THE GENETIC CONTRIBUTIONS OF INDIVIDUAL MALES AND FEMALES IN DIOECIOUS AND GYNODIOECIOUS ANGIOSPERMS

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SUMMARY

The relative genetic contributions of individual male and female zygotes in dioecious and gynodioecious populations at equilibrium sex frequencies are derived for four different genetic models.

With both the heterozygous female model (female = Mm , male = mm) and the dual male model (female = mm , male = Mm and MM), the contributions of male and female zygotes are equal.

With the heterozygous male model (female = mm , male = Mm), male zygotes contribute more than female zygotes in gynodioecious populations, but the sexes contribute equally in dioecious populations.

With cytoplasmic inheritance, male zygotes contribute at least twice as much as females.

The contributions of the adults are briefly described; with both the heterozygous female and heterozygous male models, the relative contributions of the adult sexes in dioecious populations are the inverse of both their relative survival rates and their relative frequencies.

1. INTRODUCTION

LEWIS AND CROWE (1956) expressed the view that gynodioecy "differs from all other outbreeding mechanisms such as incompatibility and dioecy, in that the two mating types contribute unequal numbers of nuclear genes to the next generation. Plant for plant a hermaphrodite contributes three times as many genes as does a female, for it supplies its own pollen and egg nuclei and also the pollen nucleus for the female." Ross and Shaw (1971) have recently pointed out that the second sentence of this quotation is valid only when the numbers of hermaphrodites and male steriles (females) in the population are equal. They noted that the relative contributions of the sexes depend partly on their frequencies. Using numerical examples, Ross and Shaw claimed that individual hermaphrodites contribute more than females and that this inequality is reduced as hermaphrodites become more frequent. They stated, for example, that "when there is 1 male sterile and 99 hermaphrodites, . . . any one hermaphrodite contributes about twice as many genes as the one male sterile".

It will be shown below that the view that individuals of the two sexes of gynodioecious populations contribute unequally to the gene pool of the next generation is not generally valid. Both pairs of authors cited above assumed that the "hermaphrodites" bear as much seed as females. But females, when this is so, are absent, with a variety of monogenic, digenic and cyto-

plasmic systems of inheritance of the sex phenotypes (Lewis, 1941; Ross and Shaw, 1971; Lloyd, 1973). Furthermore, these papers demonstrated that there is only one set of equilibrium sex frequencies for any particular mode of inheritance, level of pollinator activity and comparative seed production of hermaphrodites and females. If the sex frequencies are displaced from equilibrium, they return towards equilibrium quite rapidly, at least with the systems which have been examined to date in this respect (Lloyd, 1973). Consequently, it is appropriate to consider the genetic contributions of the two sexes primarily at equilibrium frequencies rather than at arbitrary or freely varying frequencies.

The contributions of the sex genotypes to the gene pool of the corresponding stage of the next generation in dioecious and gynodioecious Angiosperm populations at equilibrium are examined below, using the parameters and genetic models defined in Lloyd (1973). The two sexes are referred to as females and males, rather than male steriles and hermaphrodites. One advantage of this practice is that it emphasises that the two sexes of sexually dimorphic populations contribute to the gene pool of the next generation predominantly or exclusively via ovules and pollen respectively (Lloyd, 1973, and unpublished). It is assumed below that females contribute only via ovules in both dioecious and gynodioecious populations. The relative (male/female) seed fecundity, F , measures the contributions via ovules of individual males compared with females. In gynodioecious populations ($1 \geq F > 0$), males contribute one genome to each seed produced on a female plant and two genomes to each seed produced on a male. In dioecious populations, males contribute only via pollen, *i.e.* $F = 0$. It is assumed that male zygotes survive to reproductive maturity at a relative rate, S , compared with that of female zygotes, 1.

The genetic contributions of the sexes are derived below only for situations when there is more than one (x) pollinator visit to each flower. The probability that an ovule of a female plant is fertilised is then $1 - p^x$ (Lloyd, 1973), where p is the proportion of adult females in a population. With all genetic models examined, the expressions for the relative contributions of the sexes when there is less than one visit to each flower are identical to those given below for more numerous visits.

2. HETEROZYGOUS FEMALE MODEL

(Female = Mm ; male = mm)

The number of genomes contributed to the next generation by each female zygote,

$$\begin{aligned} C(\text{♀}) &= K \times \text{relative survival} \times \text{probability of fertilisation} \\ &= K(1 - p^x), \text{ (when } x > 1), \end{aligned}$$

where K is an unknown quantity depending on the total seed production of the population and the relative numbers of seeds in successive generations.

With this model, in populations with the sexes at equilibrium proportions, when $x > 1$,

$$F = \frac{(1 - p^x)(1 - p - Sp)}{2S(1 - p)} \quad (\text{from Lloyd, 1973, equation 2}).$$

Hence the number of genomes contributed by each male zygote,

$$\begin{aligned} C(\mathcal{J}) &= \text{contribution to seeds on females plus contribution to its own seeds.} \\ &= KS \left[\frac{(1-p^x)p}{1-p} + 2F \right] \\ &= KS \left[\frac{(1-p^x)p}{1-p} + \frac{2(1-p^x)(1-p-Sp)}{2S(1-p)} \right] \\ &= K(1-p^x). \end{aligned}$$

The relative contribution of the sexes,

$$\begin{aligned} C(\mathcal{J}/\mathcal{Q}) &= \frac{K(1-p^x)}{K(1-p^x)} \\ &= 1. \end{aligned} \quad (1)$$

Hence in both dioecious and gynodioecious populations, at equilibrium frequencies of the sexes the genetic contributions of individual male and female zygotes are invariably equal.

If the sexes survive at the same rate ($S = 1$), the contributions of *adult* males and females are also equal. If there is sex-differential survival, the contributions of adult males and females are unequal. Then, in dioecious populations, adults of both sexes produce adult male and female offspring in the ratio $S:1$, and the relative (male/female) contributions of adults is

$$\frac{1}{S} \left(= \frac{p}{1-p}, \text{ from Lloyd, 1973, equation 6} \right).$$

That is, the ratio of the contributions of adult males and females is equal to the inverse of the ratios of their frequencies or of their relative survival. In gynodioecious populations, the two sexes do not produce equal proportions of male and female offspring because males produce some seed. If the sexes survive at different rates, individual adults of the sex which survives better contribute less to the gene pool, but there is no simple proportionality between the relative survival of the sexes and their genetic contributions.

3. DUAL MALE MODEL

(Female = mm ; male = Mm and MM)

The genotype frequencies at equilibrium when the female is the recessive homozygote and the other two genotypes are male and fully viable were considered in Lloyd (1973) only in the absence of differential survival and when the probabilities of fertilisation of ovules on male and female plants are equal. In this case the number of genomes contributed by each female,

$$\begin{aligned} C(mm) &= K \times 1 \times 1 \\ &= K. \end{aligned}$$

Here the proportions of mm , Mm and MM are p , q and r respectively and

$$F = \frac{1-2p}{2(1-p)} \quad (\text{from Lloyd, 1973, equation 12}).$$

Therefore the number of genomes contributed by each Mm male,

$$\begin{aligned}
 C(Mm) &= K \left[\text{ratio } mm : Mm \text{ frequencies} \times \text{proportion of pollen produced} \right. \\
 &\quad \left. \text{by } Mm, \text{ plus } 2 \times \text{offspring contributed via own seed} \right] \\
 &= K \left[\frac{p}{q} \times \frac{q}{q+r} \times 1 + 2F \times 1 \right] \\
 &= K \left[\frac{p}{1-p} + \frac{2(1-2p)}{2(1-p)} \right], \quad \text{since } q+r = 1-p \\
 &= K
 \end{aligned}$$

Similarly, the number of genomes contributed by each MM male,

$$\begin{aligned}
 C(MM) &= K \left[\frac{p}{r} \times \frac{r}{q+r} + 2F \right] \\
 &= K.
 \end{aligned}$$

Therefore, under the conditions examined, individuals of the three genotypes of the dual male model contribute equally to the gene pool of subsequent generations.

4. HETEROZYGOUS MALE MODEL

(Female = mm ; male = Mm ; MM is lethal)

An additional parameter, the relative (δ determining/ φ determining) gamete success of pollen nuclei, was included in the study of sex proportions with this genetic model (Lloyd, 1973). But the effects of relative survival of the diploid sexes and relative gamete success are similar, so it will be assumed here that differential survival may operate but differential fertilisation is absent. If each flower is visited one or more (x) times, the contribution of each female,

$$C(\varphi) = K(1-p^x).$$

With this model at equilibrium (from Lloyd, 1973, equation 16),

$$F = \frac{2p(1-p^x)(Sp+p-1)}{(1-p)(1-p-2Sp)}$$

Therefore the genetic contribution of male zygotes,

$$\begin{aligned}
 C(\delta) &= KS \left[\frac{(1-p^x)p}{1-p} + 2F \right] \\
 &= KS \left[\frac{(1-p^x)p}{1-p} + \frac{4p(1-p^x)(Sp+p-1)}{(1-p)(1-p-2Sp)} \right] \\
 &= KS p \frac{(1-p^x)(-3+3p+2Sp)}{(1-p)(1-p-2Sp)}.
 \end{aligned}$$

The relative contribution of male and female zygotes,

$$C(\delta/\varphi) = \frac{Sp(-3+3p+2Sp)}{(1-p)(1-p-2Sp)}. \quad (2)$$

If $S = 1$, equation 2 reduces to

$$C(\mathcal{J}/\mathcal{Q}) = \frac{p(-3+5p)}{(1-p)(1-3p)}.$$

The complication of a lethal MM genotype with this genetic model causes the contributions of male and female zygotes to be generally unequal, even when these zygotes survive to adulthood at identical rates. In gynodioecious populations, male zygotes contribute more than female zygotes. For example, if $S = 1$ and $p = 0.4$ (which corresponds approximately to $F = 1$, depending on the pollination level), $C(\mathcal{J}/\mathcal{Q}) = 3.3$. The relative contribution of the sexes decreases as the seed fecundity of male plants decreases. In dioecious populations ($F = 0$),

$$C(\mathcal{J}) = \frac{KS(1-p^x)p}{1-p}$$

and

$$\begin{aligned} C(\mathcal{J}/\mathcal{Q}) &= \frac{Sp}{1-p} \\ &= 1, \text{ since then } S = \frac{1-p}{p} \quad (\text{Lloyd, 1973, equation 19}). \end{aligned}$$

With the heterozygous male model, equality of the zygote contributions of the sexes is confined to dioecious populations. But if the average contributions of M and m genomes among all zygotes are calculated by a procedure parallel to that used for the sex contributions, M and m genomes contribute equally in all populations at equilibrium.

As with the heterozygous female model, in dioecious populations controlled by the heterozygous male model, the relative contributions of the sexes at the *adult* stage is equal to the inverse of the ratios of their relative frequencies or of their survival rates.

5. CYTOPLASMIC MODEL

The genome contribution of each female zygote when $x > 1$,

$$C(\mathcal{Q}) = K(1-p^x).$$

If all offspring are the same sex as their seed parent,

$$F = \frac{1-p^x}{S} \quad (\text{from Lloyd, 1973, equation 22}).$$

Then the genome contribution of each male zygote,

$$\begin{aligned} C(\mathcal{J}) &= KS \left[\frac{(1-p^x)p}{1-p} + \frac{2(1-p^x)}{S} \right] \\ &= \frac{K(1-p^x)(2-2p+Sp)}{1-p} \end{aligned}$$

and

$$C(\mathcal{J}/\mathcal{Q}) = \frac{2(1-p)+Sp}{1-p}. \quad (3)$$

$$\text{If } S = 1, C(\mathcal{J}/\mathcal{Q}) = \frac{2-p}{1-p}$$

Hence with cytoplasmically controlled sex phenotypes, the zygotes of the sexes contribute unequally even if they survive at the same rate.

The numerator of equation 3 is always greater than the denominator, so male zygotes invariably contribute more nuclear genes to the next generation than do female zygotes. The smallest discrepancy occurs when females are least frequent; C approaches two as p approaches zero. Conversely, as p increases towards one ($F \rightarrow 0$), C increases towards infinity, but the extent of the greater contributions of males is limited by the impossibility of strict dioecy with cytoplasmic inheritance (Lloyd, 1973).

6. DISCUSSION

When the sexes are at equilibrium frequencies with the heterozygous female mode of inheritance of dioecy and gynodioecy, male and female zygotes contribute equally to the gene pool of the next generation. And if both sexes survive at the same rate, the adults, as well as zygotes, contribute equally with this model and also with the dual male model under the single pollination frequency examined. Equilibrium sex frequencies identical to those of the heterozygous female model have been obtained for the dual male model for general but unspecified pollination levels (Lewis, 1941) and for three different digenic models when pollination is not limiting (Ross and Shaw, 1971). In both studies, the sexes were assumed to survive at equal rates. Thus all investigated genic models which do not involve differential survival of sex genotypes produce the same equilibrium sex frequencies. At these frequencies, individual male and female adults, as well as zygotes (and with the dual male model at least, different genotypes of the same sex), contribute equally to the gene pool. So the statements of Lewis and Crowe (1956) and Ross and Shaw (1971) that in gynodioecious systems hermaphrodite (male) and female plants have unequal genetic contributions are not generally valid.

If the sex genotypes survive to reproductive maturity at different rates, males and females contribute unequally, at least at the adult stage, with both genic models investigated. The pattern of inequality differs from the suggestions of Lewis and Crowe (*loc. cit.*) and Ross and Shaw (*loc. cit.*), however, and depends on the mode of inheritance. With the heterozygous female model, zygotes still contribute equally, but the adults contribute unequally. The heterozygous male model is complicated by the lethal Mm zygotes among the seed produced on male plants, and equality of the sex contributions is confined to the zygotes of dioecious populations. With cytoplasmic inheritance, individual male zygotes contribute at least twice as much as females, whatever the relative survival of the sexes.

The contributions of the sexes at non-equilibrium frequencies have not been examined above. But in those models in which the rate of change in sex frequencies has been studied, the equilibrium is stable and populations when displaced move rapidly back towards equilibrium (Lloyd, 1973). Consequently, it may be inferred that individuals of the sex in excess of equilibrium frequencies contribute less than they do at equilibrium, while individuals of the under-represented sex contribute more than at equilibrium. This frequency-dependent selection facilitates the maintenance of a stable sexual dimorphism (cf. Ross and Shaw, 1971).

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7. REFERENCES

- LEWIS, D. 1941. Male sterility in natural populations of hermaphrodite plants. *New Phytol.*, 40, 56-63.
- LEWIS, D., AND CROWE, L. K. 1956. The genetics and evolution of gynodioecy. *Evolution*, 10, 115-125.
- LLOYD, D. G. 1973. Theoretical sex ratios of dioecious and gynodioecious Angiosperms. *Heredity*, 31, 11-34.
- ROSS, M. D., AND SHAW, R. F. 1971. Maintenance of male sterility in plant populations. *Heredity*, 26, 1-8.