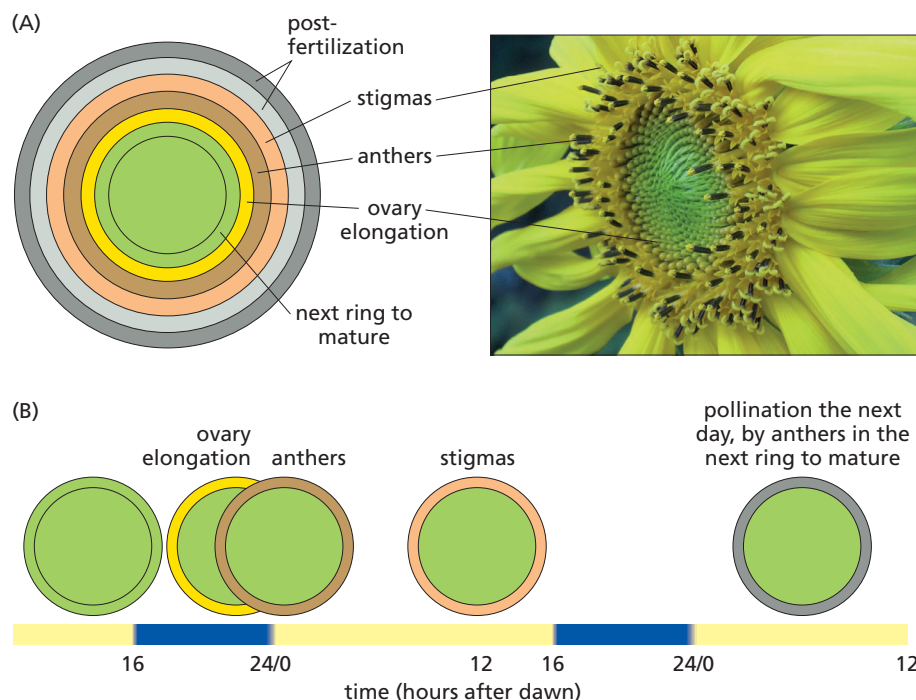


# Environmental signals

# 12

## OM12.1 CIRCADIAN CONTROL OF FLORET MATURATION IN SUNFLOWER HEADS

A striking example of the coordination of biological processes through circadian control is provided by the maturation of the florets of sunflower (*Helianthus annuus*). The head (**capitulum**) consists of numerous spirally organized florets, each of which is an individual flower (**Figure OM12.1-1**). Florets mature in discrete rings, with one ring maturing per day. Floret maturation consists of elongation of the basal ovary prior to dawn, followed by emergence of the stamens around dawn, followed by emergence of the stigmas later in the day. The stigmas will receive pollen from the stamens that emerge from the next ring to mature, on the following day. The consequences of this precisely controlled succession of events include the promotion of cross-fertilization across the capitulum – each floret inevitably receives pollen from a different floret – and the timing of pollen release to the period of the day when bee visits are most frequent, maximizing the reproductive success of the plant (see Section 11.3 for a discussion of mechanisms that prevent self-fertilization). Although different sets of genes bring about each of these processes, the timing of each process is under circadian control. As described in the text, a hallmark of processes controlled by the circadian clock is their continued rhythmicity in the absence of daily environmental cycles. In the sunflower head, the sequence of processes continues over one or a few days even when the plant is transferred to constant darkness.



**Figure OM12.1-1** Circadian control of sunflower floret development.

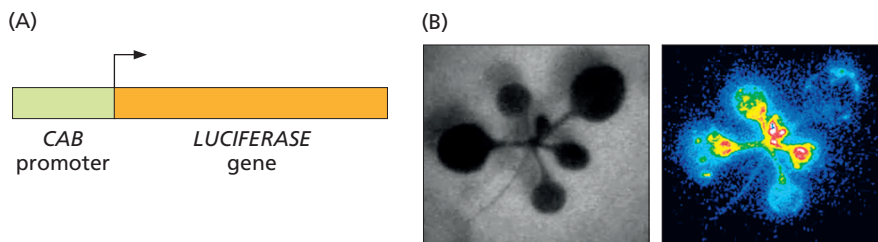
(A) The appearance of the flower head. For clarity, the diagram shows three rings of florets during the maturation process. Rings inside the maturing rings have yet to mature. The middle part is immature. In the innermost ring in which maturation has started (*yellow*), elongation of the basal ovaries causes the closed floret to increase in height. In the next ring out (*brown*), the floret has opened and anthers bearing pollen have emerged. In the next ring (*orange*), stigmas have emerged. The outermost rings (*gray*) have been fertilized and seed development is starting (these rings have not yet developed on the flower in the photograph). (B) The succession of events during maturation of florets in a single ring over a day. Ovary elongation occurs before dawn, followed by anther emergence around dawn. Stigmas emerge later in the day, after the pollen has been shed. The florets will be fertilized by pollen from the next ring to mature, on the following day. (Photo, from "Sunflower3-2012" by Rob Duval. Licensed under CC BY SA 3.0 via Wikimedia Commons.)

## OM12.2 PROMOTER–*LUCIFERASE* FUSIONS FOR CHARACTERIZING CIRCADIAN RHYTHMS

The mechanism and function of the circadian clock has been studied by creating transgenic plants that express a gene encoding a light-emitting protein fused to the promoter of an endogenous gene with a diel pattern of expression. A commonly used gene encodes the enzyme **luciferase**, found in fireflies. Luciferase (LUC) brings about the emission of light (luminescence) when it catalyzes the ATP-dependent decarboxylation of its substrate luciferin. Plants expressing promoter–*LUC* fusions emit light when treated with luciferin and ATP, and patterns of light emission can be monitored over several days using a specialized camera (**Figure OM12.2-1**). Fusion of *LUC* to genes encoding known components of the circadian clock reveals the time of day at which their expression peaks in a wild-type plant, and enables study of the performance of the clock in response to changes in day length and other environmental factors.

Expression of promoter–*LUC* fusions has also been instrumental in the identification of new clock components through the selection of mutants in which the period of the clock is longer or shorter than 24 hours. New genes with impacts on clock function continue to be identified, allowing models of the operation of the oscillator to be refined and elaborated. The much-simplified model of the clock in Figure 12.20B was largely developed from these kinds of experiments.

Fusion of *LUC* to promoters of other genes with diel patterns of expression – such as the *CAB* gene (see Figure OM12.2-1) – informs research on the role of the clock in coordinating plant processes with diel environmental changes. Although many of the components of the circadian oscillator have been identified, understanding of its operation remains incomplete and models continue to be revised and refined.



**Figure OM12.2-1 Visualizing circadian rhythms in transgenic plants.** (A) The promoter of the *CAB* (chlorophyll *a/b* binding) gene is fused to the *LUC* open reading frame encoding the firefly luciferase enzyme. This construct is used to transform *Arabidopsis* plants. (B) The presence of luciferase causes transformed plants to emit light, which can be seen with a camera able to detect luminescence (*right*). Changes in the intensity of luminescence over the diel cycle reflect the control of *CAB* expression by the circadian clock.