

Environmental Effects on Flowering

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Flower and seed development in crop plants is determined by the response of the plant to environmental factors. Understanding these relationships permits the plant breeder to obtain hybrid and self-pollinated seed from a broad range of cultivars in the field, growth chamber, or greenhouse. This chapter describes the general response of plants to environmental factors that influence flowering and shows how these factors may be manipulated to facilitate production of seed.

I. RESPONSE OF PLANTS TO ENVIRONMENT

Crop plants differ widely in their response to environmental factors. They differ among species, among cultivars within species, and among stages of plant development within a cultivar. The response reflects differences in area of adaptation and in the biological mechanisms that have evolved for coping with adverse environments.

The main environmental factors influencing flowering are day length, also referred to as photoperiod, and temperature. Species are usually classified as short-day or long-day types. A short-day plant flowers when the day length is less than its critical length and a long-day plant flowers when the day length is longer than its critical length. Some species are considered to be day-neutral, but it is unlikely that all of the cultivars of any species are completely unaffected by day length. Corn has been called a day-neutral species (Bickford and Dunn, 1972) but short-day responses have been found even in early-maturing corn hybrids (Hunter et al., 1974).

Temperature influences the rate of development and the number of flowers that produce mature seeds. Cool-season crops, such as oat and

barley produce maximum seed at about 25 C, whereas tropical crops like pigeonpea have optimum production above 30 C.

The genetic variation in response to day length and, to a lesser degree, temperature has allowed many species to adapt to a wide range of latitudes and altitudes. Soybean, a short-day species, is grown from the tropics to 50° N Lat. Soybean cultivars adapted to the tropics will not flower at day lengths of 14 hours, whereas those adapted to the higher latitudes will flower under continuous light. Genotypes from high altitudes tend to grow well at cool temperatures.

The plant is also affected differently by the environment at various phases of plant development. For example, day length may affect the initiation of flowering of a plant, but not its post-flowering development. Some soybean cultivars flower as rapidly under continuous light as on 14-hour days, but seed maturation is delayed by continuous light (Polson, 1972). The number of days of the correct day length required to induce flowering in some species decreases as plants get older (Borthwick and Parker, 1938a; Velasco and Manuel, 1955; Sasamura, 1960).

II. PHASES OF PLANT DEVELOPMENT

Germination of seed begins the life cycle of crop plants. Adequate moisture and temperature are the universal requirements for germination, although many species also exhibit some form of dormancy that must be overcome. Dormancy can be associated with hard seed coats, day-length sensitivity, the need for afterripening, or the need for exposure to low temperatures.

The juvenile phase covers the period from germination to flower bud formation. The rate at which new leaves are formed is primarily a function of temperature, but the time from emergence to flower initiation is affected by day length. Size of the mature plant is often determined by the duration of the juvenile phase because plants flowering late have initiated more leaves and, because they have more internodes, are taller than those flowering early. Rate of development is also influenced by soil moisture, soil type, and fertility.

Formation of the flower bud begins the reproductive phase. For determinate species and cultivars, the initiation of new leaves stops when flowering starts; however, leaves and stems may continue to enlarge. Corn, a determinate plant, does not initiate new leaves after the tassel is initiated. For indeterminate plants, new leaves are initiated after flowering has begun. In most indeterminate plants, the initiation of new leaves stops after the last flower forms. Cassava is an indeterminate plant that initiates flowers, leaves, and branches simultaneously. Soybean has both determinate and indeterminate cultivars.

Some winter annuals and biennials require exposure to low temperatures before reproductive development can be initiated. Vernalization is defined as the acquisition or acceleration of the ability to flower by a chilling treatment (Chouard, 1960). Vernalization does not induce flowering, but makes the plant more receptive to the day-length stimulus. Unvernalized winter rye plants flower in continuous light, but take twice as long as vernalized plants (Gott et al., 1955).

The reproductive phase lasts from initiation of the flower until fertilization of the flower. The length of this phase is determined by day length in some species. For example, the reproductive primordia of rice can revert to vegetative primordia if photoinduction of the plant is not complete (Noguchi et al., 1967); panicle emergence of rice can be delayed or prevented if the day length is too long after floral initiation (Vergara and Lilis, 1966, 1968); or the time from floral initiation to anthesis for sorghum (Quinby, 1972) and soybean (Parker and Borthwick, 1939a; Nagata, 1958) can be delayed by long day lengths. In the long-day cereals—wheat, barley, and oat—this phase is hastened by long day lengths (Guitard, 1960; Griffiths, 1961; Ormrod, 1963; Khatri, 1964).

The time from fertilization of the flower to maturation of the seed is called the ripening phase. It can be divided into three periods, according to the rate of dry matter accumulation in the seed—the lag period, the linear period, and the period when the rate levels off before maturity (Johnson and Tanner, 1972). The lag period can be as short as 1 week in wheat (Rawson and Evans, 1971) or as long as 20 days in soybean (Major et al., 1975a). Its duration also can be influenced by day length and temperature. Short days and warm temperatures shorten the lag period in soybean, a short-day species (Major et al., 1975b).

Rapid seed filling occurs during the linear period, and its rate and duration are influenced by day length and temperature. High temperatures shorten the duration of seed filling and increase the rate of seed filling in sorghum, rice, and wheat. In short-day plants, the delaying effect of cool temperatures in the fall season may be offset by the shortening day length.

III. DAY LENGTH

Day length has no effect on floral induction until the plant has attained a minimum amount of growth, a part of the life cycle often referred to as the basic vegetative phase (BVP). Species and cultivars differ widely in length of BVP. Some wheat cultivars respond to day length immediately after emergence, but most soybeans do not respond until after the unifoliate leaves have opened. The BVP of rice cultivars varies from 10 to 63 days after germination, and its length is controlled by at least two genes (Vergara et al., 1965). Variation in the BVP also has been observed in corn (Rood and Major, 1981).

After a plant has completed BVP, initiation of flowers frequently depends on the day length. The critical photoperiod is defined as the maximum day length at which a short-day plant will flower and the minimum day length at which a long-day plant will flower. The optimum photoperiod is the day length at which the plant will flower in the shortest time after BVP is completed.

Knowledge of the critical photoperiod is essential when day length is used to delay the flowering of cultivars. The critical photoperiod of 'Biloxi' soybean, a short-day cultivar, is 13.5 hours. A breeder could use a 14-hour day to prevent flowering of this cultivar until another parent was available for hybridization.

The critical photoperiod can differ markedly among cultivars of a species and frequently is associated with the latitude of adaptation. Culti-

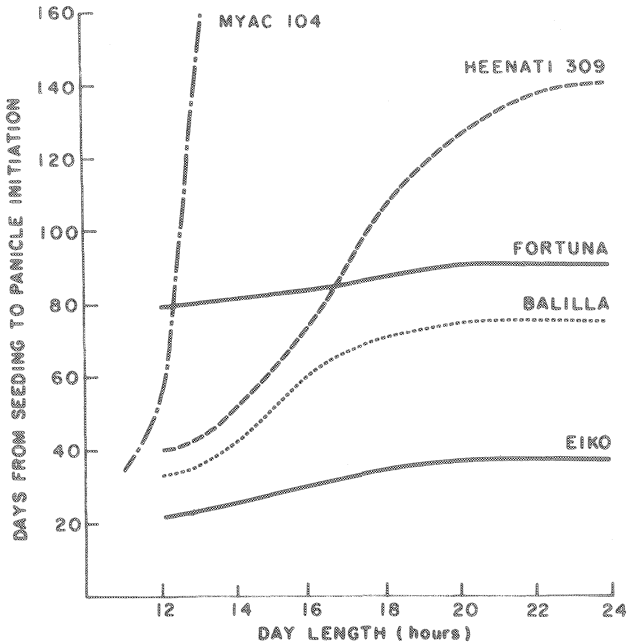


Fig. 1—Day length response curves of five rice cultivars based on data of Best (1961).

vars from low latitudes have a shorter critical photoperiod than those from high latitudes. Soybean cultivars adapted to the southern U.S. have a critical photoperiod of about 13.5 hours; those adapted to northern Minnesota and Western Canada do not have a critical photoperiod. The critical photoperiod of sorghums adapted to the United States is longer than that of tropical sorghums (Miller et al., 1968).

Knowledge of the optimum photoperiod for a species is useful for obtaining flowering and seed development in the shortest possible time. The optimum photoperiod is not known for most crop species; however, breeders commonly use about a 12-hour day to obtain rapid flowering of short-day species and 20 to 24 hours for long-day types. The reduction in number of days to flowering may or may not be linear for each hour of change in day length from the critical to the optimum photoperiod. A day-length response curve is useful in estimating when floral initiation will occur at various day lengths. The response curves in Fig. 1 are adapted from data of Best (1961) and show day-length responses of five rice cultivars. The cultivars 'Eiko' and 'Fortuna' have very low sensitivity to day length, but Eiko has a short BVP and Fortuna has a high BVP. The cultivars 'Balilla', 'Heenati 309', and 'Myac 104' have essentially the same BVP but have moderate, high, and very high day length sensitivities, respectively.

The optimum photoperiod for rapid flowering may not be optimal for obtaining desirable flowers for hybridization, because at the optimum photoperiod there may be fewer flowers, which have less pollen, and which may be more cleistogamous than at day lengths closer to the critical

photoperiod. Artificial lighting can be used to extend the day length of short-day plants to obtain suitable flowers for hybridization in winter greenhouses or in latitudes lower than their area of adaptation.

Factors to consider in creating artificial day lengths by supplemental lighting are timing, duration, level, and quality. Day length in the field or greenhouse can be extended before sunrise and after sunset, or night length can be interrupted. Night interruption is effective because the response of plants to day length is actually a function of duration of night rather than day. A short-day plant technically should be referred to as a long-night plant and a long-day plant as a short-night plant. A period of light during the night should delay flowering of short-day plants and hasten that of long-day plants.

Timing of the day length in a growth chamber can facilitate hybridization during a selected time of the day. For hybridization of peanuts, Banks (1976) began a 12-hour day at 1630 hours so that flowers were available for emasculation the next morning between 0800 and 1000 hours.

The duration of artificial lighting is a function of the critical photoperiod of the cultivar. Day length in the field depends on the light level at sunrise and sunset that is adequate for flower control. The effective day length for rice is approximately equal to the astronomical day length. Takimoto and Ikeda (1961) indicated that light levels for measuring day length of Biloxi soybean should start when the light level of daylight increased to 10 lux in the morning and decreased to 200 lux in the evening.

The light level used to extend the day length or interrupt the night is an important consideration. A relatively low level may be required in some species and cultivars. Extending the day length with supplemental illumination of only 1 lux is sufficient to delay flowering of rice (Vergara et al., 1969). As light level increases, the time from seeding to flowering of soybeans has been found to be proportionate to the level of light used to extend the natural day (Major and Johnson, 1974). Differences among cultivars must be considered, however, in establishing the minimum light requirement. Francis et al. (1970) concluded that there were three types of cultivar responses in corn: those that are insensitive to day length and light level, those that require a minimum level of 11 to 22 lux to delay flowering, and those that require a minimum level of 54 lux to delay flowering. Plant age is also a factor influencing the light level requirement. A level of 5.4 lux will prevent flowering of young Biloxi soybeans, but a higher light level is required to prevent flowering of older plants (Hamner, 1940).

Light level during the day can influence flowering and the success of hybridization. In barley, the number of days from sowing to flower initiation is linearly related to the logarithm of light level (Paleg and Aspinall, 1964). Flowers will be initiated in Biloxi soybeans in an 8-hour day provided that the light level is at least 1,076 lux (Borthwick and Parker, 1938b). Peanuts require a high light level of not less than 45% of full sunlight (Chapter 31). Potato should have at least 16 hours of light with a minimum intensity of 20 klux. Light intensity may also modify the vernalization response. Vernalization of winter broad beans is required at 18 klux, but not at 30 klux (Blondon, 1975).

Cloudiness influences light level and temperature, an effect that enhances hybridization of some species and retards hybridization of others. Flowers of sweet potato remain open longer on cloudy days than on hot,

sunny days, and hybridization of field pea is more successful when days are cool and bright than when hot, dry, and windy. Cloudy, humid weather can cause flower and pod abortion of pigeonpea. Supplemental illumination is commonly used in greenhouses to overcome low light levels during winter.

The efficiency of artificial lighting can be associated with light quality. For example, red light is at least 30 times more efficient for controlling flowering in soybean than blue light (Parker et al., 1946). Cultivars of soybean that have the *E₃* gene are sensitive to incandescent light but insensitive to fluorescent light (Buzzell, 1971), and flowering of rice is delayed slightly by green light (Kondo et al., 1942).

IV. TEMPERATURE

Temperature greatly affects development of all species, but its direct effect on floral initiation and development is highly variable among and within species. While each plant responds simultaneously to temperature and photoperiod, the degree of response to each stimulus is also variable.

The vernalization requirement for flowering of winter annuals and biennials is directly related to temperature. Temperature also is the primary factor that determines floral initiation in species with limited day-length response. Corn, for example, responds to day length for only 15 to 25 days after emergence in temperate regions, so the effect of temperature on flowering is relatively more important than that of day length (Breuer et al., 1976). The flowering and maturation of corn can be predicted by accumulating the temperatures recorded between 10 and 30 C (growing degree-days) during the growing season (Cross and Zuber, 1972).

There are critical minimum and maximum temperatures for floral initiation and development in most plants. The critical minimum for panicle differentiation of rice is 15 to 18 C (Yatsuyanagi and Takeuchi, 1959; Inouye, 1964; Noguchi and Kamata, 1965), temperatures below 21 C or above 32 C will delay floral initiation and reduce seed set of soybeans (van Schaik and Probst, 1958; Hamner, 1969), and the critical minimum and maximum temperatures for peanut flower initiation and development are 21 and 33 C, respectively (Bolhuis and de Groot, 1959).

The critical temperatures for hybridization are more restrictive than those for floral initiation and development. Cool temperatures increase the tendency for flowers to self-pollinate before they are large enough to manipulate, and coolness reduces the amount of pollen shed. On the other hand, high temperatures shorten the duration of stigma receptivity and the duration and viability of pollen. A temperature of 33 C results in low viability of peanut pollen (De Beer, 1963). Soil temperature in the podding zone is critical for development of peanuts (Ono et al., 1974); the critical minimum is 15 to 17 C, critical maximum of 37 to 39 C, and optimum of 31 to 33 C.

The response of many plants to day length is influenced by temperature. The relative importance of day and night temperatures for altering the day length response has not been the same in all studies. Manuel and Velasco (1956) found that low night temperatures hastened flowering of rice

in short days, whereas Roberts and Carpenter (1965) did not obtain separate effects of day and night temperatures. Night temperatures in controlled environments are more important than day temperatures for altering the critical photoperiod of cowpea and soybean (Parker and Borthwick, 1939b; Huxley and Summerfield, 1974), but inhibitory night temperatures probably do not occur often enough in the field to seriously affect flowering (Johnson et al., 1960).

The optimum temperature for hybridization is lower for crops adapted to temperate regions than for those adapted to the tropics. The optimum is about 19 C for potato (Chapter 34) and field pea (Chapter 23), which are cool-season crops. Hybridization of pigeonpea is successful up to 40 C (Chapter 33) and flower and seed set of pearl millet will occur between 25 and 45 C (Chapter 32).

V. MOISTURE

Adequate soil moisture is necessary to obtain vigorous plants that will have a minimum amount of flower and seed abortion. Most species and cultivars do best on soils that are well drained and have good capacity for water retention.

Species and cultivars differ in the ability to withstand excess or deficient moisture. A high percentage of flowers abort in tobacco under drought, and plants can be severely damaged or killed in 24 to 48 hours when exposed to saturated soils and high temperatures. Pearl millet does not tolerate flooding, but can be hybridized under considerable moisture stress.

Most species reduce seed production when moisture stress occurs during flowering and early seed filling. It is best to irrigate during the critical period for hybridization. If irrigation is not available, moisture stress can be reduced by providing more land area per plant and by removing excess flowers from the plant.

Soil moisture can influence seed set of species that develop fruit below ground. Optimum soil moisture content in the podding zone of peanuts is about 40% of the total soil volume in the field, regardless of soil moisture content in the rooting zone (Ono et al., 1974). Eighty to 85% of soil capacity is best for greenhouse plantings of peanut (Chapter 31).

Maturity can be hastened by reducing available water toward the end of the growing season. Some crops, such as rape, will even begin to flower again if irrigated after a dry period. If the water supply is reduced, care must be taken to ensure that the seed obtained is sufficiently large to obtain adequate viability.

Relative humidity is most important at the time of hybridization or self-pollination. There is an upper limit of relative humidity for all crops, because eventually the pollen will clump and be difficult to handle, or disease infestations may occur. When relative humidity is too high, flowers of some species can be collected and dried with a desiccant. An excessively low relative humidity can result in failure of the pollen grain to germinate on the stigma. Enclosing the stigma in its floral parts or covering the flower with a

bag may increase the relative humidity and improve the percentage of seed set.

Controlling humidity is difficult in most situations. Some growth chambers have humidity controls that can be set to the desired level and humidifying machines are available for greenhouses. Wetting the greenhouses or growth chamber floors will increase humidity.

VI. SOIL FERTILITY

Successful hybridization and seed set occur when soil fertility is maintained at a level that will sustain healthy green plants. Soil tests are useful to determine the amount of nutrients that should be added.

High N fertilization is desirable for some crop species and cultivars, but not others. Buckwheat and sweet potato produce excessive vegetative growth if soil N levels are high (De Jong, 1972). The excess vegetative growth can result in lodging, flower abortion, and delayed maturity. On the other hand, N fertilization at twice the normal rate increases seed production of tobacco.

Some species have special nutrient requirements for seed development. Peanuts require high amounts of Ca to avoid the formation of pods that are empty or contain shrivelled seeds (Chapter 31).

Restrictions on fertility and plant development are beneficial for flowering of some species. Flowering of potato is improved by placing a piece of the seed tuber on a brick and covering it with sand (Thijn, 1954). After roots from the seed tuber have penetrated the soil below the brick, the sand is washed away and tubers are removed as they are formed. Restricting root growth of sweet potato by planting in a pot can increase flowering.

VII. TECHNIQUES FOR SYNCHRONIZING FLOWERING DATES

A. Multiple Planting Dates

The most common method used to ensure the proper timing of male and female flowers is to plant on more than one date. This is particularly true when the time of flowering is not precisely known for the parents. Even when flowering dates are known, multiple planting dates can be used to increase the duration of flowering and permit the breeder to remake crosses that failed in the first attempt. When mating early and late-flowering parents, the late parent may be planted on a single date and the early parent planted on several dates thereafter.

The number of days between planting dates may not cause a corresponding change in flowering dates. A 7-day interval between planting dates may result in a 3-day or a 10-day interval between flowering dates. Reduced or increased flowering intervals are caused primarily by changes in day length and temperature that occur between planting dates. The number of days to flowering of early, midseason, and late cultivars of pigeonpea was evaluated at Hyderabad, India (17°N Lat.). Early cultivars flowered 85 days before late types when planted in July, but only 68 days earlier when both types of cultivars were planted in September (Chapter 33).

Different planting dates in the fall season have little or no effect on date of flowering for crops that require vernalization. Artificial vernalization can be used for multiple planting dates in the greenhouse or for spring planting in the field.

B. Day Length

The delay or hastening of flowering can be accomplished by manipulation of day length, as described in section III. Altering flowering date by artificial day lengths is a common practice in sugarcane, a short-day species. Early flowering is induced by decreasing the natural day length, and flowering is delayed by interrupting the dark period with light or extending the day length after floral initiation occurs naturally (Chilton and Paliatseas, 1956; Coleman, 1962; James and Miller, 1971). Cultivars of pearl millet with different day-length responses will flower simultaneously and can be hybridized under a day length of less than 12 hours (Burton and Stansell, 1971).

C. Temperature

Flowering can be manipulated by control of temperature, as described in section IV. Cool temperatures generally delay and warm temperatures hasten flowering. Excessively high temperatures can slow development of many species. Optimum temperatures for sorghum seem to be between 20 and 35 C, and flowering is delayed by temperatures outside this range. A temperature of 12 C at night results in little sorghum growth, even with optimum day temperatures (Chapter 41).

D. Plant Density

Reduced plant density encourages tillers and branches. These generally flower later than the main stem and prolong the duration of flowering of the plant. Flowers on tillers and branches, however, may be smaller and more difficult to manipulate than those on the main stem.

E. Pruning

Pruning can be used to delay or extend the flowering period. Removal of the growing point on the main stem promotes tillers and branches that flower later. In some forage species, the plants are cut back to the ground, and the secondary growth produces more flowers and seed than the first growth. Such a practice in other species could significantly reduce seed yield.

Pruning of leaves can delay flowering without damaging the main stem. The top leaves of young corn plants are sometimes destroyed by fire to delay the flowering of male plants in fields for hybrid seed production.

Removal of flowers and seed from a plant may cause it to prolong flowering. Removing all flowers each day can cause peanuts to live 240 days or more and insures that flowers will be available over a long period (Bear and Bailey, 1973). The flowering of pigeonpea can also be extended 30 to 60 days by removal of new flowers.

Girdling the stem of sweet potato can increase flowering (Edmond and Ammerman, 1971). A slanted cut is made about half way through the primary stem and a piece of wood or cardboard is wedged into the cut to prevent the stem from healing.

F. Grafting

It is possible to induce flowering of a late-flowering plant by grafting a scion of it to the stock of a plant in bloom. In soybean, a late-flowering plant introduction was grafted to a stock of an adapted cultivar that had just begun to bloom (Kiihl et al., 1977). Mature seed was obtained from the scion of the plant introduction before the nongrafted stock began to flower. The flowers on grafted scions were normal and readily used for hybridization.

In some breeding programs, potato is grafted onto tomato roots to promote flowering of difficult clones (Chapter 34). This technique increases the amount and duration of flowering and reduces the abortion of flowers before and after pollination.

G. Hormones

The flowering of plants is ultimately triggered by a hormone or a balance of hormones. This aspect of flowering is poorly understood, but has great potential in the hybridization of crop species. At present, many long-day plants can be induced to flower sooner by the addition of gibberellic acid (Thimann, 1977). Gibberellic acid may replace the vernalization requirement of *Lolium* spp. (Evans, 1969). Inducing short-day plants to flower is more difficult although some short-day plants can be induced to flower by ethylene-producing chemicals, such as chloroethane phosphonic acid. This chemical is being used commercially by pineapple growers.

VIII. CONDITIONS FOR SUCCESSFUL HYBRIDIZATION AND SELF-POLLINATION

Successful hybridization and self-pollination depend on the availability of healthy plants with an adequate number of flowers. Proper management of plants before flowering includes consideration of soil fertility, soil moisture, day length, temperature, and pest control. Both inadequate and excessive levels of soil fertility and moisture can result in plant development that is less than optimum for flower fertilization and retention. Day lengths with adequate light duration, level, and quality are of particular importance

in winter greenhouses and growth chambers. Temperatures near the optimum for the crop species should be provided whenever possible. Pest control includes elimination of weed competition and adequate management of diseases and insects.

Elimination of plant stress during flowering and the early stages of seed development will increase the chances of obtaining a high percentage of successful hybridizations and self-pollinations. An adequate moisture supply is critical, and supplemental irrigation should be available whenever possible. If moisture stress is imminent and no means are available for applying water, interplant and intraplant competition for moisture may be reduced by thinning unnecessary plants and pruning branches or tillers. Moderate temperatures and high relative humidity reduce transpiration, thereby diminishing the effect of inadequate soil moisture.

The duration of stigma receptivity and pollen viability is influenced by temperature and relative humidity. Both excessively cool or hot temperatures are unfavorable for pollination and fertilization. Cool temperatures reduce pollen shed and high temperatures shorten the duration of pollen shed and pollen viability. A reduction in relative humidity can be minimized by enclosing the stigma in the floral covering or by covering it with a bag.

IX. TECHNIQUES FOR RAPID SEED PRODUCTION

Rapid production of hybrid and self-pollinated seed can reduce the length of time required to develop a new cultivar. However, shortening the life cycle by manipulation of the environment will reduce seed yield per plant. It also may reduce flower size and increase cleistogamy, thereby limiting such techniques to the production of self-pollinated seed.

Dormancy and vernalization are survival mechanisms common to some species, and these can be overcome artificially. Seed of species that are difficult to germinate because of a hard seed coat should be scarified before seeding. Other types may require more specialized treatments to overcome dormancy. Wild rice must have the pericarp removed from around the embryo, hop needs a chilling period of 5 to 8 weeks, and some rye cultivars need an afterripening period of about 20 days. In some cases, the afterripening period can be overcome chemically with potassium nitrate or gibberellic acid (Spicer and Dionne, 1961).

Treatment of germinating seeds or seedlings in growth chambers at temperatures of 2 to 5 C will substitute for natural vernalization or overcome the biennial nature of a species. In winter wheat, exposure to 2 to 5 C in short days for 8 weeks is the most effective way of meeting the vernalization requirement (Grant, 1964). Sugarbeet is a biennial and the shortest life cycle occurs when it is exposed to 4 to 7 C for about 10 weeks during floral induction (Gaskill, 1952).

Continuous light is the most suitable method of reducing the time to flowering of long-day plants. Short day lengths promote development of short-day plants, but the actual day length used will depend on the optimum photoperiod. For plants of tropical origin, an 8-hour day may be most suitable. The use of an 8-hour day in Puerto Rico reduced the days from plant-

ing to flowering of pigeonpea by 4 months in medium maturity cultivars and 7 weeks in late cultivars (Chapter 33). A 12-hour day may be adequate for crops adapted to more temperate regions.

The temperatures most suitable for rapid seed production generally vary from about 25 to 35 C, depending on whether it is a cool or warm-season crop. Some species, such as pigeonpea or pearl millet, will develop most rapidly at temperatures above 35 C.

Moisture stress may be used to reduce the time taken from flowering to maturity, but stress should not be used until the developing seeds are well established and will not abort.

Soil fertility should be limited to the amount needed to produce a small plant with a few seeds. Nitrogen stress during the seed-filling period will result in smaller, earlier-maturing seeds. Phosphorus tends to have the opposite effect to N, so a liberal application of P may also hasten maturity.

High population densities often appear to hasten maturity, but this is probably the result of fertility and moisture stresses that occur late in the seed-filling period. With excess fertility and moisture, increased population density may actually delay maturity.

Most crops harvested for their seed have been selected for large seed. The embryos of such seed may reach maturity long before maximum seed dry weight is reached. Thus it may be possible to harvest seed 10 to 15 days after the linear phase of seed filling has begun. The seed may be small and shrivelled, but may still have excellent viability. When this procedure is followed, it is advisable to cut the entire plant and dry it in the field or the greenhouse. This method essentially imposes severe moisture stress, and curing the whole plant allows some translocation of sugars and minerals into the seed during the drying period.

REFERENCES

- Banks, D. J. 1976. Peanuts: germplasm resources. *Crop Sci.* 16:499-502.
- Bear, J. E., and W. K. Bailey. 1973. Effect of seed treatment and germination on seed dormancy of peanuts, *Arachis hypogea*. *J. Am. Peanut Res. Educ. Assoc.* 3:122-126.
- Best, R. 1961. Some aspects of photoperiodism in rice (*Oryza sativa* L.). Elsevier Publishing Co., N.Y. 87 p.
- Bickford, E. D., and S. Dunn. 1972. Lighting for plant growth. The Kent State Univ. Press, Kent, Ohio.
- Blondon, F. 1975. Les exigences pour la floraison de trois lignes de *Vicia faba* L. (feverole). *C. R. Acad. Agric.* 61:1068-1081.
- Bolhuis, G. G., and W. de Groot. 1959. Observations on the effect of varying temperatures on the flowering and fruit set in three varieties of groundnut. *Neth. J. Agric. Sci.* 7:317-326.
- Borthwick, H. A., and M. W. Parker. 1938a. Effectiveness of photoperiodic treatments of plants of different age. *Bot. Gaz.* 100:245-249.
- , and ———. 1938b. Photoperiodic perception in Biloxi soybeans. *Bot. Gaz.* 100:374-387.
- Breuer, C. M., R. B. Hunter, and L. W. Kannenberg. 1976. Effects of 10- and 20-hour photoperiod treatments at 20 and 30 C on rate of development of a single-cross maize (*Zea mays*) hybrid. *Can. J. Plant Sci.* 56:795-798.

- Burton, G. W., and J. R. Stansell. 1971. An automatic darkbox to induce flowering in short-day plants in midsummer. *Crop Sci.* 11:595-596.
- Buzzell, R. I. 1971. Inheritance of a soybean flowering response to fluorescent-day-length conditions. *Can. J. Genet. Cytol.* 13:703-707.
- Chilton, S. J. P., and E. D. Paliastseas. 1956. Studies on the flowering of sugar cane. *Proc. Int. Soc. Sugar Cane Technol.* 9:652-656.
- Chouard, P. 1960. Vernalization and its relations to dormancy. *Annu. Rev. Plant Physiol.* 11:191-238.
- Coleman, R. E. 1962. Control of flowering and the use of pollen storage as techniques in a sugar cane breeding programme. *Proc. Int. Soc. Sugar Cane Technol.* 11:553-540.
- Cross, H. Z., and M. S. Zuber. 1972. Prediction of flowering dates in maize based on different methods of estimating thermal units. *Agron. J.* 64:351-355.
- De Beer, J. F. 1963. Influences of temperature on *Arachis hypogea* L. with special reference to its pollen viability. *Versl. Landbouwk. Onderz. (Wageningen)* N.R. 69.2:1-81.
- De Jong, H. 1972. Buckwheat. *Field Crop Abstr.* 25:389-396.
- Edmond, J. B., and G. R. Ammerman. 1971. Sweet potatoes: Production, processing, marketing. AVI Publishing Co., Westport, Conn.
- Evans, L. T. 1969. The induction of flowering. MacMillan and Co., N.Y.
- Francis, C. A., D. Sarria V, D. D. Harpstead, and C. Cassalet D. 1970. Identification of photoperiod insensitive strains of maize (*Zea mays* L.). II. Field tests in the tropics with artificial lights. *Crop Sci.* 10:465-468.
- Gaskill, J. O. 1952. A new sugarbeet breeding tool—two seed generations in one year. *Agron. J.* 44:338.
- Gott, M. B., F. G. Gregory, and O. N. Purvis. 1955. Studies in vernalisation of cereals. XIII. Photoperiodic control of stages in flowering between initiation and ear formation in vernalised and unvernalsed Petkus winter rye. *Ann. Bot. (Lond.)* 19:87-126.
- Grant, M. N. 1964. Vernalization and days to anthesis of winter wheat under controlled temperature and light. *Can. J. Plant Sci.* 44:446-450.
- Griffiths, D. J. 1961. The influence of different daylengths on ear emergence and seed setting in oats. *J. Agric. Sci.* 57:279-288.
- Guitard, A. A. 1960. The influence of variety, temperature, and stage of growth on the influence of spring barley to photoperiod. *Can. J. Plant Sci.* 40:65-80.
- Hamner, K. C. 1940. Interrelation of light and darkness in photoperiodic induction. *Bot. Gaz.* 101:658-687.
- . 1969. *Glycine max* (L.) Merrill. p. 62-89. In L. T. Evans (ed.) The induction of flowering; some case histories. Cornell Univ. Press, Ithaca, N.Y.
- Hunter, R. B., L. A. Hunt, and L. W. Kannenberg. 1974. Photoperiod and temperature effects on corn. *Can. J. Plant Sci.* 54:71-78.
- Huxley, P. A., and R. J. Summerfield. 1974. Effects of night temperature and photoperiod on the reproductive ontogeny of cultivars of cowpea and of soyabean selected for the wet tropics. *Plant Sci. Lett.* 3:11-17.
- Inouye, J. 1964. Effect of temperature on flower bud initiation and fruiting of rice plants grown on artificial culture medium. *Proc. Crop Sci. Soc. Jpn.* 32:330-332.
- James, N. I., and J. D. Miller. 1971. Photoperiod control in the USDA sugar cane crossing program. *Proc. Int. Soc. Sugar Cane Technol.* 14:341-347.
- Johnson, D. R., and J. W. Tanner. 1972. Calculation of the rate and duration of grain filling in corn (*Zea mays* L.). *Crop Sci.* 12:485-486.

- Johnson, H. W., H. A. Borthwick, and R. C. Leffel. 1960. Effects of photoperiod and time of planting on rates of development of the soybean in various stages of the life cycle. *Bot. Gaz.* 122:77-95.
- Khatri, M. I. 1964. Photoperiodic and vernalization studies in New Zealand wheat. *Pak. J. Sci.* 16:307-311.
- Kiihl, R. A. S., E. E. Hartwig, and T. C. Kilen. 1977. Grafting as a tool in soybean breeding. *Crop Sci.* 17:181-182.
- Kondo, M., A. Terasaka, and M. Umino. 1942. Experimental studies on photoperiodism in rice (III). *Nogaku Kenkyu* 33:1-24.
- Major, D. J., and D. R. Johnson. 1974. Effect of light intensity on the development of field grown soybeans. *Crop Sci.* 14:839-841.
- , ———, and V. D. Luedders. 1975a. Evaluation of eleven thermal unit methods for predicting soybean development. *Crop Sci.* 15:172-174.
- , ———, J. W. Tanner, and I. C. Anderson. 1975b. Effects of daylength and temperature on soybean development. *Crop Sci.* 15:174-179.
- Manuel, F. C., and J. R. Velasco. 1956. Further observations on the photoperiodic response of *Elon-elon* rice. *Philipp. Agric.* 40:421-432.
- Miller, F. R., D. K. Barnes, and H. J. Cruzado. 1968. Effect of tropical photoperiods on the growth of sorghum when grown in 12 monthly plantings. *Crop Sci.* 8:499-502.
- Nagata, T. 1958. Studies on the flowering and fruiting of summer vs. autumn soybean types. *Proc. Crop Sci. Soc. Jpn.* 27:87-90.
- Noguchi, Y., and E. Kamata. 1965. Studies on the control of flower bud formation by temperature and daylength in rice plants. V. Response of floral induction to temperature. *Jpn. J. Breed.* 15:86-90.
- , T. Nakajima, and T. Yamaguchi. 1967. Studies on the control of flower bud formation by temperature and daylength in rice plants. VII. Elimination of photoinductive effects by keeping under long-day conditions. *Jpn. J. Breed.* 17:20-24.
- Ono, Y., K. Nakayama, and M. Kubota. 1974. Effects of soil temperature and soil moisture in podding zone on pod development of peanuts. *Proc. Crop Sci. Soc. Jpn.* 43:247-251. [English summary.]
- Ormrod, D. P. 1963. Photoperiodic sensitivity of head differentiation, culm elongation, and heading in some spring wheat and spring barley varieties. *Can. J. Plant Sci.* 43:323-329.
- Paleg, L. G., and D. Aspinall. 1964. Effects of daylength and light intensity on growth of barley. II. Influence of incandescent light on apical development. *Bot. Gaz.* 125:149-155.
- Parker, M. W., and H. A. Borthwick. 1939a. Effect of photoperiod on development and metabolism of the Biloxi soy bean. *Bot. Gaz.* 100:651-689.
- , and ———. 1939b. Effect of variation in temperature during photoperiodic induction upon initiation of flower primordia in Biloxi soy beans. *Bot. Gaz.* 101:145-167.
- , S. B. Hendricks, H. A. Borthwick, and N. J. Scully. 1946. Action spectrum for the photoperiodic control of floral initiation of short-day plants. *Bot. Gaz.* 108:1-26.
- Polson, D. E. 1972. Day-neutrality in soybeans. *Crop Sci.* 12:773-776.
- Quinby, J. R. 1972. Influence of maturity genes on plant growth in sorghum. *Crop Sci.* 12:490-492.

- Rawson, H. M., and L. T. Evans. 1971. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. *Aust. J. Agric. Res.* 22:851-863.
- Roberts, E. H., and A. J. Carpenter. 1965. The interaction of photoperiod and temperature on the flowering response of rice. *Ann. Bot. (Lond.)* 29:359-364.
- Rood, S. B., and D. J. Major. 1981. Diallel analysis of the photoperiodic response of maize. *Crop Sci.* 21:875-878.
- Sasamura, S. 1960. Studies on the relation between the plant age and the degree of sensibility to short day length in the late paddy rice variety Zuiho. *Proc. Crop Sci. Soc. Jpn.* 28:355-358.
- Spicer, P. B., and L. A. Dionne. 1961. Use of gibberellin to hasten germination of *Solanum* seed. *Nature (Lond.)* 189:327-328.
- Takimoto, A., and K. Ikeda. 1961. Effect of twilight on photoperiodic induction in some short day plants. *Plant Cell Physiol.* 2:213-229.
- Thijn, G. A. 1954. Observations on flower induction with potatoes. *Euphytica* 3: 28-34.
- Thimann, K. V. 1977. Hormone action in the whole life of plants. Univ. of Massachusetts Press, Amherst.
- van Schaik, P. H., and A. H. Probst. 1958. Effects of some environmental factors on flower production and reproductive efficiency in soybeans. *Agron. J.* 50: 192-197.
- Velasco, J. R., and F. C. Manuel. 1955. The photoperiodic response on Elon-elon rice. *Philipp. Agric.* 39:161-175.
- Vergara, B. S., T. T. Chang, and R. Lilis. 1969. The flowering response of the rice plant to photoperiod. A review of the literature. *Int. Rice Res. Inst. (Los Banos) Tech. Bull.* 8.
- , and R. Lilis. 1966. Studies on the responses of the rice plant to photoperiod. II. Effect of the number of photoinductive cycles on a seasonal rice variety BPI-76. *Philipp. Agric.* 50:9-14.
- , and ———. 1968. Responses of the rice plant to photoperiod. III. Effect of different photoperiods after panicle initiation on the emergence of the panicle. *Philipp. Agric.* 52:61-65.
- , S. Puranabhavung, and R. Lilis. 1965. Factors determining growth duration of rice varieties. *Phyton Rev. Int. Bot. Exp.* 22:177-185.
- Yatsuyanagi, S., and T. Takeuchi. 1959. Ecological studies of rice variety. III. The problem of the temperature and the efficiency during the generative growth period. *Proc. Crop Sci. Soc. Jpn.* 18:164-168.