

## Sexual strategies in plants

### III. A quantitative method for describing the gender of plants

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**Abstract** Gender (maleness or femaleness) is a quantitative phenomenon in plants. For accurate descriptions of gender, numerical estimates of the relative capabilities of plants as pollen and ovule parents have advantages over the verbal morphological descriptions of gender that are traditionally used. Full descriptions require the distribution of gender among subsets of a sexual class (e.g., among individual plants) to be indicated as well as the average condition. Estimates of gender can be based on the pollen and ovule or seed production of each subset independently (phenotypic gender), or else the pollen and ovule or seed production of the whole population can be taken into account to assess the functional gender of any subset. The functional gender of a plant estimates the proportions of its genes which are transmitted through pollen (its maleness) or through ovules (its femaleness). Prospective estimates of functional gender are based on the relative maternal and paternal investments before anthesis (gamete estimates) or until the maturation of seeds (seed estimates). These estimates provide an ideal measure of the gender strategies of plants as sexual parents, but do not necessarily correspond closely with the actual success of a plant in leaving descendants through its male and female gametes. Equations for obtaining estimates of functional gender are derived for populations with random cross-fertilisation and for those with varying frequencies of self-fertilisation and random cross-fertilisation. The cosexual nature of plants of monomorphic populations and the separate male and female sexes of dimorphic populations are discussed.

**Keywords** sex; gender; strategies; plants

#### INTRODUCTION

The sexual nature, or gender, of plants is customarily described in morphological terms. To describe the distribution of stamens and carpels within angiosperm populations, Linnaeus (1737 and subsequently) and Darwin (1877) distinguished the conditions of hermaphroditism, monoecy, andromonoecy, gynomonoecy, dioecy, androdioecy, gynodioecy, polygamomonoecy, and polygamydioecy. In many instances, the classes they recognised are simple and convenient to apply. A brief examination of the size and nature of the sporophylls on a few plants at the appropriate stage of development often allows a population to be placed in one or other category with confidence. As a result, these morphological terms have been universally adopted as the standard nomenclature for sex conditions in flowering plants.

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The apparent simplicity and ease of application of the morphological terminology of sex conditions is somewhat deceptive, however. It is frequently assumed that plants in one population and with the same general sex form are identical in their gender, but different plants of the same general phenotype can vary considerably in their precise gender. The traditional classes of sex conditions are often treated as though they are clearly distinct from one another, although there are frequent and diverse intergrades between the major sex conditions, as Darwin (1877) pointed out. There is, for example, an unbroken continuum from hermaphroditism through gynodioecy to dioecy (Lloyd 1976, Webb 1979) and another series from monoecy to dioecy (Lloyd 1972, 1979b; Charlesworth & Charlesworth 1978). The basic Linnaean-Darwinian terminology has been supplemented by additional terms, such as subdioecy, trioecy, etc., which have been applied inconsistently to individuals and populations which

do not fit easily into any of the major classes. Altogether, the boundaries of the sex classes are often uncertain.

The discrete, typological nature of the morphological terms does not lend itself readily to the recognition of intermediate conditions or to the description of differences in the relative pollen and ovule contributions of flowers and individuals of the same morphological type. Morphological descriptions of sex tend to rely on appearance rather than function. Moreover, they ignore the fact that the sexual performance of a flower or plant depends not only on its own nature, but also on the gametes produced by other flowers and plants in the same population.

This paper aims to provide simple and general techniques for describing the gender of plants in more detailed and precise ways than the classical, verbal terms allow. Morphological and genetical measures of gender are considered and compared. Applications of these methods are presented elsewhere (Lloyd 1979b, Primack & Lloyd 1980).

#### TYPES OF GENDER MEASUREMENTS

Higher plants have an open system of growth whereby the various organs are repeated many times on one individual. An angiosperm plant typically produces many flowers, each with an androecium and/or a gynoecium. Whether sporophylls, sporangia, or gametes are used as the descriptive units of sex, the relative proportions of male and female organs may vary over the entire range between the all-male and all-female extremes. The intermediate conditions are often fully functional. Detailed descriptions of plant gender should therefore be quantitative.

Full descriptions of the gender of a sex phenotype should indicate the distribution of gender as well as the average condition. Individuals or parts of individuals which have the same general sexual form may differ in their precise position on a quantitative scale of gender. Horovitz & Harding (1972), Willson & Rathcke (1974), Ross (1977), Bawa (1977), and Horovitz (1978) have pointed out that in various circumstances the plants of hermaphrodite or monoecious populations may vary in their relative pollen and ovule propensities. By making special assumptions, I have elsewhere recorded the quantitative variation in gender among plants of the "same sex" in several monoecious, gynodioecious, and dioecious populations (Lloyd 1972, 1975, 1976). The methods proposed below allow the distribution of gender to be examined among phenotypically similar plants (or other subsets of a population, e.g., capitula in a population of Compositae) with any kind of sex expression.

The easiest descriptions of gender to achieve are those which simply record the occurrence of

microsporophylls and megasporophylls, as in the classical terminology. Descriptions of the gross morphology of flowers are of great value for identification and taxonomic comparison, but they are too imprecise for many other purposes. Non-functional androecia or gynoecia may be fully developed or they may be conspicuously modified or reduced, but there is no non-arbitrary size or shape beyond which they can be unambiguously scored as present. If descriptions of sex are to document how plants function rather than their outward appearance, they must be based on their expected or realised performance as parents in sexual reproduction.

Estimates of sexual performance differ in whether or not the estimate for one plant uses information on the production of gametes and seeds by the rest of the population. "Phenotypic" measures of gender rely entirely on the pollen and ovules (or seeds) produced by the plants or parts of plants being described. Phenotypic estimates of gender, such as the proportion of flowers that have ovaries with functional ovules, are really only refinements of the traditional verbal descriptions of sex. Such measures do not take account of the sexual behaviour of other plants in the population, and they therefore record the potential of a plant rather than its relative prospects as a pollen parent and as an ovule parent in an interbreeding population. The success of a plant in cross-fertilisation depends not only on its own performance, but also on that of the other members of the population.

The ultimate criterion of the relative performance of a plant as a pollen parent and as an ovule parent is its success in passing on its genes through male and female gametes. Consequently, the measures of gender adopted here are estimates of the proportions of genes transmitted by a plant (or other subset) through pollen (maleness) and through ovules (femaleness) to plants at the same stage of the next sexual generation.

A plant with many flowers mates repeatedly and "promiscuously" in one reproductive season, because the removal and/or deposition of pollen occurs separately (and often more than once) at each flower. Consequently, it is not possible to ascertain by direct observation of any reasonably large sample of plants what paternal success each plant has had through its pollen achieving fertilisation. Even if a measure of the use of pollen such as the number of pollinators visiting each plant is available, knowledge of the paternal contributions a plant makes to seeds is invariably incomplete. In addition, the fate of seeds is uncertain. One plant may produce 10 times more seeds than another, and yet the former plant may leave fewer mature progeny derived from its seeds than the latter. (And often, neither leave any adult descendants).

The accumulation of uncertainties throughout a complete sexual generation makes it a formidable

task to estimate the "effective gender" of a plant, i.e., the relative success that a plant eventually has in leaving descendants through its male and female gametes. It is comparatively easy to record the relative investments that a plant makes as a paternal parent and as a maternal parent by measuring the investments in androecia and gynoecia. Moreover, if the average genetic value of expenditure on paternal and maternal structures is known, one can calculate the relative expectations in terms of fitness returns for expenditure on androecia and gynoecia. Prospective estimates of the functional gender of a plant calculate the proportions of a plant's genes that are most likely to be transmitted through pollen (its maleness) or through its own seeds (its femaleness), based on expenditure on androecia and gynoecia.

Unlike the traditional descriptions of plant sex, estimates of functional gender can readily incorporate the performance of a plant as a maternal parent after the fertilisation of its ovules. There are two kinds of estimates of functional gender, which differ in the way the female contributions are assessed. "Gamete estimates" are based on the numbers of pollen grains and ovules (or polliniferous and ovuliferous flowers) produced by a sample of plants or parts of plants. "Seed estimates" of gender are based on the numbers of pollen grains and seeds (or polliniferous flowers and fruits) produced by various subsets of a population. Seed estimates incorporate more information and are therefore superior to gamete estimates as indicators of the likely reproductive success of a subset. However, gamete and seed estimates of gender are also indicators of reproductive strategies up to different stages in the process of sexual reproduction. From this point of view, gamete and seed estimates have different but equally valid uses.

#### METHODS FOR ESTIMATING FUNCTIONAL GENDER

The maternal fitness of a subset of a population (i.e., the number of offspring derived from female gametes produced in the subset's gynoecia) is denoted as  $g_i$ . The paternal fitness of a subset,  $a_i$ , is the contribution to fitness achieved through pollen produced in androecia. Then the total sexual fitness of the subset,

$$w_i = g_i + a_i.$$

Gender can be measured as functional femaleness,  $G_i$ , the proportion of genes most likely to be transmitted through gynoecia, or as functional maleness,  $A_i$ , the proportion of genes most likely to be transmitted through androecia.

Then

$$G_i = \frac{g_i}{g_i + a_i}, \quad (1a)$$

and

$$A_i = \frac{a_i}{g_i + a_i}, \quad (1b)$$

where

$$G_i + A_i = 1.$$

Various units can be used to estimate maternal and paternal expectations. Estimates are preferably based on counts of the pollen and either ovules or seeds produced, but in many instances only the numbers of flowers bearing pollen and ovules or seeds will be available. Whatever the descriptive units are, the androecial units must be weighted so that the genetic value (the average contribution to fitness) of one weighted unit equals that of one gynoecial unit. This can be done by noting that each zygote is derived from fusion of a male and a female gamete, and hence the total ovule or seed fitness of all subsets of a population is equal to the total pollen fitness of all subsets. That is,

$$\sum_i a_i = \sum_i g_i.$$

A plant cannot control or even perceive the success that its pollen achieves in fertilisation or the success that seeds to which it contributes have in growing to maturity. Presumably, maternal and paternal investments are outlaid under those circumstances in which the ratio of the fitness benefits to resource costs exceeds, on average, the benefit to cost ratio for alternative activities. Thus, as far as a plant can predict, every androecial investment is about equally likely to provide a fitness return and each gynoecial investment has a similar chance of success.

Assume that all androecial units (pollen grains or polliniferous flowers, denoted by  $l$ ) have the same probability,  $p_a$ , of contributing genes to adults of the next generation and that all gynoecial units (ovules, seeds, ovuliferous flowers or fruits, denoted by  $d$ ) have an equal probability,  $p_g$ , of contributing genes to the next generation. Then,

$$\frac{p_a}{p_g} = \frac{\sum_i d_i}{\sum_i l_i} = E,$$

where the equivalence factor,  $E$ , is the quantity by which the number of androecial units must be multiplied so that the adjusted pollen fitness is commensurable with the recorded ovule or seed fitness. The functional femaleness of a subset is then

$$\begin{aligned} G_i &= \frac{d_i p_g}{d_i p_g + l_i p_a} \\ &= \frac{d_i}{d_i + l_i E}. \end{aligned} \quad (2a)$$

Similarly,

$$A_i = \frac{l_i E}{d_i + l_i E}. \quad (2b)$$

Regardless of the distribution of gender values among the members of a population, the weighted

average of femaleness (or maleness) of all members is always one-half.

The gynoeceal units in a population may vary in their prospects of success as maternal parents of sexual progeny. For example, the seeds of different individuals may vary in size, or seeds borne in different positions on one plant may have distinctive germination requirements. Information on the relative fitness or quality,  $q_i$ , of samples of seeds or seedlings from subsets of a population can be incorporated into estimates of functional gender. Then,

$$E = \frac{\sum_i d_i q_i}{\sum_i l_i}$$

If androecial units vary in their probabilities of contributing to zygotes, they may be similarly weighted.

Equations (2a) and (2b) are applicable only if the paternal fitness of a subset can vary independently of its maternal fitness. This is a reasonable assumption if all embryos in a population result from cross-fertilisation. But in self-fertilisation a plant contributes both gametes to a zygote. A plant therefore contributes genes equally through pollen and ovules to its self-fertilised progeny. Unless the frequency of self-fertilisation and the relative fitness of selfed progeny do not vary between subsets of a partially self-fertilised population, the androecial and gynoeceal fitnesses cannot be estimated simply from the production of pollen and ovules or seeds. Equations (2a) and (2b) must be modified by finding the pollen production,  $l_{ix}$ , and equivalence factor,  $E_x$ , applicable to crossed seeds only.

Suppose that the ovules of some or all subsets of a population are fertilised by self-fertilisation in proportion  $s_i$  and by random cross-fertilisation in proportion  $t_i$ . Let the subscripts  $s$  and  $x$  denote the components of  $w$ ,  $a$ ,  $g$ ,  $d$ ,  $l$ ,  $A$ , and  $G$  (defined as above) that are associated with self- and cross-fertilisation respectively. Let the average fitness of seeds of subset  $i$  that are derived from crossing be  $q_{ix}$ , and that of seeds derived from selfing be  $q_{ix}l_i$ , where the average relative fitness of (inbred) seeds from self-fertilisation,  $l_i$ , varies between 0 and 1. The average fitness of seeds from cross-fertilisation in the whole population is  $\bar{q}_x$ . Then,

$$G_{is} = A_{is} = 1/2,$$

and

$$E_x = \frac{\sum_i t_i d_i}{\sum_i l_{ix}}$$

and

$$G_i = \frac{g_{ix} + g_{is}}{w_{ix} + w_{is}} = \frac{d_i q_{ix}(t_i + s_i l_i)}{d_i q_{ix}(t_i + 2s_i l_i) + l_{ix} E_x q_x} \quad (3)$$

To calculate the functional gender of a plant or other subset that experiences some self-fertilisation, one should know the seed production, the pollen available for crossing, the frequencies of self- and cross-fertilisation, and the relative fitnesses of selfed and crossed seeds for that subset and for a representative sample of the whole population. If some of this information is not available, a prospective estimate of gender may still be possible by making simplifying assumptions. For example, if the pollen used in selfing is not considered ( $l_{ix} = l_i$ ), and the crossed seeds from all plants have equal fitnesses, then equation (3) reduces to

$$G_i = \frac{d_i(t_i + s_i l_i)}{d_i(t_i + 2s_i l_i) + l_i E} \quad (4)$$

Extra assumptions will obviously decrease the accuracy of gender estimates, but these estimates are more practicable and they may still be superior to those obtained by assuming that there is no selfing or to measurements of phenotypic gender.

The general effect of self-fertilisation on the gender of a plant may be seen by allowing the subsets of a population to vary in their proportions of self- and cross-fertilisation and in the inbreeding depression experienced by selfed seeds. Assume that all subsets have the same quantity of seeds and of pollen available for crossing and their crossed seeds all have the same fitness; i.e.,

$$d_i = \bar{d}, l_{ix} = \bar{l}_x, q_{ix} = \bar{q}_x.$$

Then

$$E_x = \bar{t} \bar{l}_x,$$

and equation (4) reduces to

$$G_i = \frac{t_i + s_i l_i}{\bar{t} + t_i + 2s_i l_i} \quad (5)$$

If  $t_i < \bar{t}$ ,  $G_i < 1/2$ . If  $t_i > \bar{t}$ ,  $G_i > 1/2$ .

A plant that has ovules that are crossed less (or more) frequently than the average contributes its genes more (or less) through pollen than through ovules. Self-fertilisation has this effect on gender because a plant contributes pollen as well as ovules to a selfed seed.

Agamospermy also results in a plant transmitting two sets of genes to each of its agamospermous offspring. Hence, equations (3) or (4) could be applied (with redefined symbols) to plants of a population reproducing by a combination of sexual reproduction and agamospermy.

#### MONOMORPHIC AND DIMORPHIC POPULATIONS

In populations which contain only one sexual phenotype, pollen and ovule functions are combined in the same plants which on average must transmit their

genes equally in the category of gynomonoeceal monoecy. There is a need for populations. the plants of "equisexual" the equal contribution, it contributes equally to both populations (Lloyd & Lloyd 1980). monomorphic indicates that functions join individual plants through pollen or seed (Lloyd 1980, L

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genes equally through pollen and ovules. Populations that are monomorphic in gender include those in the categories of hermaphroditism, monoecy, gynodioecy, andromonoecy, and polygamo-monoecy recognised by Linnaeus and Darwin. There is a need for a term to collectively describe the gender of plants of these diverse monomorphic populations. I have previously (Lloyd 1975) called the plants of gender-monomorphic populations "equisexual". Although this term calls attention to the equal contribution through pollen and ovules on average, it could also lead to a supposition that every plant or other subset of a monomorphic population contributes equally through pollen and ovules. This is probably far from true in many monomorphic populations (Horovitz 1978, Lloyd 1979b, Primack & Lloyd 1980), so I now prefer to describe plants of monomorphic populations as "cosexual". This indicates that they belong to a sexual class which functions jointly as "male and female", although individual plants need not contribute genes equally through pollen and ovules and may even lack either pollen or seeds under certain conditions (Primack & Lloyd 1980, Lloyd 1979c).

In populations which are dimorphic in gender, there are two distinguishable morphological classes of plants, one of which produces proportionately more ovules and seeds than the other. Dimorphic populations include those in the classes of dioecy, gynodioecy, androdioecy, and (when not mislabelled) polygamodioecy distinguished by Linnaeus and Darwin. It follows from equations (2), (3), and (4) that the class of plants with proportionately more ovules, seeds, ovuliferous flowers, or fruits also has higher average femaleness ( $\bar{G}$ ) than the other class, which accordingly has a greater average maleness ( $\bar{A}$ ). I have proposed that the two morphs of populations which are dimorphic in gender on the definition above should be uniformly described as male and female sexes, although they are not always, or even characteristically, strictly unisexual or "constant" (Lloyd 1972, 1975, 1976).

Individual male and female plants or the male or female sexes as a whole are subsets of a dimorphic population. Their functional gender can therefore be estimated from equations (2)–(4) above, where the appropriate equivalence factor is derived from the total androecial and gynoecial fitness of both sexes. The gender of the sexes of dimorphic populations can be estimated without any knowledge of the mode of inheritance of sex. (If cytoplasmic factors are involved, the gender estimates include all nuclear genes but not the cytoplasmic factors.) The methods proposed above supersede the special techniques used previously to estimate the gender of plants of some dioecious and gynodioecious populations (Lloyd 1975, 1976).

## DISCUSSION

The quantitative measures of functional gender advocated here are useful for several approaches to the sexual behaviour of plants. Firstly, they are valuable as a means of obtaining more precise descriptions of sexual behaviour than are provided by the traditional verbal terms. Precise gender descriptions are not only useful for their own sake, but they also supply a framework for genetical, developmental, and physiological analyses of sexual behaviour. Gender estimates are a suitable basis for documenting the course of evolutionary changes in sexual conditions.

Estimates of functional gender are superior to measures of phenotypic gender as estimators of sexual behaviour in several respects. Functional gender measurements use a standardised scale varying from 0 to 1, with the average of all individuals (weighted by their total fitness) always being 0.5. Seed estimates of functional gender incorporate not only the gamete production of individuals but also the post-anthesis development of seeds, which is equally important for maternal fitness. And since the gender measurements are based on the actual investments that a plant makes as a sexual parent, they provide an ideal measure of gender strategies. The use of functional gender in exploring gender strategies is illustrated elsewhere (Primack & Lloyd 1980, Lloyd 1979b).

The functional gender of a plant can only be calculated if the sexual nature of an adequate sample of the population is known. Functional gender has no meaning for single plants considered apart from the population in which they would interbreed. Moreover, calculations of functional gender usually assume that all pollen grains or pollen flowers (and separately all ovules, seeds or fruits) have equal prospects, and they may also require assumptions about the frequency of self-fertilisation or the degree of inbreeding depression. If these assumptions are questionable, it is safer to use the less complete information of intrinsic gender rather than misleading estimates contained in inaccurate calculations of functional gender.

Prospective gender estimates do not necessarily provide accurate measurements of the relative success, if any, that a plant actually has in leaving descendants through pollen and seeds. This, the effective gender of a plant, could be estimated more accurately (and with additional effort) by measures of paternal and maternal fitness other than the simple quantities recording parental allocations. The pollen removed from anthers would be a better estimator of the paternal fitness realised than is the pollen produced, particularly in plants in which the pollen produced by a flower is removed as one or a few units, as in orchids and asclepiads (e.g., Wyatt 1976). The pollen produced by a plant could be weighted by various factors, such as the number of pollinator

visits to a plant or the number of departures from the plant. Another type of refinement would entail modifying gender calculations by using a series of equivalence factors for different subsets of a population. Varying equivalence factors could be based on several criteria, including the relative numbers of male and female gametes in a population at different times throughout a flowering season, the proximity of the pollen of each individual to ovules of other plants, or the numbers of plants which are cross-compatible with each individual. A special case of the latter kind involving heterostylous populations is considered elsewhere (Lloyd 1979a).

Similarly, there are better measures of maternal fitness than ovule or seed production if one wishes to measure the fitness realised from parental investments rather than parental strategies. Estimates of effective gender could incorporate, for example, observations of seed dispersion from different maternal parents to areas suitable for germination or the relative germination rates within the area of the seed shadow of each maternal parent. However, studies of the success of pollen in achieving fertilisation and of the fates of seeds from different individuals are so time-consuming that they cannot be routinely included in studies of the distribution of gender in natural populations. It must also be recognised that although the inclusion of events occurring after parental investment has ended would improve the estimates as a record of the fitness actually achieved, it would also render the gender estimates less suitable as measures of plant strategies.

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#### IV.

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