Flowering of plants

PLANTS CAN DO IT WITH OR WITHOUT SEX

Life relies on the fact that living organisms can perpetuate themselves in time by generating offspring. This can be done in different ways. Bacteria just divide themselves, while more evolved organisms may use sexual reproduction to benefit from the genetic mix of traits from the parents. While humans use sexual reproduction as the sole means of reproduction, plants may reproduce both sexually and asexually. You may have already noticed that plants have the amazing capacity to generate a new organism from a part of their leaves, roots or stems (*see figure 1*). We call this asexual reproduction, since it does not involve the sexual organs of the plants, that is to say, the flowers. The new asexually generated plant will be genetically identical to its "mother". Just like humans, plants also reproduce sexually to generate the next generation. Flowering plants, also called angiosperms (*see box 1*), have their reproduction organs harbored in the flower. In nature there are also plants that do not produce genuine flowers, for example the gymnosperms such as mosses, ferns or pine trees (*see box 1).* These more ancient vegetal species have been "quickly" outnumbered by the emerging flowering plants in the last 100 million years.

***Box 1**: Angiosperms and Gymnosperms*

Angiosperms and Gymnosperms are both Spermatophyta plants, meaning that they produce seeds. The angiosperms have flowers, harboring the sexual organs, and produce fruits that contain the seeds. Fruits provide protection to the seeds and help their dispersal. The gymnosperms, instead of producing fruits, generate naked seeds, often contained in cones. Just to mention some: the pine trees, cypress trees and ginkgo. The angiosperms probably evolved from a now-extinct group of gymnosperms and have a major economical impact as they constitute the basis of human alimentation. Examples of food products derived from angiosperms are potatoes, beans, limes, cherries, strawberries, apples, wheat, barley and rice. The gymnosperms, on the other hand are used to produce paper, wood, perfumes and soap.

Figure 1: Leaf of a species of the Bryophyllum genus. All 40 species of this genus are able to generate plantlets on the edge of their leaves. Once the plantlet is mature, it falls on the ground and generates a new plant, genetically identical to the mother plant. Photograph made by J. Zicola

"BEAUTY" AS A SUCCESSFUL REPRODUCTION STRATEGY

Flowers have been so important in human culture that we can find them in literature, religion and poetry of almost any civilization. They often have flashy colours, sweet odors and beautiful shapes.

All this beauty could make us forget what their primary task is in nature: to ensure successful reproduction. Indeed, the nice colours, nectar and the good smell they produce is not meant to attract humans, but insects, birds or even bats that will carry the pollen from one flower to the other (*see figure 2a*). Note that while humans and animals can move to meet their sexual partner, plants are fixed to the ground and need to use other strategies to exchange their precious genetic material. To bring their pollen from one flower to the other, angiosperms can use either animals or wind as carrier. Species using wind as carrier, e.g. cereals, have small flowers, since they do not have to attract animals but just deliver their pollen to the wind. On the other hand, some plants developed such attractive flowers that they do not even need to reward their visitor with precious nectar. These flowers are called deceptive flowers. About one third of the estimated 30,000 orchid species produce deceptive flowers. These flowers have various shapes that look like the sexual partners or the food of their pollinators (*see figure 2b*). They can even emit scents that mimic the sex pheromones of their pollinator. Note that the majority of flowering plants do reward their pollinators as such strategy provides a higher rate of pollination compared to producing deceptive flowers.

a)

b)

Figure 2: a) Bee pollinating a flower. b) Example of orchids mimicking its pollinator (photograph Fir0002/Flagstaffotos).

RIGHT CONDITIONS AND TIME TO FLOWER

Flowering plants adjust the time at which they flower (also called flowering time) to maximize the number and quality of offspring they can produce in a given environment. To ensure a large number of seeds, and thereby progeny, a flower needs to be fertilized at the right moment. For example, if a plant flowers too early at locations with cold winters, its pollinators may still be in hibernation. Such timing mismatch will lead to a fatal lack of pollination, leading to no seeds and therefore no offspring for the plant. In order to flower at the appropriate time, plants are able to sense different signals coming from their environment. Plants are for example able to sense the length of the day, what we also call the photoperiod. Photoperiodic flowering plants can be classified as either long-day or short-day plants. Long-day plants flower when the day length is longer than the night as for example during the late spring and summer. In contrary, short-day plants need a longer night and flower when days are getting shorter, what typically happens after the 21st of June in the Northern hemisphere. Short-day plants flower when the day length is shorter than the night. We can also distinguish “obligate photoperiodic” plants, which absolutely require long or short days to trigger flowering, and “facultative photoperiodic” plants, which flower at the appropriate day length, but eventually also flower regardless of the day length. For example, the pea, lettuce and barley are obligate long-day plants, while oat is a facultative long-day plant. An example of obligate short-day plants is the common cocklebur (*Xanthium strumarium*). Known facultative short-day plants are the crops rice, cotton, and hemp. There are also plants whose flowering time is not depending on the photoperiod; they are called day-neutral. Day-neutral plants use other signals than the photoperiod, and these signals can be external such as the ambient temperature or internal such as the developmental stage of the plant or the production of phytohormones by the plants (*see figure 3*). Cucumber, tomato, sunflower and rose are well-known day-neutral plants.

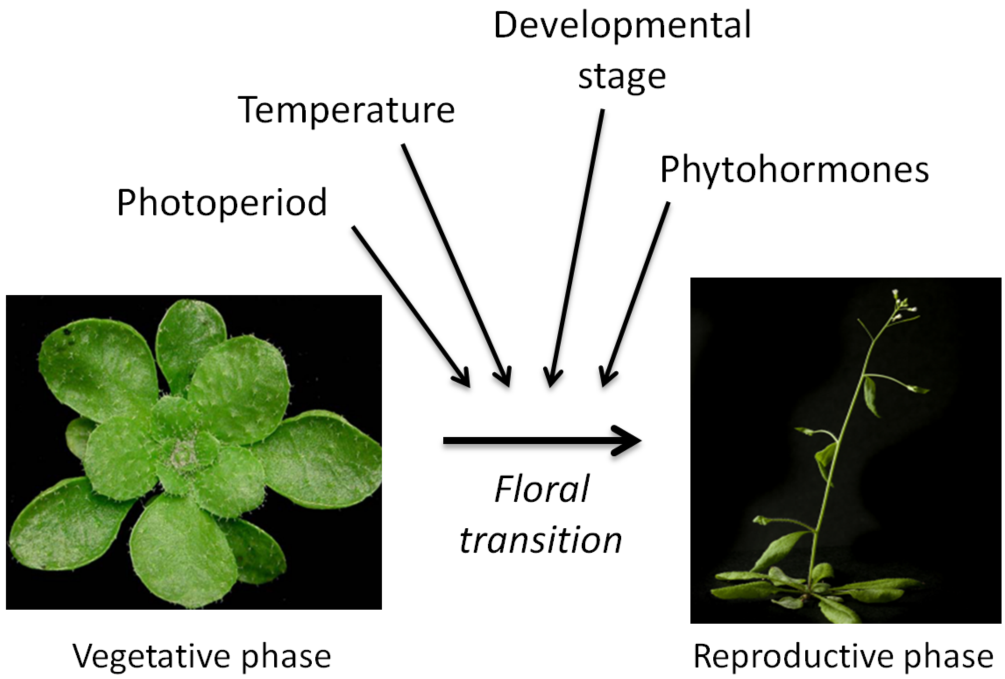


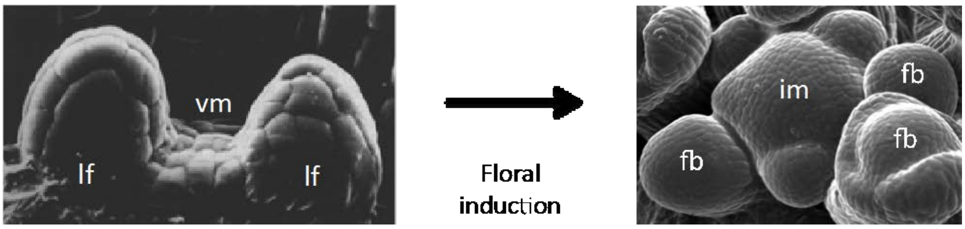
Figure 3: Example of factors influencing the induction of flowering. Flowering is a key developmental stage in the life cycle of a plant. For flowering to occur the plant has to undergo a transition from the vegetative phase (the growth of all vegetative organs like leaves and roots) to the reproductive phase (development of flowers). Pictures made by S. Del Prete.

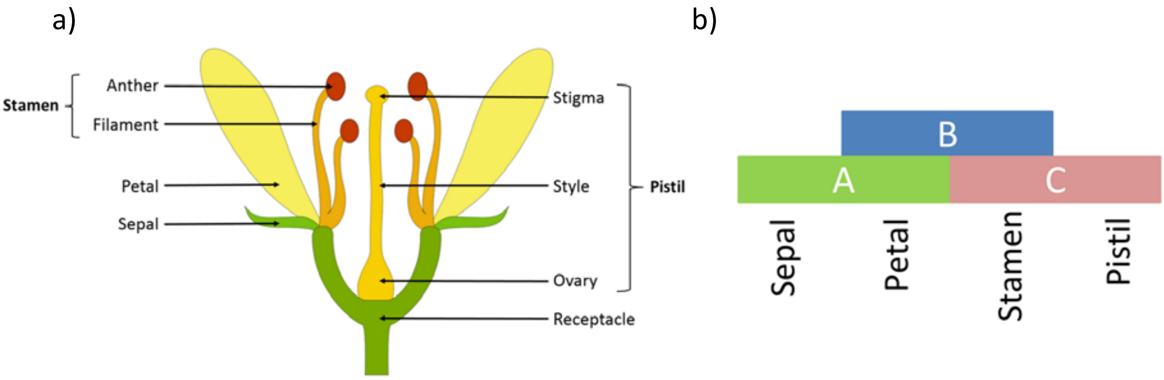
HOW A FLOWER IS SHAPED

The flowering process causes radical changes to the cells present in the meristem (*see box 2*). The vegetative meristem that is producing leaves becomes an inflorescence meristem during the floral transition; the latter meristem produces flowers. Angiosperm flowers are the most common flowers that we can see around us every day. They are composed of four different types of organs that are arranged in concentric circles or whorls. From the outside to the center, we can find sepals, petals, stamens (filament and anther) and pistil (ovary, style and stigma; *see figure 4a*). Sepals and petals form the vegetative part, stamens and carpels the reproductive parts. Sepals protect the inner part of the flower, while the coloured petals can attract pollinators and also have a protective function. The filament and the anther, which produces the pollen, together form the stamen that constitutes the male sexual organ. The female sexual organ is represented by the pistil. The stem to which the flower organs are attached is called the receptacle. The receptacle can in some cases expand after fertilization and become the edible part of a fruit, for example in strawberries. The proper development of the different parts of the flower described in *figure 4a* is dependent on various genes. These genes are classified in three groups called A, B, and C. The combination of expression of these three groups of genes determines which flower parts develop, according to the so-called ABC model (*see figure 4b*). The loss-of-function of one of these groups of genes leads to aberrant flower development, as illustrated in *figure 4c*. By using different mutants, scientists could determine the respective role of the genes in flower development and discover the ABC model.

Box 2: *Meristem*

A meristem is a region of cells capable to divide and form different types of tissues and organs. During the vegetative development of a plant (see figure 3), the meristem (i.e. the vegetative meristem) produces leaves. After the floral transition, the meristem at the shoot tip turns from a vegetative meristem into an inflorescence meristem. In the left picture, you can see a vegetative meristem (vm) surrounded by immature leaves (lf). After the floral induction, the vegetative meristem turns into an inflorescence meristem (im) from which floral buds (fb) appear (shown in the right picture) that will turn into flowers. Pictures taken by scanning electron microscopy from the model plant Arabidopsis thaliana; kindly provided by P. Laufs (IJPB-INRA Versailles, France).





c)

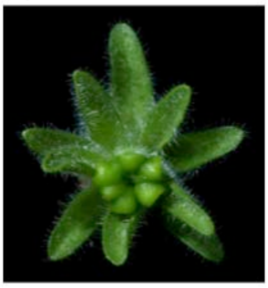


Figure 4: a) Flower anatomy. b) ABC model. The production of petals involves genes of groups A and B while for sepal formation only genes of group A should be active. The production of stamen needs the activity of genes of groups B and C, while for the pistil on genes of group C should be active. Drawing made by J. Zicola. c) Mutant petunia flower in which a B gene is inactive. The flower is composed of two whorls of sepals and two whorls of pistils. It shows sepals instead of petals and pistils instead of stamens (photograph kindly provided by G. Angenent, WUR, The Netherlands).

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