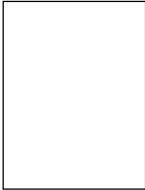


Gender in Plants

1. Why Do Plants Change Sex?

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Complex evolutionary forces determine whether plants are male, female or hermaphrodite throughout their lives or whether they switch from one sex to another. This article explores these often conflicting forces and seeks answers for sex change in plants.

In classical Greek mythology, Hermaphroditus, son of Hermes and Aphrodite, spurned the advances of Salmacis, guardian nymph of a lovely pond. Salmacis plunged into the water after Hermaphroditus and entangled him perforce in a powerful embrace. Whilst thus entwined, Salmacis entreated the gods to unite her eternally with her love. The gods were kindly and merged Salmacis with Hermaphroditus so that they were but one androgynous body ever after. This is why plants and animals in which both male and female sexual organs are present in the same individual are called hermaphrodites.

A Conceptual Framework

The ancestral angiosperms or flowering plants had bisexual, perfect flowers (*Figure 1*). From this condition arose the variety of sexual systems found in seed plants today (*Box 1*). About three-fourths of all flowering plants have the ancestral perfect-flowered condition, while about ten percent are either dioecious or monoecious, the rest being a mixture of sexual types.

An hermaphroditic plant is one in which the male reproductive structures (stamens) and female reproductive structures (carpels) are produced on the same plant either in the same or within separate flowers, either simultaneously or sequentially. Sequential hermaphrodites are those that change sex at varying time scales. Why do hermaphrodites adopt one or the other strategy? Are these strategies equivalent and merely different



answers to the same evolutionary problem of maximising an individual's fitness? Darwinian fitness is the measure of an individual's survival and reproductive success in terms of the number of offspring produced. Reproductive success in plants can be achieved either through male or female functions via pollen or ovules. The fitness of an hermaphrodite is, therefore, the combined fitness of its male component in terms of the number of progeny sired by its pollen, and of its female function in terms of the number of seeds produced.

Simultaneous Versus Sequential Hermaphroditism

In 1969, Michael Ghiselin wrote an influential paper in an attempt to explain patterns of hermaphroditism in animals. His theories have now been applied to plants. The *low density* theory of Ghiselin predicts that simultaneous hermaphroditism could have an advantage in a population which is at a low density when in such populations the probability of successful pollen transfer between individuals is also low. This co-occurrence of sexes would be especially advantageous under such conditions if the hermaphrodite could self-fertilise. Moreover, in such sparse populations, even self-incompatible hermaphrodites, i.e. those unable to self-fertilise, would have a greater opportunity of mating with the opposite sex, compared with a low density population in which the sexes are separated in individual plants. For example, in an extreme case where a population of simultaneous hermaphrodites was reduced to only two individuals, each individual would have twice the probability of mating with the opposite sex than if it were either male or female at any given moment.

Interest in theories of sex change was largely evoked by the sex reversals found in many invertebrates like crustaceans and molluscs, and many species of fishes. In these animals, individuals are of one sex when young and change sex when older or larger. Ghiselin's *size-advantage* theory which was developed for animals has often been invoked to explain the phenomenon of sequential hermaphroditism. In this theory,

Box 1. Terminology Related to Mating Systems in Plants

Perfect or bisexual flower: Flower with male and female reproductive parts

Hermaphrodite: Plant with bisexual or monoecious flowers

Monoecy: Hermaphrodite plant with unisexual male and female flowers on the same plant

Dioecy: Male and female flowers on separate plants

Andromonoecy: Hermaphrodite plant with bisexual and unisexual male flowers on the same plant

Gynomonoecy: Hermaphrodite plant with bisexual and unisexual female flowers on the same plant

Androdioecy: Coexistence of hermaphrodite and male plants in the population

Gynodioecy: Coexistence of hermaphrodite and female plants in the population



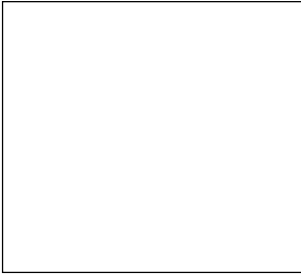


Figure 1. The perfect flower of the glory lily waits to be pollinated and have its pollen taken away.
(Courtesy: Ulhas Rane)

sex change is favoured if either male or female functions are best performed by individuals of different sizes. In multicellular animals and plants, there is usually a considerable difference in size between male and female gametes produced by an individual. Male gametes – sperm or pollen, are considerably smaller than female gametes – eggs or ovules. This condition of a large size difference between the gametes of opposite sexes is referred to as anisogamy. So, it is generally assumed that pollen is less expensive to produce than seeds. Therefore, maleness should be favoured in smaller, younger plants and femaleness in older, larger plants with greater resource reserves.

Resource Budget for Reproduction

It is also often assumed that an individual plant has a resource budget demarcated for reproduction. This may be a fixed or a variable proportion of its total resource budget, the rest of which could be spent on many other functions. Although the size advantage model has been influential in stimulating research into the relationship between age, size and reproductive success, other factors such as the resource cost of sex change, length of reproductive life, and the rate of increase in reproductive success after the sex change need also to be considered.

Why be an Hermaphrodite?

Figure 2. Many snake lilies change sex. They are males when young and later become female.
(Courtesy: Ulhas Rane)



The conditions under which individual plants should allocate resources from their reproduction budget to both sexes or only to one sex have been explored in a fundamental analysis by Eric Charnov, John Maynard Smith and James Bull (*Box 2*) who showed that in populations at equilibrium, if the sum of the pollen and ovule production of an hermaphrodite relative to that of a male or a female is > 1 , hermaphrodites with bisexual or monoecious flowers should be expected. In other words, if the combined male and female reproductive success of an hermaphrodite is greater than that of a unisexual individual, hermaphroditism rather than dioecy would be selected for in the population (see *Box 2* for fundamental assumptions made by



this theory). Populations are said to be at equilibrium with regard to a particular evolutionary strategy, if the population at that stable state cannot be replaced by individuals employing other more successful strategies. In this case, the evolutionarily stable strategy for all individuals in the population could be either hermaphroditism or dioecy. Explanations for the presence of hermaphrodites as well as unisexual individuals in the same population are more complex.

The Gene Lottery

It is important to remember, however, that fitness is not just a function of production of offspring. Offspring should also survive and ultimately reproduce to ensure gene transmission. Males or females that produce offspring that are either more genetically variable or that disperse their progeny into a greater variety of environments may have greater fitness because of the increased probability of the survival of such offspring to their own reproductive stages. The greater the genetic variation among offspring, the larger the proportion of offspring that will survive under the fluctuating demands of a single environment. This is like ensuring that you have many lottery tickets with different numbers. Correspondingly, the greater the diversity of environments that offspring are dispersed into, the greater the

Box 2. When should a Plant be an Hermaphrodite?

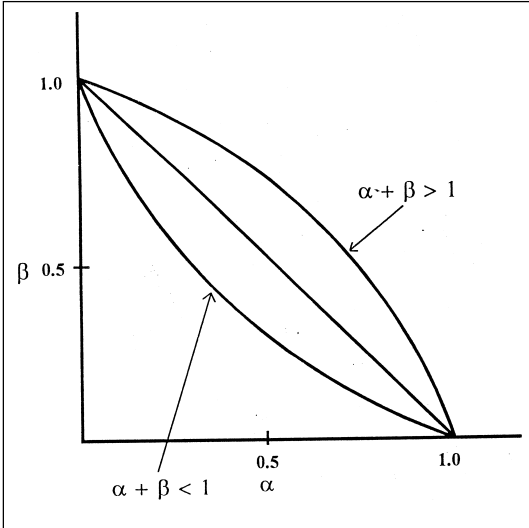
Let m = number of males, f = number of females, and h = number of hermaphrodites in a population. Let N = number of pollen grains produced by a male and n = number of ovules by a female. Then α and β = amount of pollen and ovules produced by an hermaphrodite as a fraction of the pollen and ovules produced by a male or female. Therefore, an hermaphrodite produces αN pollen + βn ovules.

Assumptions: 1. Random mating 2. All individuals have the same survivorship to adulthood. 3. Population is at equilibrium. 4. Self-incompatibility 5. Sexual type is determined by genes.

Let R = total number of offspring produced; W_m , W_f and W_h = the fitnesses of males, females and hermaphrodites = expected number of offspring produced by each sexual type.

Box2. continued...





Total pollen produced by males = Nm

Total pollen produced by hermaphrodites = αNh

And, total pollen produced by males and hermaphrodites = $N(m + \alpha h)$. Similarly, total ovules produced by females and hermaphrodites = $n(f + \beta h)$

Since each offspring has one father and one mother, R offspring will have R haploid genomes contributed by pollen grains and R haploid genomes contributed by ovules. $N(m + \alpha h)$ pollen grains result in R haploid genomes. Therefore N pollen

grains (produced by a male) will result in $NR/[N(m + \alpha h)]$ haploid genomes (offspring). Therefore the fitness of a male will be $W_m = R/(m + \alpha h)$. The fitnesses of females and hermaphrodites can be similarly derived.

Therefore, $W_m = R\left(\frac{1}{m + \alpha h}\right)$ $W_f = R\left(\frac{1}{f + \beta h}\right)$ and $W_h = R\left(\frac{\alpha}{m + \alpha h} + \frac{\beta}{f + \beta h}\right)$.

In a population at equilibrium, the fitnesses of all sexual phenotypes i.e. males, females and hermaphrodites, should be equal.

In a dioecious population at equilibrium, $h = 0$ and $W_m = W_f$

Such a dioecious population can resist invasion by an hermaphrodite mutant only if $W_m = W_f > W_h$

i.e. when $R\left(\frac{1}{m + \alpha h}\right) > R\left(\frac{\alpha}{m + \alpha h} + \frac{\beta}{f + \beta h}\right)$

or when $R\left(\frac{1}{m + \alpha h}\right) > R\left(\frac{\alpha}{m + \alpha h} + \frac{\beta}{m + \alpha h}\right)$

[Since $W_m = W_f$, $m + \alpha h = f + \beta h$]

Therefore, dioecy will prevail if $\alpha + \beta < 1$, while hermaphroditism will be selected for if $\alpha + \beta > 1$

(adapted from Charnov, Maynard Smith and Bull, 1976)

probability that the genotype of the offspring is suited to that environment. This is like having many lottery tickets with the



same number but ensuring that they all come from different lotteries! This mixing and matching of offspring genes and environment is also important in the fitness that a reproducing individual actually attains. Therefore, mere numbers of offspring produced do not necessarily translate directly into fitness.

Bateman's Principle

The **Bateman principle**¹ when applied to plants states that male reproductive success should be limited, i.e. have its upper boundaries set, by the number of ovules its pollen can access, while female reproductive success should be limited by access to nutrient and energy resources for seed and fruit production. However, if parental fitness is also dependent on the genotype of the offspring, female success may also be limited by the genotypes of the pollen received. It is now known that seed production can be limited in some cases also by the amount of pollen received by the female. This can occur when pollinators are generally scarce, as sometimes happens in high altitude plants. It could also occur when the number of flowers on the plant or the quantity of nectar is insufficient to attract an adequate number of pollinators (see conflict between the sexes with regard to this same feature later). Bateman's principle needs to be applied cautiously since factors such as pollen genotypes and pollen quantity can also limit both the male and female components of reproductive success.

Pollen and Seed Shadows

There is another fundamental conceptual issue regarding the possible benefits of dual sex expression in plants. In a unisexual male plant, there could be a point beyond which increasing expenditure on reproduction will not proportionally increase reproductive success because there are no more unfertilised ovules available within its pollen shadow. The shadow is the area over which the pollen of a flower or a plant is dispersed (see *Box 3*). At this point, it would be preferable either to be an hermaphrodite or to change sex. Similarly for a female plant whose seeds are usually dispersed close to the maternal plant and

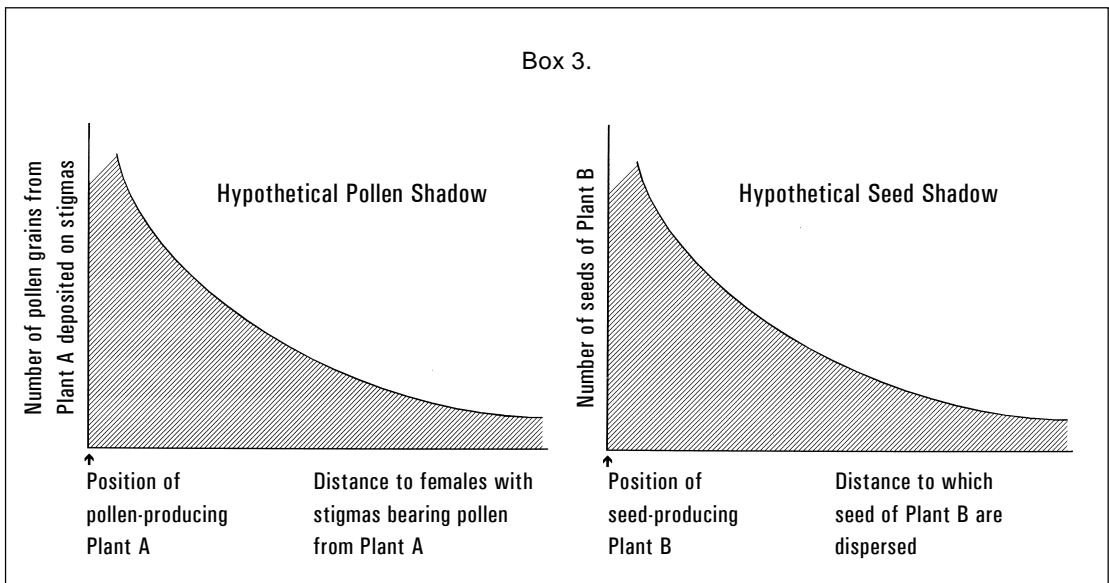
¹ In 1948, A J Bateman observed that individual male fruitflies showed greater variation in number of offspring produced than females. The vast numbers of male gametes produced, owing to their smaller size and consequent lower costs of production relative to female gametes, cause a disparity between the sexes in gamete mating opportunity.



only a small proportion of seeds is deposited further away. Most of the seeds near the parent plant are likely to compete intensively for nutrients and for space and only a few may be able to occupy available sites for seedling establishment. Due to this seed competition, a stage could be reached when further expenditure on female function will not result in a proportional increase in female reproductive success. These are examples of the *law of diminishing returns*. Moreover, the distance to which a male's genes can be transmitted is usually greater than a female's genes because male genes move first through pollen to fertilise seeds and then subsequently through the dispersal of those seeds. Therefore, a male's progeny may be placed in more diverse microhabitats than those of a female. This may also influence the increase in fitness achieved by specialising only on one sex by being either male or female.

The Plot Thickens!

Still further complications lie ahead. If a plant is both self-compatible as well as capable of outcrossing, and if most of its pollen shadow is cast over itself, then it would produce more seeds by self-pollination rather than by outcrossing. This



reduction in opportunities for outcrossing due to the movement of pollen and thereby genes within plants rather than between plants is called *pollen discounting*. One way in which a pollen shadow can linger over the same plant is if the plant produces very showy and nectar-rich flower displays so that pollinators tend to move from flower to flower on the same plant rather than between plants (note earlier opposite effect on female reproductive success). This can have further serious consequences for a plant incapable of self-fertilisation as the stigmas of its flowers may get clogged with useless self-pollen. Therefore, the law of diminishing returns can apply not only to the total pollen production on a plant over the entire flowering season, but also to the total pollen presented to pollinators at any given time. This means that it might be better for plants to present pollen in small amounts to reduce pollen discounting which could influence the pattern of male versus female optimal requirements for reproduction. This may hold true for animal-pollinated plants but for wind-pollinated plants, massive pollen production at any given time might be important.

It should be evident by now that the world of sex and consequently of sex change in plants is extremely complex, and is even further complicated by the modular structure of plant reproductive units. One can refer to the reproductive success of an individual flower, an individual branch, or that of the whole plant. In theory it is possible to write equations that sum up reproductive success across plant modules but for biologists to measure the parameters to test the models is an extremely challenging task. It should also be clear by now that there are multiple, complex and often opposing factors which are acting simultaneously on the male and female within each hermaphroditic plant. Therefore, models too are at best approximations of the real world.

Why do plants change sex? We should have figured it all out by now or can we? Sex change will be explored further in the next part of this article along with specific examples.

Suggested Reading

- ◆ Eric L. Charnov. *The Theory of Sex Allocation*. Princeton University Press. 1982.
- ◆ John Maynard Smith. *The Evolution of Sex*. Cambridge University Press. 1978.
- ◆ Mary F. Willson. *Plant Reproductive Ecology*. John Wiley. 1983.

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