inferences

Ratio[a]	Grain yield	Ear length	Ear girth	Kernel rows	Plant height	Ear height	Days to silk
R_1 (MAS)	0.519	0.779	0.644	1.409	0.893	–	–
R_1 (J607)	5.767	29.833	1.144	1.637	2.587	0.638	–
R_2	0.724	0.567	0.902	0.732	1.013	0.823	1.847
R_3	1.112	1.048	0.789	1.480	1.141	0.819	0.707
R_4	0.574	2.300	–	0.712	1.424	1.059	0.827
R_5	0.349	0.862	0.229	0.514	2.103	0.593	0.538
$R_{6(1)}$	1.387	–	1.985	1.055	1.020	0.767	3.447
$R_{6(2)}$	–	0.381	1.057	0.840	0.738	0.662	1.332

[a] R_1 (dominance to additive genetic variance in MAS) $= \sigma^2_{D11}/\sigma^2_{A11}$; R_1 (dominance to additive genetic variance in J607) $= \sigma^2_{D22}/\sigma^2_{A22}$; R_2 (average intra- to inter-population male components) $= \sigma^2_{m11} + \sigma^2_{m22})/(\sigma^2_{m12} + \sigma^2_{m21})$; R_3 (average intra- to inter-population female components) $= (\sigma^2_{f11}/\sigma^2_{f22})/(\sigma^2_{f12} + \sigma^2_{f21})$; R_4 (covariance of intra-to inter-population male effects in MAS compared to J607) $= \sigma_{m11m12}/\sigma_{m22m21}$; R_5 (S_1 progeny variance in MAS compared to J607) $= \sigma^2_{s1}/\sigma^2_{s2}$; $R_{6(1)}$ (covariance of S_1 and intra-population male effects to S_1 and inter-population male effects in MAS) $= \sigma_{s1m11}/\sigma_{s1m12}$; and $R_{6(2)}$ (covariance of S_1 and intra-population male effects to S_1 and inter-population male effects in J607) $= \sigma_{s2m22}/\sigma_{s2m21}$

(Appendix 6). S_1 variance in MAS, in comparison to J607, R_5, gave a ratio of 0.349. This also indicated a higher gene frequency in MAS than J607 ($p > x$). A value of $p = 0.9$ and $x = 0.7$ to 0.8 gave theoretical values ranging from 0.45 to 0.28 with $0.50 > a > 0.75$ (Appendix 5). Covariance of intra- to inter-populations male effects in MAS compared to J607, R_4, is free of level of dominance (Appendix 4). The observed ratio was 0.574, which can be realized with $p = 0.8$ to 0.9 and $x = 0.7$ to 0.8.

These ratios indicate $p + x > 1$ but the ratio of average intra- to inter-population male component, R_2, indicates that $p + x < 1$. On the whole, it may be assumed that $p = 0.8$ to 0.9 and $x = 0.7$ to 0.8. All these ratios agree to the point that MAS has a slightly higher average gene frequency than J607 for grain yield.

Ear length

Only σ^2_A was significant in MAS and σ^2_D in J607. Assuming partial dominance in MAS ($a = 0.75$ approximately) the R_1 indicated $p = 0.9$ (Appendix 1). In J607, the gene frequency seemed to be a little lower, i.e. $x = 0.8$ assuming $a = 1.5$, R_1 being 29.833. Two other ratios, R_3 and R_5, also suggested that MAS had a slightly higher gene frequency than J607. All such ratios can be obtained if $p = 0.8$ to 0.9 and $x = 0.7$ to 0.8. However, R_4 and $R_{6(2)}$ did not agree and indicated that the gene frequency in MAS is probably lower than that in J607 ($p = 0.7$ and $x = 0.9$). The ratio of average intra- to inter-population male component indicated that $p + x < 1$. Most of the ratios indicated high level of favourable genes in both populations, MAS having little higher gene frequency (0.8 to 0.9) than that in J607 (0.7 to 0.8).

Ear girth

No consistent trend was observed for ear girth. The ratio R_1 indicated $p = 0.8$ to 0.9 when $a = 0.75$ and $x = 0.6$ to 0.7 with $a = 1.0$. A similar trend was observed from R_5. However, $R_{6(1)}$ indicated that the average gene frequency in MAS ($p = 0.6$) seemed to be lower than that in J607 ($x = 0.8$ to 0.9). From these comparisons between observed and theoretical ratios it appeared that $p + x > 1$. However, R_2 and R_3 suggested that $p + x < 1$. The observed value of R_2 was 0.902, which is quite near to one, being obtainable when $p = x$. This observation is also supported by $R_{6(2)}$. Thus, it is possible that $p = x = 0.8$ for ear girth. It may be added that for this trait neither σ^2_D nor σ^2_A was significant in J607, which may be the cause of the inconsistencies found in the results.

Kernel rows

Both σ^2_A and σ^2_D were significant in MAS as well as in J607. R_1 was greater than one in both cases. Considering $a = 1$, it seemed that MAS and J607 have a gene frequency in between 0.7–0.8. However, R_3 indicated that both populations had a range of 0.7 to 0.9 whereas $R_{6(1)}$ and $R_{6(2)}$ indicated an average gene frequency of 0.7 to 0.8 in both populations. A comparison of the observed values of R_4 with the theoretical value revealed that these ratios agree if p and x are assumed to be 0.7 to 0.9 and 0.7 to 0.8, respectively. The reported ratio of R_5 is obtainable assuming a gene frequency of 0.7 to 0.9 in MAS and 0.7 to 0.8 in J607. Thus, it appears that $p+x > 1$, whereas R_2 indicates that $p+x < 1$. Various ratios, except those of average intra- to inter-population male components, indicated that the gene frequency for this trait ranged between 0.7 to 0.9 in both populations, through p may be a little larger than x.

Plant height

Significant estimates of σ^2_A as well as σ^2_D were obtained in both populations. R_1 was 0.893 in MAS and 2.567 in J607. Assuming complete dominance ($a=1$), these ratios indicated a gene frequency between 0.6 to 0.7 in MAS and 0.8 to 0.9 in J607. The ratios R_2, R_3, $R_{6(1)}$ and $R_{6(2)}$ indicated that p may be in the range of 0.6 to 0.7 whereas $x=0.7$ to 0.8. The ratios R_4 and R_5 narrowed down the values, p being 0.6 and x being 0.8.

Ear height

For ear height only σ^2_A was significant in both populations and the R_1 ratio suggested a high gene frequency in J607 ($x=0.8$ to 0.9) while no indication was available regarding the gene frequency in MAS. Most of the other ratios, such as R_4, R_5 and $R_{6(1)}$ suggested that p is in the range of 0.5 to 0.7 and x in the range of 0.4 to 0.6. According to the ratios R_2 and R_3, $p+x < 1$ and a higher gene frequency can be assigned to MAS ($p=0.5$ to 0.7) than that to J607 ($x=0.4$). These ratios showed that the gene frequency was relatively higher in MAS than in J607 but the results pertaining to $R_{6(2)}$ were not in confirmity with this observation.

Days to silk

In the inheritance of this trait, σ^2_A was significant, whereas σ^2_D was negative, in both populations. The ratio R_1, being negative, did not provide any clue regarding gene frequency. The ratios R_4 and R_5 indicated that p may be 0.7 to 0.8 and x may be 0.4 to 0.6. The computed ratio of $R_{6(2)}$ is obtainable if p and x are assumed to be 0.7 and 0.4, respectively. However, R_2, R_3 and $R_{6(1)}$ did not support these observations regarding p and x. Moreover, R_2 indicated that $p+x > 1$ whereas R_3 indicated $p+x < 1$. On the basis of these results, it is difficult to draw a conclusion but the indications are that $p=0.7$ to 0.8 and $x=0.4$ to 0.6.

General comments

The expression of heterosis is dependent on the differences in the gene frequency in the parents and the dominance effects. Goodrich et al. (1975) suggested that to draw useful conclusions about gene frequencies, there should be a minimum of 5% heterosis in the hybrid. In the present study heterosis was greater than 5% only for grain yield (15.45%) and plant height (8.16%). It was nearly 5% for ear height (4.79%). The heterosis was significant for all traits and, therefore, gene frequency in the two populations was expected to differ for all traits. The results showed, however, that the differences with respect to gene frequency in the two populations were distinct for plant height only and there were similar indications for grain yield and ear height. Gene frequencies seemed to be 0.6 in MAS and 0.8 in J607 for plant height. For grain yield and ear height, the gene frequency seemed to be higher in MAS than in J607 but the differences were not as evident as in case of plant height. The gene frequency seemed to be 0.8 to 0.9 in MAS and 0.7 to 0.8 in J607 for grain yield and 0.5 to 0.7 in MAS and 0.4 to 0.6 in J607 for ear height. The two populations differed widely for days to silk but various ratios indicated either no differences between two populations or inconsistent results with respect to gene frequency, which is in agreement with the observation of Goodrich et al. (1975). It may be added that the estimates of gene frequencies relate to an average measure over all loci segregating. Thus, even if the estimates of gene frequencies in the two populations were the same, the frequency of individual loci could differ between the populations and lead to heterosis.

The mean performance of various populations should show an agreement with the gene frequency estimates, the mean performance being higher when frequency of the favourable alleles with positive dominance is higher provided the effect of the fixed loci is same in both the populations. In the present study the mean performance and the estimates of gene frequency agreed only for plant height and were contradictory for grain yield. The average ear height of the two populations did not differ much from each other. The relationship between mean performance and gene frequency may be disturbed by the direction of dominance, number of fixed loci and environmental influences.

The procedures used to estimate gene frequency have various limitations and provide only approximate information. The theoretical values are calculated for a single locus and the observed values are based on phenotypic observations, the end result of many loci which do not necessarily behave similarly. No information is obtainable on the number of genes fixed in the homozygous condition. The observed values of genetic variance and covariances are based on various assumptions which may not be fulfulled. The assumption of no epistasis is difficult to meet. Two populations may have different alleles – giving rise to the problem of multiple allelism. Epistasis and multiple alleles may result in biases which could not be determined in the present study. In addition to this the non-significant estimates of variance components have also been used in the present study. S_1 lines may be more influenced by GE interactions than half-sib-full-sib progenies thereby influencing the results. The progenies in the study were evaluated in only one year hence progeny component of variance may be biased by genotype × year interaction. Such bias may be more pronounced in the characters having low heritability such as grain yield. Since the environments in this study are quite diverse, the bias may not be serious. Moreover the levels of dominance 'a' actually may be different in the two populations. To make inferences about gene frequencies, levels of dominance in combination with gene frequencies are considered which give approximately the same value as the corresponding observed ratios. There were a number of such combinations in theoretical tables which may give same observed value but in making inferences about gene frequency only meaningful combinations were considered.

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Appendix 1. Theoretical ratio of dominance variance to additive variance $\sigma^2_D/\sigma^2_A = R_1$ calculated for a single locus and for various values of a and p

a[b]	p[a]								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.50	0.023	0.047	0.073	0.099	0.125	0.148	0.164	0.163	0.125
0.75	0.040	0.086	0.140	0.204	0.281	0.374	0.482	0.595	0.633
1.00	0.056	0.125	0.214	0.333	0.500	0.750	1.167	2.000	4.500
1.25	0.070	0.163	0.292	0.480	0.781	1.333	2.625	8.000	0.281
1.50	0.084	0.199	0.369	0.639	1.125	2.204	5.906	72.000	10.125

[a] p is frequency of favourable allele in the population

[b] a is level of dominance

Appendix 4. Theoretical ratio of $\sigma_{m11m12}/\sigma_{m22m21} = R_4$ for a single locus for various values of p and x

p[a]	x[a]								
	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.1	1.000	0.503	0.429	0.375	0.360	0.375	0.429	0.563	1.000
0.2	1.778	1.000	0.762	0.667	0.640	0.667	0.762	1.000	1.778
0.3	2.333	1.313	1.000	0.875	0.840	0.875	1.000	1.313	2.333
0.4	2.667	1.500	1.143	1.000	0.960	1.000	1.143	1.500	2.667
0.5	2.778	1.563	1.190	1.042	1.000	1.042	1.190	1.563	2.778
0.6	2.667	1.500	1.143	1.000	0.960	1.000	1.143	1.500	2.667
0.7	2.333	1.313	1.000	0.875	0.840	0.875	1.000	1.313	2.333
0.8	1.778	1.000	0.762	0.667	0.640	0.667	0.762	1.000	1.778
0.9	1.000	0.563	0.429	0.375	0.360	0.375	0.429	0.563	1.000

[a] p is gene frequency in population 1 and x is gene frequency in population 2

Appendix 2. Theoretical ratios of $(\sigma^2_{m11}+\sigma^2_{m22})/(\sigma^2_{m12}+\sigma^2_{m21}) = R_2$ calculated for a single locus for various values of p, x and a

p[a]	x[a]	a[b]			
		0.50	0.75	1.00	1.25
0.1	0.1	1.000	1.000	1.000	1.000
	0.2	0.959	0.946	0.936	0.928
	0.3	0.885	0.849	0.821	0.799
	0.4	0.806	0.747	0.702	0.668
	0.5	0.735	0.658	0.602	0.560
	0.6	0.680	0.594	0.533	0.490
	0.7	0.662	0.573	0.515	0.478
	0.8	0.712	0.638	0.595	0.573
	0.9	1.000	1.000	1.000	1.000
0.2	0.2	1.000	1.000	1.000	1.000
	0.3	0.979	0.971	0.966	0.960
	0.4	0.936	0.913	0.894	0.878
	0.5	0.893	0.855	0.824	0.799
	0.6	0.868	0.822	0.786	0.758
	0.7	0.885	0.845	0.815	0.794
	0.8	1.000	1.000	1.000	1.000
	0.9	1.444	1.633	1.744	1.778
0.3	0.3	1.000	1.000	1.000	1.000
	0.4	0.988	0.984	0.980	0.976
	0.5	0.969	0.956	0.945	0.935
	0.6	0.963	0.948	0.935	0.923
	0.7	1.000	1.000	1.000	1.000
	0.8	1.143	1.208	1.259	1.293
	0.9	1.632	1.988	2.247	2.233
0.4	0.4	1.000	1.000	1.000	1.000
	0.5	0.996	0.994	0.993	0.991
	0.6	1.000	1.000	1.000	1.000
	0.7	1.042	1.063	1.083	1.101
	0.8	1.185	1.287	1.381	1.453
	0.9	1.653	2.108	2.509	2.667
0.5	0.5	1.000	1.000	1.000	1.000
	0.6	1.004	1.006	1.009	1.011
	0.7	1.039	1.061	1.085	1.110
	0.8	1.162	1.266	1.378	1.480
	0.9	1.569	1.034	2.536	2.778
0.6	0.6	1.000	1.000	1.000	1.000
	0.7	1.016	1.026	1.038	1.053
	0.8	1.104	1.179	1.273	1.381
	0.9	1.424	1.816	2.340	2.667
0.7	0.7	1.000	1.000	1.000	1.000
	0.8	1.037	1.066	1.110	1.176
	0.9	1.252	1.510	1.941	2.333
0.8	0.8	1.000	1.000	1.000	1.000
	0.9	1.089	1.189	1.404	1.778
0.9	0.9	1.000	1.000	1.000	1.000

[a] p is gene frequency in population 1 and x is gene frequency in population 2. As p and x are interchangeable, their reciprocal combinations of p and x have same value of R_2 and hence are omitted

[b] a is level of dominance (partly adapted from Goodrich et al. 1975)

Appendix 3. Theoretical ratios of $(\sigma^2_{f11}+\sigma^2_{f22})/(\sigma^2_{f12}+\sigma^2_{f21}) = R_3$ for various values of p, x and a

p[a]	x[a]	a[b]			
		0.50	0.75	1.00	1.25
0.1	0.1	1.000	1.000	1.000	1.000
	0.2	0.966	0.959	0.954	0.952
	0.3	0.902	0.881	0.868	0.860
	0.4	0.832	0.800	0.775	0.763
	0.5	0.767	0.718	0.691	0.777
	0.6	0.715	0.657	0.627	0.613
	0.7	0.691	0.629	0.599	0.588
	0.8	0.730	0.675	0.652	0.647
	0.9	1.000	1.000	1.000	1.000
0.2	0.2	1.000	1.000	1.000	1.000
	0.3	0.982	0.977	0.975	0.973
	0.4	0.945	0.931	0.923	0.918
	0.5	0.907	0.884	0.871	0.864
	0.6	0.883	0.854	0.838	0.831
	0.7	0.896	0.869	0.856	0.851
	0.8	1.000	1.000	1.000	1.000
	0.9	1.424	1.572	1.632	1.628
0.3	0.3	1.000	1.000	1.000	1.000
	0.4	0.990	0.987	0.986	0.985
	0.5	0.973	0.966	0.961	0.959
	0.6	0.967	0.958	0.953	0.951
	0.7	1.000	1.000	1.000	1.000
	0.8	1.133	1.176	1.197	1.201
	0.9	1.610	1.875	1.995	1.982
0.4	0.4	1.000	1.000	1.000	1.000
	0.5	0.997	0.996	0.995	0.995
	0.6	1.000	1.000	1.000	1.000
	0.7	1.038	1.051	1.058	1.060
	0.8	1.174	1.240	1.273	1.277
	0.9	1.640	1.969	2.130	2.105
0.5	0.5	1.000	1.000	1.000	1.000
	0.6	1.004	1.005	1.006	1.006
	0.7	1.036	1.049	1.056	1.058
	0.8	1.155	1.221	1.255	1.258
	0.9	1.569	1.904	2.078	2.041
0.6	0.6	1.000	1.000	1.000	1.000
	0.7	1.015	1.021	1.024	1.025
	0.8	1.101	1.149	1.174	1.174
	0.9	1.435	1.722	1.879	1.833
0.7	0.7	1.000	1.000	1.000	1.000
	0.8	1.037	1.056	1.066	1.065
	0.9	1.268	1.464	1.577	1.533
0.8	0.8	1.000	1.000	1.000	1.000
	0.9	1.099	1.182	1.227	1.206
0.9	0.9	1.000	1.000	1.000	1.000

[a] p is gene frequency in population 1 and x is gene frequency in population 2. As p and x are interchangeable, their reciprocal combinations have same value of R_3 and hence are omitted

[b] a is level of dominance

Appendix 5. Theoretical ratio of $\sigma^2_{s1}/\sigma^2_{s2} = R_5$ for a single locus for various values of p, x and a

p[a]	x[a]	a[b]			
		0.50	0.75	1.00	1.25
0.1	0.1	1.000	1.000	1.000	1.000
	0.2	0.608	0.624	0.637	0.648
	0.3	0.503	0.532	0.556	0.576
	0.4	0.481	0.526	0.565	0.599
	0.5	0.507	0.577	0.642	0.699
	0.6	0.584	0.697	0.808	0.913
	0.7	0.744	0.941	1.153	1.369
	0.8	1.099	1.494	1.979	2.531
	0.9	2.228	3.329	4.951	7.244
0.2	0.2	1.000	1.000	1.000	1.000
	0.3	0.827	0.852	0.873	0.889
	0.4	0.790	0.842	0.887	0.925
	0.5	0.833	0.924	1.007	1.079
	0.6	0.960	1.116	1.269	1.409
	0.7	1.223	1.507	1.810	2.114
	0.8	1.808	2.394	3.105	3.909
	0.9	3.665	5.332	7.770	11.187
0.3	0.3	1.000	1.000	1.000	1.000
	0.4	0.955	0.988	1.016	1.040
	0.5	1.007	1.084	1.154	1.213
	0.6	1.160	1.310	1.454	1.585
	0.7	1.478	1.768	2.074	2.376
	0.8	2.185	2.809	3.558	4.395
	0.9	4.429	6.256	8.901	12.577
0.4	0.4	1.000	1.000	1.000	1.000
	0.5	1.054	1.097	1.135	1.167
	0.6	1.214	1.325	1.430	1.525
	0.7	1.548	1.789	2.040	2.286
	0.8	2.288	2.842	3.500	4.227
	0.9	4.637	6.329	8.757	12.098
0.5	0.5	1.000	1.000	1.000	1.000
	0.6	1.152	1.208	1.260	1.306
	0.7	1.468	1.630	1.798	1.959
	0.8	2.170	2.590	3.084	3.622
	0.9	4.399	5.769	7.716	10.366
0.6	0.6	1.000	1.000	1.000	1.000
	0.7	1.274	1.350	1.427	1.499
	0.8	1.884	2.145	2.447	2.773
	0.9	3.818	4.777	6.123	7.935
0.7	0.7	1.000	1.000	1.000	1.000
	0.8	1.478	1.589	1.715	1.849
	0.9	2.996	3.539	4.292	5.293
0.8	0.8	1.000	1.000	1.000	1.000
	0.9	2.027	2.227	2.502	2.862
0.9	0.9	1.000	1.000	1.000	1.000

[a] p is gene frequency in population 1 and x is gene frequency in population 2. As p and x are interchangeable, their reciprocal combinations have same value of R_5 and hence are omitted

[b] a is level of dominance (partly adapted from Goodrich et al. 1975)

Appendix 6. Theoretical ratio of $\sigma_{s1m11}/\sigma_{s1m12}$ or $\sigma_{s2m22}/\sigma_{s2m21} = R_6$ for a single locus for various values or p, x and a

p[a]	x[a]	a[b]			
		0.50	0.75	1.00	1.25
0.1	0.1	1.000	1.000	1.000	1.000
	0.2	1.077	1.103	1.125	1.143
	0.3	1.167	1.231	1.286	1.333
	0.4	1.273	1.391	1.500	1.600
	0.5	1.400	1.600	1.800	2.000
	0.6	1.555	1.882	2.250	2.667
	0.7	1.750	2.286	3.000	4.000
	0.8	2.000	2.909	4.500	8.000
	0.9	2.333	4.000	9.000	∞
0.2	0.2	1.000	1.000	1.000	1.000
	0.3	1.083	1.115	1.143	1.167
	0.4	1.182	1.261	1.333	1.400
	0.5	1.300	1.450	1.600	1.750
	0.6	1.444	1.706	2.000	2.333
	0.7	1.625	2.071	2.667	3.500
	0.8	1.857	2.636	4.000	7.000
	0.9	2.167	3.625	8.000	∞
0.3	0.3	1.000	1.000	1.000	1.000
	0.4	1.091	1.130	1.167	1.200
	0.5	1.200	1.300	1.400	1.500
	0.6	1.333	1.529	1.750	2.000
	0.7	1.500	1.857	2.333	3.000
	0.8	1.714	2.364	3.500	6.000
	0.9	2.000	3.250	7.000	∞
0.4	0.4	1.000	1.000	1.000	1.000
	0.5	1.100	1.150	1.200	1.250
	0.6	1.222	1.353	1.500	1.667
	0.7	1.375	1.643	2.000	2.500
	0.8	1.571	2.091	3.000	5.000
	0.9	1.833	2.875	6.000	∞
0.5	0.5	1.000	1.000	1.000	1.000
	0.6	1.111	1.176	1.250	1.333
	0.7	1.250	1.429	1.667	2.000
	0.8	1.429	1.818	2.500	4.000
	0.9	1.667	2.500	5.000	∞
0.6	0.6	1.000	1.000	1.000	1.000
	0.7	1.125	1.214	1.333	1.500
	0.8	1.286	1.545	2.000	3.000
	0.9	1.500	2.125	4.000	∞
0.7	0.7	1.000	1.000	1.000	1.000
	0.8	1.143	1.347	1.500	2.000
	0.9	1.333	1.751	3.000	∞
0.8	0.8	1.000	1.000	1.000	1.000
	0.9	1.167	1.375	2.000	∞
0.9	0.9	1.000	1.000	1.000	1.000

[a] p is gene frequency in population 1 and x is gene frequency in population 2. As p and x are interchangeable, their reciprocal combinations have same value of R_6 and hence are omitted

[b] a is level of dominance (partly adapted from Goodrich et al. 1975)