

Gender in Plants

2. More About Why and How Plants Change Sex

Renee M Borges



Renee Borges is at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore. Her research interests are behavioural ecology and plant-animal interactions.

What is the difference between plant sex and plant gender? Why does stress sometimes cause maleness and other times result in femaleness? Do plant hedge mating bets using sex change? This article addresses these and other evolutionary questions about plant gender.

The Modular Nature of Plants

Johann Wolfgang von Goethe, the German literary genius immortalised for such triumphs as *The Tragedy of Doctor Faust*, was also a natural scientist. He believed that every flowering plant had six stages consisting of seed, leaves, calyx, corolla, sex organs and fruit. Each plant was supposed to be made up of fundamental units which were leaf organs that then metamorphosed through these six stages. In his *Essay on the Metamorphosis of Plants* (1790), he spoke of the concept of a plant archetype (*Urpflanze*) which gave rise to the diversity of plants based on a unified plan. Shoots of the plant archetype consisted of these serially repeated leaf organs. Although the idea of metamorphosis from leaf organs is now obsolete, Goethe in Germany and Georges Cuvier in France were largely responsible for the view that many plants and animals are composed of serially repeated units called metamers or modules. Metameric animals have a fixed or determinate number of units, which does not keep increasing during the life of the animal. In many plants, however, modules continue to be added on each year from meristematic tissue; meristems may die with seasonal periodicity only to grow again and produce leaf and reproductive tissue; meristems within certain portions of the plant may produce reproductive tissue while those in the rest of the plant are quiescent.

In hermaphrodite plants, male and female reproductive units are thus scattered through the plant in a repeated fashion.

¹ Part 1 of this article Why do Plants Change Sex? appeared in *Resonance*, Vol. 3, No. 4, 1998.



Recent studies have shown, however, that many hermaphrodite plants do not contribute genes equally through male and female function to the next generation. Individual plants range from being relatively more or less male to relatively more or less female. This finding coupled with the modular and indeterminate nature of plant growth and reproduction led to the important perspective that sex expression in plants is a quantitative phenomenon, i.e. it depends on the relative proportion of reproductive units of both sexes within an individual plant. From this point of view, the term **plant sex** denotes the various mating systems of plants such as monoecy or androdioecy while the term **plant gender** refers to the relative representation of male and female function in the entire plant. The **phenotypic gender** of a plant then signifies the relative proportions of male and female reproductive units in terms of flowers, pollen or ovules at any given time on the plant (see *Box 1*). The **functional gender** of a plant is its relative contribution to the next generation via the male and female functions in terms of how many offspring it has sired or how many seeds it has matured.

Mating Neighbourhoods and Mating Environments

Let us imagine an insect-pollinated plant, one in which the insect vector is a weak flier that normally moves between plants that are no more than 50 m apart. Then, all plants of the same species within a radius of 50 m may be considered to be within the mating neighbourhood of a particular individual plant. Those plants to which this focal plant can either donate pollen to or receive pollen from constitute the mating neighbourhood of the plant. This neighbourhood concept helps to relate the phenotypic gender of a plant to that of the other plants in the local population. This is done using a measure known as the **standardised phenotypic gender** (see *Box 1*). A major assumption in this measure is that the plants included within the local population do actually belong to the mating neighbourhood of the focal plant and, therefore, they affect the functional outcome of maleness and femaleness of the focal plant either by receiving pollen from or donating pollen to the

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Box 1.

The **phenotypic gender** (P_{id}) of a focal plant i on any given day d can be calculated by the formula:

$$P_{id} = \frac{D_{id}}{D_{id} + L_{id}}$$

where D_{id} is the total number of open female flowers in the sample from the i th plant on day d and L_{id} is the total number of open male flowers in the sample from the i th plant on day d . This measure can vary from 0 (male phase only) to 1 (female phase only).

The **standardised phenotypic gender** can be calculated by the formula:

$$S_{id} = \frac{D_{id}}{D_{id} + (L_{id}E_{id})}$$

E_{id} is an equivalence factor and is given by the formula: $E_{id} = (\sum(D_{id}/L_{id}))i$

E_{id} is the average ratio of female to male flowers within the samples for all plants sampled on a given day and assumed to be within the mating neighbourhood of the focal plant. S_{id} also varies from 0 (male phase only) to 1 (female phase only).

(adapted from Lloyd and Bawa 1984)

focal plant. If it is assumed that all pollen grains produced by all flowers within a mating neighbourhood have an equal chance of mating with all ovules in the neighbourhood (panmixia or random mating), and that all seeds have an equal chance of survival and establishment, then the standardised phenotypic gender of a plant may be considered to be equivalent to its functional gender.

The mating neighbourhood of an individual plant is difficult, however, to determine. It depends on the pollen shadows of neighbours (see Part 1 of this article in *Resonance* April 1998) and is a function either of pollinator movement and efficiency or of factors such as wind velocity, air currents and the electrostatic properties of pollen in wind-pollinated plants. Random mating is also an assumption that is usually violated. Therefore, the operational validity of the standardised phenotypic gender and the real correspondence between the functional and phenotypic genders is often not known. Despite this, the value of the standardised phenotypic gender of a mostly male plant bearing

only a few female flowers, and surrounded by all-male plants, will indicate femaleness (examine this yourself by putting in imaginary numbers into the formulae in *Box 1*). This illustrates intuitively how the phenotypic, standardised phenotypic and functional genders are related and how the gender phenotype and the functional phenotype of the same plant can be quite different from each other. The phenotypic maleness or femaleness of the plants in the local mating neighbourhood of the focal plant constitutes its **mating environment** and thereby influences its male or female functionality.

Gender Switches from Season to Season

There are two major ways in which individual plants can change gender with time. Gender can be adjusted continually within a single individual throughout the flowering season by shifts in proportions of maleness and femaleness or by switches from all-male to all-female phases. A single plant can also be either all-male or all-female for an entire flowering season. The switch between male and female phases from season to season is called **diphasy**. Diphasic plants suppress one or the other sex in an entire season probably by arresting male or female function in flower primordia.

Eric Charnov and James Bull believe that it is sometimes disadvantageous for sex expression to be genetically fixed (see also their model with John Maynard Smith predicting when a plant should be an hermaphrodite in Part 1 of this article). According to their **patchy environment model**, labile sex determination should be favoured by natural selection when an individual's fitness as either male or female is strongly influenced by the environment, and where the individual has little control over its environment. Such conditions could prevail when resources in terms of mates or nutrients are patchily distributed. A local mating environment with an excess of males or females could bring about severe local competition for mates of either sex. An individual that changes to the minority sex will be favoured in such an environment.

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Nutrients may be patchily distributed resulting in localised sites favouring maleness or femaleness. Owing to the differential costs of male versus female function, with female function particularly seed production being more costly, the direction of environmental sex determination is often predictable. Sunlit patches favour photosynthesis, and therefore, femaleness because of the greater opportunities for resource accumulation. Stress usually results in maleness. Xeric conditions, therefore, usually result in shifts to maleness while more mesic conditions cause femaleness. Cucumbers, for example, often produce male flowers under conditions of low soil moisture or low relative humidity. Physical trauma, however, in the form of damage to the terminal axis or major wounds often results in a switch to femaleness as observed in papaya. Some maples (*Acer pennsylvanicum*) do not grow as canopy trees but come up quickly in temporary openings or gaps in the forest caused by natural tree falls or logging. The seedlings start growing in the high light environments of these gaps and male flowers are the first to be produced on the young treelet. As more saplings and treelets grow up in the tree gap, the canopy starts closing over this tree and soon the prevailing light conditions become unsuitable for the tree and the tree may even die in the shade. However, just before canopy closure, the tree switches sex and becomes female and allocates all its resources to maternal function in one large reproductive burst. This is a 'now or never' type of response and is analogous to the response to trauma in the papaya.

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Experimental manuring of plants especially with high nitrogen fertilisers has been observed to cause shifts from maleness to femaleness in *Arisaema* (snake lily), *Zea mays* and *Begonia*. Experimental removal of underground storage tissue often has a reverse effect. In the forests of central India, the leaves of the *tendu* tree (*Diospyros melanoxylon*) are used extensively in making *bidis* (local cheroots). In this economically important dioecious species, females have been reportedly found predominantly on more mesic sites. It is worth investigating whether this is a result of environmentally induced sex change and, therefore,

whether sex is rigidly determined in this species since even some so-called dioecious species are now known to change sex.

Models for diphasy generally assume a size-advantage for sex change. In a species of snake lily also popularly called the jack-in-the-pulpit (*Arisaema triphyllum*), the minimum plant size for female expression measured as leaf area was found to be 220 cm² and 280 cm² in two sites. Most plants below this size were males and it is believed that this is because individual fruits are costly to produce. Correlated with these observations, it was found that plants in the male phase occurred in shaded habitats where growth was retarded. When such plants were transplanted into sunny sites they came into the female phase. In an interesting experiment in which two connected shoots of this species were given different environmental treatments, one shoot behaved as male while the other functioned as female. This experiment and the results from the transplantations showed that gender phase in this plant is related to environmental conditions for resource acquisition. A similar phenomenon occurs in a group of orchids. Interestingly, these orchids produce between 2 and 4 million seeds per fruit and it could be argued that such fruits are costlier to produce compared to pollen grains resulting in resource constraints on femaleness.

In two neotropical woody cucurbit vines that grow to the top of the canopy, there is also a threshold size for femaleness. A non-fruiting initial male phase is followed by male and female inflorescences in alternating cycles. The size at which female flowers and fruit are first produced may be predicted by the average basal stem diameter at which the plants attain a height allowing optimal photosynthesis. In some wind-pollinated plants, however, the opposite pattern for size advantage prevails. Here, femaleness is greater in younger and shorter individuals. This may have to do with male function because taller plants should be better able to propagate pollen using wind currents. The pollen would then travel over greater distances creating longer shadows.



In individual Bridelia trees, male (left) and female (right) flowering phases alternate several times throughout the flowering season.

It is also possible that a mortality factor such as predation that is both patchy and sex-specific could favour a sex change. This has not been well studied in any plant species.

Gender Switches within Seasons

Within seasons, gender can be switched in several ways. In plants with bisexual flowers, this can be achieved by a mechanism called **dichogamy**, which involves the synchronisation of protandry or protogyny in all open flowers throughout the plant (see *Box 2*). In such plants, a majority of the flowers on the plant come into the male or female phase at the same time via synchronised maturation of anthers (anthesis) or synchronised stigma growth and receptivity. The equivalent of this phenomenon in monoecious plants is **second-order dichogamy** in which the plant produces male and female flowers in alternating synchronous sequences. Gender change via synchronised dichogamy or second-order dichogamy is called **temporal dioecy** because the same plant alternates between being male or female within a single flowering season. *Bridelia retusa* (Euphorbiaceae), a common monoecious tree in moist deciduous Indian forests, exhibits temporal dioecy in which the interval between successive male and female phases is only one week. Interestingly, this species has been variously described

Box 2. Terminology Related to Mating Systems in Plants

Protogyny: Maturation of female component of bisexual flower before male component

Protandry: Maturation of male component of bisexual flower before female component

Dichogamy: Temporal separation of male and female phases in a bisexual flower

Diphasy: Alternation between male and female phases in an individual plant from season to season

as monoecious or dioecious in different flora probably depending on whether the herbarium specimens were collected from an all-male or all-female phase or from an intersex in the process of changing between phases.

Some *Zizyphus* species (belonging to the *ber* family) exhibit temporal dioecy via synchronised protandry. These plants are self-incompatible and produce flowers that last a single day. Populations contain two types of plants. Flowers of 'early type' plants are male in the early morning (staminate phase) and become female (pistillate phase) by mid-afternoon. Flowers of 'late type' plants open late in the morning, are male in the afternoon and become female the following morning when the flowers of the 'early type' plants are male. This beautiful system ensures that these self-incompatible plants receive cross-pollen only. Temporal dioecy could also maximise fitness by minimising pollen discounting (see Part 1 of this article) in self-compatible species and thereby maximising outcrossing.

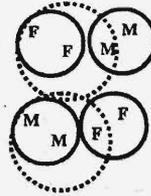
Gender Alternations as Bet-hedging Strategies

One major disadvantage of diphasy compared to continual gender adjustments in a single season is that a gender choice for a whole flowering season could be considered as a relatively long-term commitment to gender especially if the current mating and abiotic environments favour the opposite sex. If soil nutrient concentrations, moisture and light levels or some other environmental factors change at small spatial scales (say 50 m^2), then neighbouring plants of the same species will experience different environmental conditions and may respond appropriately to produce either a male- or female-biased phenotype. This may result in both males and females being included within a mating neighbourhood (see *Box 3*). However, if environmental factors responsible for gender change vary at larger spatial scales (say 200 m^2), then a mating neighbourhood may consist entirely of one gender phase, male or female, which would be dysfunctional from the aspect of pollen movement. In the former case, the environment is fine-grained (as in fine sand

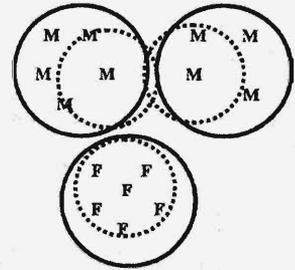
Box 3. Grain Size and Mating Environment

The closed circles indicate patches of nutrients/moisture/light levels or any other spatially variable environmental parameter that favour maleness (M) or femaleness (F). The dotted circles indicate the normal extent of the mating neighbourhood based on pollen movement due to biotic or abiotic factors.

With a fixed mating neighbourhood size, the mating environment of a fine-grained patch is more likely to contain both males and females than that of a coarse-grained one.



Fine-grained patches



Coarse-grained patches

particles forming a pattern of smaller scale units) and in the latter situation, the environment is coarse-grained (as in coarse gravel with a pattern consisting of larger scale units).

If most individuals within a patch respond to the patchy environment in the same way, then the relative fitness advantage accruing to any particular individual making a particular gender change will be reduced. Only if all individuals in a population do not have the same environmental sensitivity or if the nutrient or environment landscape is fine-grained enough for each individual to have a different response resulting in a spatial mosaic of individuals in different gender phases will a mating environment of different genders be created. Diphasy is in this sense very different from temporal dioecy in which an individual can obtain the benefits from functioning either as male or as female at different times of the same breeding season. In temporal dioecy, it is possible that females may be able to exercise mate choice and even abort developing seeds or fruit from earlier female phases if they subsequently receive better quality pollen in later female phases. This needs experimental verification. Gender alternations via temporal dioecy therefore enable plants to hedge their bets and alternate between male or female function at much smaller time scales compared to diphasy, if diphasy can be considered as bet-hedging at a longer time

scale. However, if diphasy is entirely environmentally determined, the question of bet-hedging is moot.

Complexity of Gender Issues and Challenges for Research

As more plant species and their populations are being investigated, the following facts are becoming increasingly clear. Firstly, most populations of plants with a traditionally designated sex expression, such as dioecy or gynodioecy, could actually be a collection of hermaphrodite individuals expressing various degrees of gender adjustments as has been found for papaya and several orchids. Secondly, even within a single population, there may be a mixture of labile environmentally determined gender, strict genetic canalisation or cytoplasmically determined gender expression. Only long-term observation of marked individuals (sometimes stretching over many years), measurement of the appropriate parameters of the mating and abiotic environments, and a comparison of the gender dynamics of different populations will facilitate an understanding of these complex gender issues. There is a need to investigate the nutrient and mating environments of plants on a much more fine-grained level. It is possible that there is no optimum strategy for an entire population but rather that there are multiple optima for individuals or groups of individuals within environments of slight spatiotemporal differences. The *raisons d'être* of sex change in plants await experimental verification. There are fascinating mysteries to be solved not only about **why** plants change sex but also **how** they go about this process. An abundance of challenges awaits the patient, intrepid and innovative researcher.

Suggested Reading

- [1] Robert W Cruden. Temporal dioecism: systematic breadth associated traits and temporal patterns. *Botanical Gazetteer*. 149. 1–15, 1988.
- [2] David G Lloyd and Kamaljit S Bawa. Modifications of the gender of seed plants in varying conditions. *Evolutionary Biology*. 17. 255–338, 1984.

Address for Correspondence
Renee M Borges
Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560 012, India