

## How Flowers Work

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Colin J. Webb, DSIR Land Resources, Private Bag, Christchurch

Most people see flowers as things of beauty, often used directly or indirectly as elements of decoration in their lives. To botanists, flowers, and the fruits which follow them, provide the most useful characters in plant classification. From a pollinator's point of view, flowers are a source of food, and many scientists interested in plant reproductive biology see flowers in this way, classifying flowers by their pollination classes. In this article, I would like first to look at pollination classes, giving a few familiar examples, but then I would like to look at the process of pollination from the plant side - the mechanisms plants use to ensure that pollination is successful.

Plants which produce seed predominantly through deliberate selfing, as in many of our native willowherbs (*Epilobium*), are not included in this discussion. Of course many plants that are normally outcrossed are also selfed to some degree; these are included.

### Pollination syndromes

Pollination syndromes can be grouped into two broad classes; abiotic pollination, where the pollen vector is inanimate, and biotic, where an animal of one form or another helps to transfer pollen.

#### Abiotic pollination

Plants with abiotic pollination systems are characterised by flowers without attractive petals, scent or nectar, there being no pollinator to be attracted or rewarded. In fact, the petals and sepals are often very reduced or absent and so the flowers are inconspicuous.

*Wind pollination.* The commonest form of abiotic pollination is that carried out by wind. In addition to the above features, wind-pollinated flowers usually have feathery stigmas to pick up pollen from the air, and dangling anthers that release many small pollen grains into the air. The grains are usually small and dry so that they are easily transported. These characteristics or variations on them can be seen in the flowers of such native genera as *Coprosma*, *Urtica* (nettles), and *Carex* (sedges).

*Water pollination.* This is much less common, but there are many interesting and specialised flowers that are pollinated by water. In most plants that adopt this means of pollen dispersal stigmas are held at the water surface and the pollen is thread-like and floats along until it comes into contact with a stigma. In the native flora the marine angiosperm *Zostera muelleri* (seagrass) shows these characters.

#### Biotic pollination

Flowers pollinated by biotic means usually have distinct attractants (conspicuous petals or their equivalent, and a strong scent) and rewards (usually pollen and/or nectar, but sometimes other rewards such as shelter or brood sites). The types of attractants and rewards vary remarkably according to the type of pollinator. Some of the commonest syndromes are outlined here.

*Moth pollination.* Moth flowers are usually white, with a narrow floral tube containing a little nectar, and are scented in the evening and at night with a strong heavy scent that some people find unpleasant and may blame for hayfever. Typical examples are privet, jasmine, and many native epacrids.<sup>1</sup> *Pittosporum* have the typical scent of moth flowers, are mostly scented in the evening, and are visited by moths, but are unusual in often having dark or almost black flowers.

**Butterfly pollination.** Butterfly flowers are similar to moth flowers but are usually brightly coloured and are scented during the day. Examples are butterfly bush (*Buddleja*) and *Lantana*.

**Bee pollination.** Bees are the world's most successful and diverse pollinating group, and are therefore of great commercial importance. We have only a few native bees, but they are nevertheless important in the pollination of many native plants. Most of our native daisies are bee-pollinated and nearly all of our native brooms are too. Bee flowers vary greatly as do bees themselves. Generally they are scented and offer nectar as a reward, though some nectarless flowers are pollinated by pollen-collecting bees (kiwifruit for example). Flower colour varies, but red is unusual, and the flowers may have markings in ultraviolet - visible to bees but not to us.

**Fly pollination.** Some groups of flies are important pollinators, with some plants producing vile scents mimicking rotten meat to attract them to their flowers. Among our native plants, the large inflorescences of spaniards and flowers of at least some forget-me-nots are fly-pollinated. Fly pollination may also be important on some isolated islands where other pollinators are few or lacking. The flowers of the Chatham Island forget-me-not for example are visited by several different types of fly in its native habitat.

**Bird pollination.** Flowers pollinated by birds are usually robust to withstand the impacts of their large visitors, produce copious nectar for the demanding feeders, have exposed sexual parts to contact the visitor, and generally lack a scent, most birds having a poor sense of smell. Most bird-pollinated flowers are red as in rewarewa and rata, but there are many exceptions, our native kowhai being but one.

**Bat pollination.** Bat flowers are usually pale, often held well up in the forest, and produce a lot of nectar. Two native candidates for bat pollination are *Collospermum* and *Tecomanthe*.

There are other pollinating groups as well, beetles and marsupials for example, but the above outline includes those you are most likely to come into contact with amongst our native and garden floras.

### The Structure and Function of Flowers

Most plants produce flowers that are hermaphroditic, that is they contain both anthers and pistils. Species with separate male and female individuals (dioecious) or male and female flowers on the same plant (monoecious) are in the minority although they are relatively common in New Zealand. Here I am going to concentrate on hermaphroditic flowers, mentioning separate sexes only in passing.

Hermaphroditic flowers carry out two functions: they dispatch pollen from male parts (anthers), and they receive pollen on female parts (stigmas). The better they are at doing these two things the more successful they will be at producing seed. However, there is an inherent conflict in trying to do these two things within the one flower: in order to successfully transfer pollen from the anthers of one flower to the stigmas of another, pollen should be placed on a restricted area of the pollinator's body and picked up from the same place, but if the flower is trying to do both the functions of pollen dispatch and pollen receipt, the two actions may interfere with each other. Potentially, the more precise the pollination system is, the more is the likelihood of self-interference. In talking about interference we are not just meaning the avoidance of self-pollination, but maximising the efficiency of pollen transfer. In fact, many species that have mechanisms that avoid interference are self-incompatible (unable to set seed when selfed); clearly in these cases the mechanisms have nothing to do with avoiding selfing.

Plants overcome the above dilemma in two main ways, by separating pollen dispatch and receipt either in time (**dichogamy**) or in space (**herkogamy**). I will consider each of these in turn with examples, and describe some of the variations found in nature. I am not going to describe all of the mechanisms known - that would be too confusing - but will mention all the common ones, plus a few rarer ones that I find interesting.

#### Dichogamy

Dichogamy is the presentation of pollen and stigmas within a flower or within a plant at different times. In many cases the stigmas and the anthers perform their functions in

precisely the same position within the flower, and are either moved into or out of position so that, along with the temporal separation, any interference is avoided.

The order in which stigmas and anthers are presented in dichogamous flowers allows recognition of two groups: when stigmas are presented first this is called protogyny, when anthers are presented first this is called protandry.

**Protogyny.** Many wind-pollinated flowers are protogynous. In native tutu (*Coriaria*) feathery red stigmas are presented before the dangling anthers, and flowers on a flowering branch are all in the same phase at once. In the female phase (stigmas presented and receptive to pollen), the anthers are tucked away and the casual observer could be forgiven for thinking the plant to be a female one. During the male phase (anthers presented and pollen available to be dispersed), the stigmas have usually withered up and dropped off. Native and naturalised plantains provide a further example of wind-pollination and protogyny.

Primitive angiosperms are another group of plants in which protogyny is common. This can be seen in garden magnolias and in many, but not all, native buttercups. In the Mount Cook lily, the anthers are tucked in under the carpels with splayed receptive stigmas above them when the flowers first open. Later the styles fold inwards, out of the way, and the anthers are raised up on elongated filaments.

**Protandry.** Protandry is common in native and naturalised plants alike. In matagouri (*Discaria*), pollen is presented first, and once it has been removed by pollinators the 3-lobed stigma unfolds, each lobe with a droplet of liquid to collect pollen. In this species the removal of pollen alone creates the space needed for the stigma to open unimpeded.

In native geraniums, the anthers drop off the filaments after the male phase, and the filaments move inwards as the stigmas unfurl to form a star just where the anthers were previously.

In kanuka, the anthers are tucked in and swing outwards after presenting pollen and before the stigma is receptive in the centre of the flower.

The naturalised mallows show protandry very clearly, and the mechanism involved here was described 200 years ago by the German botanist Sprengel. In *Malva sylvestris* the anthers form a cylinder of pollen in the centre of the newly opened flower; later the supporting filaments collapse and the stigmas then unfurl in the centre of the flower.

Harebells (*Wahlenbergia*) exhibit another form of protandry and this can be clearly seen in our native representatives. Pollen is placed on specialised collecting hairs at the top of the style on the outside of the closed stigmas, with the anthers themselves falling to the bottom of the flower. The pollen is gradually released onto insect visitors as the supporting hairs retract. Later the flower enters its female phase as the stigma opens to replace the pollen in the centre of the petal tube. This complex mechanism is characteristic of the bell flower family (Campanulaceae) and can be seen clearly in a number of garden campanulas. The related lobelia family (Lobeliaceae), sometimes merged with the Campanulaceae, has a similar protandrous mechanism: the anthers are fused into a tube and the pollen is pushed up through this by the growing style before the stigmas open. The daisy family (Asteraceae) is characterised by a mechanism very similar to that of the lobelia family. In fact all three of these families are considered closely related to each other. Of course in the daisy family each head is a cluster of small flowers, and if you examine them closely you can see the flowers opening in sequence from the outside to the centre of the head, the pollen appearing first and the stigmas later.

Our native *Rhabdothamnus* provides an excellent example of the avoidance of interference through protandry. The anthers present the pollen first, at the top of the flower in the centre; later, the anthers drop to the bottom of the flower revealing the receptive stigma in just the same place the anthers were earlier.

Most native gentians show protandry beautifully. The anthers open first, facing outwards from the centre of the flower; after several days they swing outwards on their filaments, sometimes right through the petal lobes, and then the 2-lobed stigma opens to replace them in the flower's centre. However, the situation is, in fact, a little more complicated than this. Firstly, in two species I have studied, anthers and stigmas function at the same time with the anthers dehiscing inwards directly onto the stigmas when the weather is rainy or overcast, but with the anthers pulled back from the stigmas by the petals opening when it is fine. This seems to give these two species the option of selfing or outcrossing depending on the weather and the likelihood of insect visitors. The second complication is that gentian flowers shut

each night and open again in the morning. Once pollinated, they shut that night and do not open again. Clearly only protandry would work for them, for if they were protogynous and shut after the stigmas received pollen, the anthers would be trying to function inside an already closed flower!

One of the advantages of dichogamy is that all the flowers on an inflorescence or even on a plant can be synchronised so that flowers of only one phase, female (stigmas) or male (pollen), are presented at one time. This was discussed earlier for our native tutu, and is a common mechanism in the carrot and ivy families. Unfortunately, our natives in these latter two families provide few examples as in many species the sexes are separated onto different plants. Instead look for this in naturalised and cultivated plants - rice paper plant (*Tetrapanax*) is a good example. Some native *Ourisia* species show synchronised protogyny, with the whorls of flowers all in the same sexual phase.

### Herkogamy

Herkogamy is the presentation of pollen and stigmas within a flower or plant at the same time but separated in space.

*Approach herkogamy.* The commonest form of herkogamy, and one which can be seen easily in many native and garden flowers, is where the stigmas and pollen are placed along the pathway that the pollinator takes to get to nectar within the flower: stigmas are outermost so that they are contacted first and incoming pollen is deposited, anthers are placed next so that the pollen to be dispatched can be picked up on the same part of the insect's body, and finally the pollinator is rewarded for its efforts. This arrangement is called approach herkogamy and achieves precise pollination while avoiding interference. Native and cultivated hibiscuses provide clear examples, as do fuchsias, lilies, many Amaryllidaceae, and numerous other plants.

*Movement herkogamy.* This is a rare but interesting variation in which either the stigmas or the anthers are moved into or out of the presentation position, although technically both are in a functional condition at the same time. The cultivated *Mimulus cardinalis* displays one form of movement herkogamy. The stigma is presented forward of the anthers and is sensitive so that it closes after contact with the pollinator; this exposes the anthers and gets the stigma out of the way. This is not an unusual mechanism in the foxglove family (Scrophulariaceae) and Cheeseman described it for our native *Glossostigma* last century.

The triggered anthers of barberry (*Berberis*), which spring inwards to dust the pollinator with pollen, are another example. In several of our native parahebes, the anthers are moved inwards out of their specialised petal folds actively by the pollinator as it grasps the filaments to position itself within the flower. At this stage the stigma has already contacted the pollen left by another flower on the insect's tummy. European veronicas are described as having just this mechanism also.

*Reciprocal herkogamy.* This class includes species that have flowers of two or more forms, each presenting pollen and stigmas at the same time but in different positions in each of the forms. There are no native examples of either of the two types of reciprocal herkogamy, but there are examples in the naturalised and cultivated floras.

Enantiomorphous plants are those that have left and right handed flowers, sometimes within a plant as in some cassias, and sometimes on different plants. An example of the latter is in the cultivated and naturalised South African *Wachendorfia*. Some plants have flowers with one anther and the style bent to the right and two anthers bent to the left and other plants have the reverse.

Heterostylous plants have the anthers and stigmas at two or rarely three different levels within the flower, this varying among plants. Generally flowers can only produce seed when pollinated with pollen from an anther at the same level on another plant. This complex mechanism seems to promote the efficient transfer of pollen to stigmas and can be seen for example in the naturalised and cultivated purple loosestrife (*Lythrum*), many *Oxalis* species, true flaxes (*Linum*), primroses (*Primula*), and some daffodils, for example *Narcissus triandrus*. In many cases only one form of plant will be grown as a clonally propagated garden variety, or only one form will be wild, meaning that the plants will not produce seed - perhaps fortunate in the case of the weedy oxalises.

*Interfloral herkogamy.* In some species the flowers on a single plant may be either male or female, so we may regard this as an extreme way of separating the two pollination surfaces. In many such cases the plants are dichogamous as well.

Nikau provides an interesting example. Here the separate male and female flowers are borne on the same inflorescence in groups of three, each female accompanied by two males. But as well as this separation in space, the plant is protandrous with the male flowers opening first and falling from the plant before the females function.

Raupo (*Typha orientalis*) also has separate male and female flowers on the one inflorescence and, as in many wind-pollinated species, is protogynous. The typical inflorescence has two segments, the upper male and the lower female. The female segment opens first as a mass of glistening stigmas. After it has finished the male segment functions producing clouds of pollen - later the male flowers drop off to leave the typical spike at the top of the stalk seen in dried flower arrangements.

#### Conclusions

There are some differences between dichogamy and herkogamy that may not be immediately obvious from what I have outlined above. Dichogamy, because of the separation of the male and female function in time, requires two pollinator visits to the flower in order for it to perform both functions, whereas in herkogamous flowers pollen can be deposited and picked up on a single visit. This may give an advantage to herkogamous flowers where pollinators are scarce. On the other hand, as noted above, dichogamous plants can have all flowers in the same sexual phase across an inflorescence or plant - an advantage not available to herkogamous species.

Another difference between dichogamy and herkogamy is that, in nearly all cases, dichogamous mechanisms involve the movement of male or female parts, or both, into or out of the pollination area. Most herkogamous species do not show such movements - the exception being the few plants that have movement herkogamy. The ease of movement, or even loss, of stamens or stigmas and style is one of the factors that determines whether dichogamous plants are protandrous or protogynous. The feathery stigmas of wind-pollinated species for example are easily lost and this may explain why so many wind-pollinated plants are protogynous. On the other hand, the stout stigmas of many insect-pollinated plants are not easily discarded and so it is the anthers that are lost following their release of pollen, so favouring protandry.

Mechanisms that avoid interference between pollen receipt by stigmas and pollen dispatch from anthers through the separation of these two functions in time (dichogamy) or space (herkogamy) are almost universal in flowering plants. Avoiding interference and increasing pollination efficiency are important factors which, along with the type of pollinator, determine the shape and function of flowers. Understanding them is a major part of understanding how flowers work. There are a great variety of pollination mechanisms displayed by our native, naturalised and introduced floras, with many of them still waiting to be discovered by those who care to look closely and carefully at flowers.