PHOTOPERIODISM:
(MONITORING DAY LENGTH)

As we have seen, the circadian clock enables organisms to determine the time of day at which a particular molecular or biochemical event occurs. Photoperiodism, or the ability of an organism to detect day length, makes it possible for an event to occur at a particular time of year, thus allowing for a seasonal response. Circadian rhythms and photoperiodism have the common property of responding to cycles of light and darkness. Precisely at the equator, day length and night length are equal and constant throughout the year. As one moves away from the equator toward the poles, the days become longer in summer and shorter in winter. Not surprisingly, plant species have evolved to detect these seasonal changes in day length, and their specific photoperiodic responses are strongly influenced by the latitude from which they originated. Photoperiodic phenomena are found in both animals and plants. In the animal kingdom, day length controls such seasonal activities as hibernation, development of summer or winter coats, and reproductive activity. Plant responses controlled by day length are numerous, including the initiation of flowering, asexual reproduction, the formation of Perhaps all plant photoperiodic responses utilize the same photoreceptors, with subsequent specific signal transduction pathways regulating different responses. Because it is clear that monitoring the passage of time is essential to all photoperiodic responses, a timekeeping mechanism must underlie both the time-of-year and the time-of-day responses. The circadian oscillator is thought to provide an endogenous time-measuring mechanism that serves as a reference point for the response to incoming light (or dark) signals from the environment. How changing photoperiods are evaluated against the circadian oscillator reference will be discussed shortly.

Plants Can Be Classified by Their Photoperiodic Responses

Numerous plant species flower during the long days of summer, and for many years plant physiologists believed that the correlation between long days and flowering was a consequence of the accumulation of photosynthetic products synthesized during long days. This hypothesis was shown to be incorrect by the work of Wightman Garner and Henry Allard, conducted in the 1920s at the U.S. Department of Agriculture laboratories in Beltsville, Maryland. They found that a mutant variety of tobacco, Maryland Mammoth, grew profusely to about 5 m in height but failed to flower in the prevailing conditions of summer. However, the plants flowered in the greenhouse during the winter under natural light conditions. These results ultimately led Garner and Allard to test the effect of artificially providing short days by covering plants grown during the long days of summer with a light-tight tent from late in the afternoon until the following morning. These artificial short days also caused the plants to flower. This requirement for short days was difficult to reconcile with the idea that longer periods of radiation and the resulting increase in photosynthesis promote flowering in general.

Garner and Allard concluded that the length of the day was the determining factor in flowering and were able to confirm this hypothesis in many different species and conditions. This work laid the foundations for the extensive subsequent research on photoperiodic responses. The classification of plants according to their photoperiodic responses is usually based on flowering, even though many other aspects of plants’ development may also be affected by day length. The two main photoperiodic response categories are short-day plants and long-day plants:

1. Short-day plants (SDPs) flower only in short days (quantitative SDPs), or their flowering is accelerated by short days (quantitative SDPs).
2. Long-day plants (LDPs) flower only in long days (qualitative LDPs), or their flowering is accelerated by long days (quantitative LDPs).

The essential distinction between long-day and shortday plants is that flowering in LDPs is promoted only when the day length exceeds a certain duration, called the critical day length, in every 24-hour cycle, whereas promotion of flowering in SDPs requires a day length that is less than the critical day length. The absolute value of the critical daylength varies widely among species, and only when flowering is examined for a range of day lengths can the correct photoperiodic classification be established.

Long-day plants can effectively measure the lengthening days of spring or early summer and delay flowering until the critical day length is reached. Many varieties of wheat (Triticum aestivum) behave in this way. SDPs often flower in fall, when the days shorten below the critical day length, as in many varieties of Chrysanthemum morifolium. However, day length alone is an ambiguous signal because it cannot distinguish between spring and fall. Plants exhibit several adaptations for avoiding the ambiguity of day length signal. One is the coupling of a temperature requirement to a photoperiodic response. Certain plant species, such as winter wheat, do not respond to photoperiod until after a cold period (vernalization or overwintering) has occurred. Other plants avoid seasonal ambiguity by distinguishing between shortening and lengthening days. Such “dual–day length plants" fall into two categories:

1. Long-short-day plants (LSDPs) flower only after a sequence of long days followed by short days. LSDPs, such as Bryophyllum, Kalanchoe, and Cestrum nocturnum (night-blooming jasmine), flower in the late summer and fall, when the days are shortening.
2. Short-long-day plants (SLDPs) flower only after a sequence of short days followed by long days. SLDPs, such as Trifolium repens (white clover), Campanula medium (Canterbury bells), and Echeveria harmsii (echeveria), flower in the early spring in response to lengthening days.