

12 Flowering and Fruiting

THE PRODUCTION of seeds is often the primary objective in crop production. Seed production results from numerous physiological and morphological events that lead to flowering and fruiting in response to *photoperiod* (length of day) and *temperature*. Flowering and fruiting responses to these environmental factors have been the subject of intensive investigation for more than 50 years.

Studies in the 1920s (Garner and Allard 1920, 1923, 1925) led to the identification of *photoperiod* as a controlling environmental factor in flowering. Later studies demonstrated that the *nyctoperiod* (length of night), rather than length of day, was actually the operative factor in control of plant responses. If the dark period is interrupted by short exposures of light at low energy, the result is a long-day effect. Interruption of the light period by dark exposures, however, has no effect on flowering. Later studies by other USDA scientists identified *phytochrome* as the photoreceptor (pigment) in the control of developmental processes such as flowering, and demonstrated how phytochrome reacted in relation to light quality in the red part of the spectrum. The role of mature leaves as the production site of a flowering stimulus (hormone) and its transport to and activation of the meristems have been matters of keen interest in research since the pioneer work. /

Latitude and time of year (sun declination) are the determinants of photoperiod and temperature, both of which vary widely from season to season and from the equator to the poles. Although nearly constant year-round at the equator, photoperiod can vary by 24 hr per day between June and December (summer and winter solstices) at the poles (Fig. 12.1).

The dominant role of photoperiod and temperature on flowering and fruiting and ultimately on seed production emphasizes the importance of cultivar selection. Photoperiodically sensitive cultivars of soybean are adapted to a narrow latitudinal range, often no more than 200 to 250 km. Water, nutrients, and other factors at most can only modify the response to photoperiod or temperature. On the other hand, certain crops, such as tomato, are insensitive to photoperiod and can be produced in any latitude within broad temperature limits.

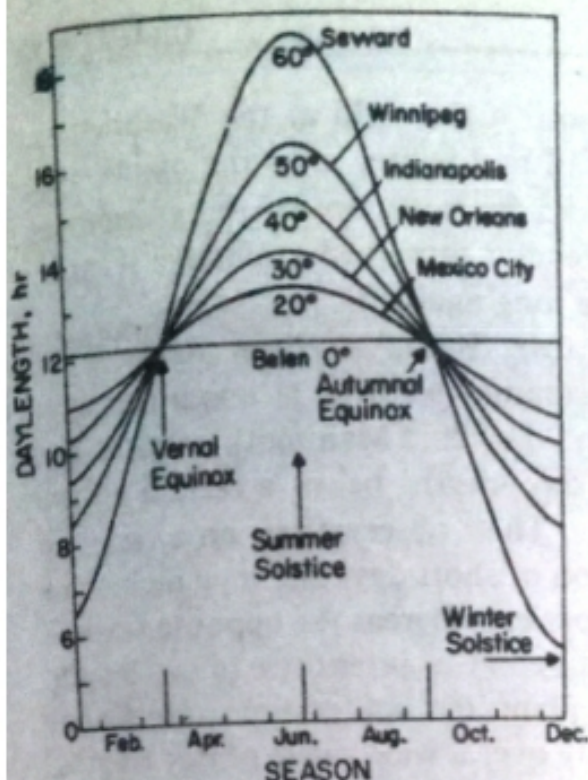


Fig. 12.1. Annual changes in day length (sunrise to sunset) in relation to latitude. (From Leopold and Kriedemann 1975)

Transition to Flowering

Shoot meristems produce either leaf or inflorescence primordia, depending on photoperiod and possible interactions with temperature. Indeterminate growth initially produces leaves. In a few species the same bud first produces leaves, then floral structures, and then leaves again. In *monocarpic* plants (annuals), the transformation of a vegetative (leaf producing) bud to flowering ends further leaf production. The initiation of flowering in these plants may be thought of as a final commitment of energy resources. After flowering and fruiting the plant dies. Such growth is *determinate*. On the other hand, only partial commitment is made to sexual reproduction in perennials; vegetative growth may continue indefinitely, separately or concurrently with flowering. Axillary buds that have adequate food reserves renew vegetative growth if leaf formation is terminated by flowering of older shoots, such as in alfalfa, or the old shoots may continue to grow, as in trees. Biennials characteristically produce a stemless rosette growth in the first year and stems, flowers, and fruits in the second year, a *monocarpic* habit much like an annual.

Photoperiodism

The effect of day length on flowering was first alluded to by Tournis in France and by Klebs in Germany just after the turn of the century (Evans 1969). Although these researchers came close to the recognition of photoperiodism, the actual discovery is credited to two USDA scientists, W. W. Garner and H. A. Allard (1920; 1923, 1925), working near Washington, D.C. They coined the term *photoperiodism* to define plant response to day length. Their observations were on two short-day crop cultivars, 'Maryland Mammoth' tobacco and 'Biloxi' soybean (maturity group VIII). The tobacco plants did not

produce flowers during the growing season in the field at the Washington, D.C., latitude but flowered later in the fall and winter after the plants were moved into the greenhouse. Axillary shoots from stumps of the greenhouse plants flowered in the short days of winter but remained vegetative if emergence occurred in spring, when days were long again.

Garner and Allard observed field-grown 'Biloxi' soybean plants. Field plantings made from early spring to midsummer matured at about the same time in autumn. They concluded that both 'Maryland Mammoth' tobacco and 'Biloxi' soybean flowered in response to day lengths below a certain critical length; that is, they were short-day plants. Their observations on a range of species clearly illustrated that a combination of short days and long nights in a 24-hr cycle promoted flowering in many species, whereas the opposite favored flowering in others. Some species were indifferent or insensitive to day length. However, even photoperiodically sensitive plants did not require a specific day length for flowering but flowered optimally over a wide range of day lengths, generally becoming less sensitive with increasing plant age (Fig. 12.2). Day lengths longer than optimum delayed flowering of short-day plants until a critical length was reached, above which the plant remained vegetative. Similarly, day length below a critical length caused long-day plants to remain vegetative. Both types of crop species became sensitive to photoinductive conditions after a required basic vegetative phase (BVP) (Vergara and Chang 1976; Major 1980).

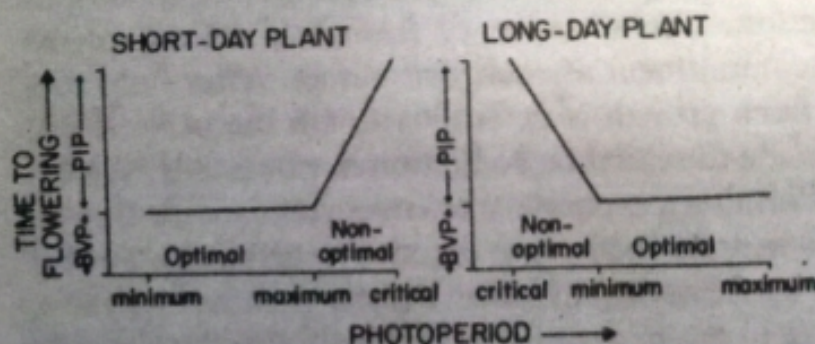


Fig. 12.2. Generalized model of plant response to day length. BVP is basic vegetative phase; PIP is photoperiod-induced phase (Major 1980, by permission).

In spite of the complexity of responses to a range of day lengths and the various interactions with other environmental factors, the following classification scheme outlined by Hillman (1962) is useful in understanding the day-length responses of crop and wild species.

I. Short-day plants (SDPs). Flowering is promoted by day lengths shorter than a critical maximum (which varies among species and varieties) and usually is influenced by other environmental factors, such as temperature (Kasperbauer 1973). 'Maryland Mammoth' tobacco, 'Biloxi' soybean, and cocklebur are classic SDPs. Since they are highly sensitive to photoperiod, they have been used in numerous photoperiod studies.

2. Long-day plants (LDPs). Flowering is promoted by day lengths longer than a critical minimum (which is influenced by genotype and other environmental factors). 'Wintex' barley and black henbane (*Hyoscyamus niger*), a biennial, are classic LDPs and have been used extensively in photoperiod research.

3. Short-long-day plants (SLDPs). Flowering is promoted by exposure to a sequence of short days prior to an exposure to long days. Many temperate-zone, perennial grasses (e.g., orchardgrass) fit this category, although their responses are more complex than even this indicates because a cold period (vernalization) is also required between exposures to short and long days (Gardner and Loomis 1953).

4. Long-short-day plants (LSDPs). Flowering is promoted by exposure to a sequence of long days prior to exposure to short days. Night jasmine (*Cestrum nocturnum*) is regarded as a LSDP.

5. Day-neutral plants (DNPs). Flowering is insensitive to photoperiod but is associated with an age factor. Generally flowers commence after a minimum age or size is attained. Dandelion, tomato, and buckwheat are DNPs. These species are adapted to any latitude within broad temperature limits. 'Big Boy' tomato cultivar, for example, can be produced from Mississippi to Canada. Many plants of tropical origin are DNPs, but others are SDPs (e.g., tropical soybean cultivars).

As mentioned before, classification of plant response is made on the basis of the relationship of flowering to the length of day (light period in a 24-hr cycle), but the actual controlling factor is the length of uninterrupted darkness, or *nyctoperiod*, rather than the photoperiod. Some plants do not fit any of these categories. For example, sunflower is a LDP in juvenile stages but becomes insensitive with plant age.

Generally it can be assumed that crop and wild species that flower and fruit in midsummer are LDPs, and those that flower and fruit in autumn are SDPs. Winter annuals (e.g., wheat), biennials (e.g., sugar beet), and numerous perennials (e.g., orchardgrass), are obligatory LDPs. These plants, however, flower only after vernalization, or a cold period. Maize, sorghum, and soybean are SDPs. There is considerable overlap between the ranges for short- and long-day plants.

Categorizing the flowering response of soybean cultivars adapted to northern latitudes, which have long summer days, presents an interesting problem. These cultivars (maturity groups 0 and 00) can flower under 16- to 18-hr days, whereas the critical day length for 'Biloxi' cultivar is about 12 hr. However, a classification other than SDP for such cultivars would not be correct, since flowering occurs even earlier or in fewer days on plants with fewer nodes as photoperiods shorten (e.g., from 16 to 8 hr).

Modern cultivars of such biennial crops as sugar beet and celery have been selected for a high vernalization requirement because stems bearing inflorescences the first year (*bolting*) are undesirable in a commercial crop. Annual types (which flower without vernalization) have been selected from biennial sugar beet, black henbane, and sweet clover.

LOCUS OF VERNALIZATION

Evidence that the cold stimulus is produced in the meristems or buds rather than in the leaves is derived from four phenomena: (1) imbibed seeds are readily vernalized; (2) cold exposure of only leaves, roots, or stems was not effective (Salisbury 1963); (3) developing seeds on a mother plant can be, and sometimes are, vernalized if cold persists before the seeds become dry; and (4) plants regenerated from adventitious buds from a vernalized leaf were induced to flower (Wellensiek 1962).

LOSS OF VERNALIZATION

Vernalization in seeds can be nullified by exposure to adverse conditions, such as desiccation or high temperatures (30–35°C) for a period of days (Purvis and Gregory 1937; Lang and Melchers 1947). It is difficult to reconcile these findings with the agricultural practice advocated by Lysenko in the USSR of vernalizing winter cereal grains and holding them for spring seeding. It would seem that holding the seeds in a dry state would devernalyze them. At any rate, the Lysenko practice has not persisted anywhere, probably because adapted spring-type cultivars became available.

Vernalization in certain perennial grasses is more complex; in addition to cold, some short photoperiods are necessary (Peterson and Loomis 1949; Cooper 1950). In orchardgrass, floral induction occurred naturally by November 15 at Ames, Iowa (42°N) (Gardner and Loomis 1953). A requirement for short days in conjunction with vernalization has not been observed in biennials and winter annuals; that is, only cold is required for floral induction in these species.

Flowering

FLORAL INDUCTION

Gardner and Loomis (1953) recognized three discrete phases in orchardgrass flowering, each with distinctive photoperiodic and thermal requirements (Fig. 12.5):

1. Floral induction: production of the flowering stimulus (a chemical change in the shoot apex) in response to the cold (nongrowth) temperatures and short days of autumn
2. Floral initiation: transformation of induced but morphologically vege-

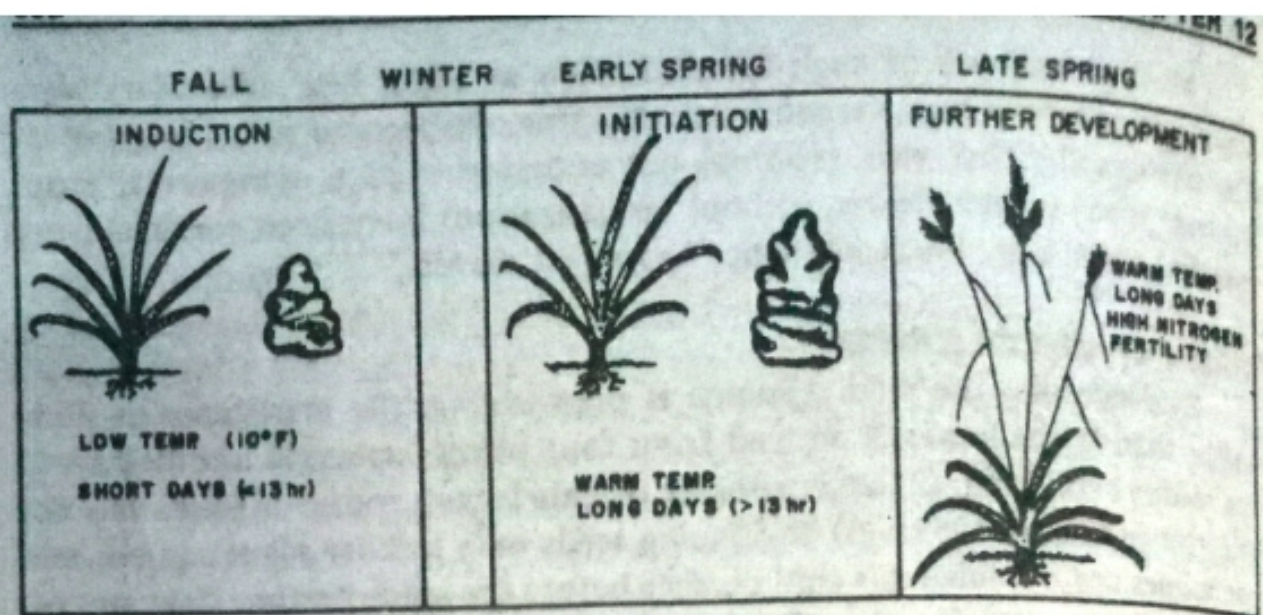


Fig. 12.5. Flowering of orchardgrass in relation to seasonal temperature and photoperiod (Gardner and Loomis 1953).

tative growing points to floral primordia in response to the long days and moderately warm temperatures of spring

3. Further floral development: growth and development of floral initials into mature flowers and inflorescences in response to the long days and moderately warm temperatures of spring (also favored by high nitrogen fertility)

In orchardgrass the flowering stimulus produced in the shoots exposed to induction conditions was not transferred to tillers that did not receive both cold and short days, although an organic connection is presumed to exist (Fig. 12.6). The fact that only the tillers exposed to light flowered, while the many hidden in leaf sheaths did not, supports the concept that leaves are the photoperiodic receptors.

Such a three-phase response usually is not delineated for flowering in most other studies, although it is probably universal among species. Generally emphasis has been on *floral induction* (production of the flowering stimulus) and *floral expression* (development). Much of the classic work on microdissected buds of soybean and cocklebur described early morphological changes, defined as floral initiation. The requirements for floral induction and floral initiation are the same in a SDP, such as soybean; consequently these two phases are not separable as they are in orchardgrass. The requirements for floral initiation and expression appear to be different in soybean; inflorescences were initiated (after induction) under long days, but flowers aborted if the plants were maintained under long days after initiation (Fisher 1962).

With the aid of low magnification of a dissecting microscope, a system of staging floral development has been described for cocklebur (Salisbury 1955), soybean (Borthwick and Parker 1938), and lambsquarters (Kasperbauer et al. 1964). Photoinduced plants of these SDPs readily produce floral initials under