6 Crop Developmental Responses to Temperature, Photoperiod, and Light Quality

The development of plants can be influenced by temperature (i.e., the rate of production of nodes), by either heat units or photoperiod (i.e., the triggering of flowering), and by light quality. *Development* should be distinguished from *growth*, which involves increase in mass, length, volume, or area of a plant or organ. The life cycle of adapted plants is synchronized with the seasonal changes in average weather (climate) through affects of photoperiod and/or temperature on development that result in an optimal phenology (Bunting, 1975). Phenology is the sequence of developmental events during the plants' life cycle as it is determined by environmental conditions. Annual crop plants are sown when the environment permits effective germination, emergence, and establishment. Adapted cultivars grow vigorously and then flower on an optimal date, enabling them to produce fruit and/or seed during a period of the year when average environmental conditions permit the plant to produce many fruit and/or seed of good quality. Bunting (1975) provides examples from England and West Africa of how plant breeders and agronomists have developed cultivars and management methods that enable annual crops to have an optimal phenology with respect to the timing and duration of their period of reproductive development such that it fits the available season and results in maximum productivity. Clearly, when breeding improved cultivars, it is important to be able to predict their dates of flowering and harvest, and methods have been developed for making these predictions.

HEAT-UNIT SYSTEMS FOR PREDICTING PLANT DEVELOPMENT

Heat-unit systems are empirical approaches used to predict the rate of development of plants (or insects) where the process and genotype are insensitive to photoperiod. They may be used to predict dates of flowering or harvest or the locations and dates

where a particular fruit quality can be achieved, such as with citrus or grapes. An example is presented of the development of a heat-unit system for predicting date of flowering of an annual plant, which includes an interaction with genotypic heat tolerance and photoperiod.

1. Sow the cultivar at different dates and in different locations to provide different but reasonable (effective for commercial production) thermal regimes during the vegetative period.
2. Record dates of sowing and first flowering.
3. Measure daily (24 hour) maximum (T_{max}) and minimum (T_{min}) air temperatures in a standard weather station shelter at each location.
4. Analyze the data by plotting average rate of development $1/D$, where D is the number of days from sowing to flowering, versus average daily temperature = $[\Sigma(T_{max} + T_{min})/2]/D$ over the period from sowing to flowering (Figure 6.1). Where the curve is linear, with an acceptable correlation coefficient, this indicates that rate of development can be modeled as being proportional to degrees average air temperature above a base temperature (T_{base}). The projected intercept on the x axis is T_{base} and, for the cowpea data in Figure 6.1, it is 8.5°C. The inverse of the slope of the line is the total heat unit (degree-days) for the process as described by Equation (6.1) and in Figure 6.1 it is 734°C day.

$$\text{Heat units} = \sum_{i=D}^{i=1} \frac{T_{max} + T_{min}}{2} - T_{base} \qquad (6.1)$$

where T_{max} and T_{min} are daily data from sowing to first flowering, and T_{base} is a constant for a particular cultivar and developmental process. The heat-unit value should be effective for predicting the number of days from sowing to flowering of the specific cultivar in the range of environments over which the model was developed, as long as average daily air temperatures do not exceed threshold values (T_t). Where average daily air temperatures exceed threshold values, the model may be modified by including an algorithm stating that for $T > T_t$, $T = T_t$. This modification assumes that $1/D$ becomes constant once T exceeds T_t, which is approximately consistent with the data in Figure 6.1. For the example presented in Figure 6.1, however, it would be necessary to have two different threshold values for the different types of cultivars. The heat-susceptible cowpea lines exhibited a lower T_t, because their floral bud development was suppressed by high temperatures, whereas the floral bud development of the heat-tolerant lines was not affected as much by these high temperatures. Note that the experiments of Figure 6.1 were conducted under long-day conditions. Under the short-day conditions that prevail in many environments near the equator, the floral bud development of cowpea is not suppressed by high temperatures (Dow el-madina and Hall, 1986), and Equation (6.1) can be used with no modifications needed based on upper threshold temperatures for all of the cowpea lines described in Figure 6.1. Other effects of photoperiod on photoperiod-sensitive plants are described later in this chapter.

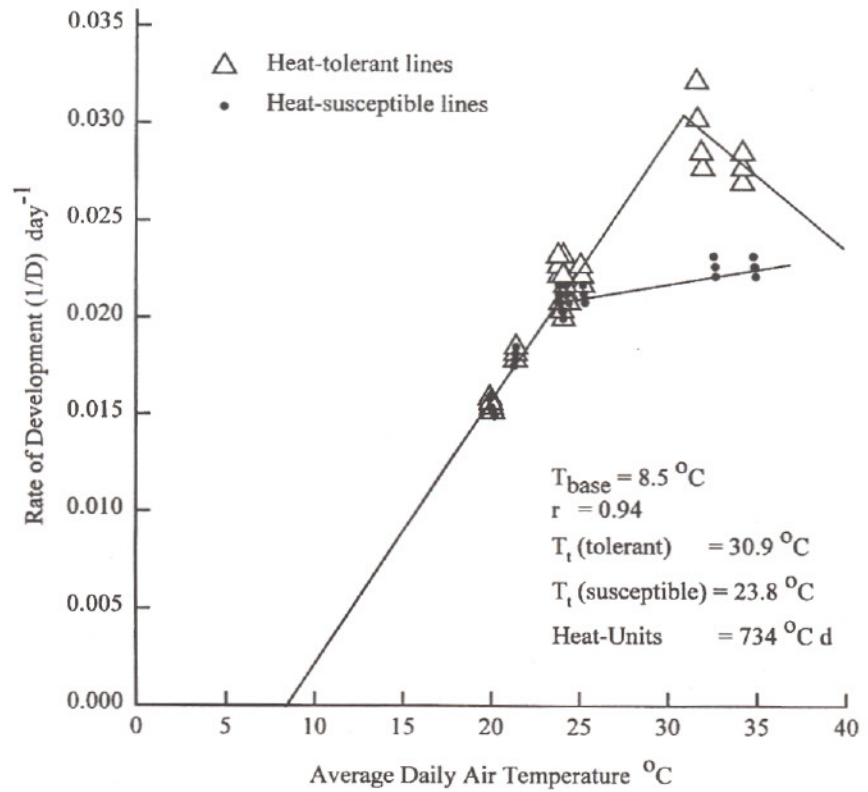

FIGURE 6.1 Rate of development (1/D) of heat-tolerant and heat-susceptible cowpea lines, where D is the period between sowing and first flowering as a function of average air temperature. The heat-unit and r values are based on the linear part of the curve. Ismail, A.M., and A.E. Hall, Positive and potential negative effects of heat-tolerance genes in cowpea. *Crop Sci.* 38: 381–390.

Heat-unit values can differ between different cultivars and developmental processes, but the T_{base} values tend to be similar for different cultivars and developmental processes but different for different types of species. For example, cool-season species such as pea have T_{base} values of about 4°C, whereas warm-season species, such as sweet corn and cowpea have T_{base} values of 8 to 10°C.

Heat-unit systems are used to guide the commercial production of annual crops that are suitable for market only over a few days, i.e., fresh sweet corn or peas for freezing. If the objective with sweet corn is to supply a major market, such as July 4th in the United States, the cultivar used and sowing date must be chosen such that the crop is ready for market just before July 4th. By using average daily air temperature data and working backward in time, it is possible to predict the combination of cultivar (heat-unit requirement and T_{base}) and sowing date that will produce a crop that is ready for harvest on, say, July 2nd. (Note that the actual temperatures during the cropping season probably will differ from the climatic average and that the soil

must be warm enough at sowing to permit emergence as discussed in Chapter 5.) For producing packets of frozen peas and other crops, it is necessary to achieve a continuous flow of fresh produce from farms to the processing factory. This can be done by choosing cultivars with different heat-unit requirements from sowing to the date when crop quality is optimal, and sowing on different dates and in regions with different thermal regimes.

The heat-unit system described by Equation (6.1) has been used to define climatic zones for growing different varieties of grapes for different end-uses in California. In this case, a base temperature of 10°C is used, and the heat units are obtained by summing average degree-days over the growing season from April 1st through October 31st. Cooler zones with a specific small number of degree-days are useful for producing good dry wines; hotter zones with more heat units can produce sweeter wines; and the hottest zones, with even more heat units, are effective for producing table grapes or raisins. Different citrus scions have different heat-unit requirements for producing high-quality fruit. For example, most grapefruit cultivars require more heat units than oranges, except that two new grapefruit cultivars (*Citrus* sps.) have been developed, Oroblanco and Melogold, that have heat-unit requirements for fruit development similar to those of Navel oranges.

Different types of heat-unit systems have been used. In some cases, it is assumed that the diurnal curve of air temperature is a sinewave, and average temperature is determined based on this assumption. The overall objective is to develop an empirical method that is effective in predicting the specific developmental process in a particular commercial production region using available weather station data. Some different heat-unit models are described on the web site www.ipm.ucdavis.edu.

CHILLING REQUIREMENTS OF PLANTS

Optimal development of some plants requires that they experience chilling. For example, deciduous trees can require chilling during winter to overcome bud dormancy. Insufficient chilling results in delayed foliation. A tree may have a small tuft of leaves near the tips of the stems and be devoid of leaves for 30 to 50 cm below the tips. Lower buds may break eventually, and substantial suckering can occur from lower parts of the tree. Bloom can be delayed, and the flowers can be abnormal, so that fruit set is reduced. To avoid these problems, deciduous tree species and cultivars must be chosen whose chilling requirements will be met in the environment where they are to be grown. The physiologically effective temperatures are between 1 and 12°C but, in earlier years, chilling requirements of different varieties were defined on the basis of the number of hours experienced with air temperatures <7°C. More effective models have been developed such as one based on the hours when air temperatures were between 0 and 7°C or the more complex Utah Model, which includes negative effects on chilling units of high temperatures. Average chilling units for different locations in California for November 1st through March 31st are presented in the web site of the Fruit & Nut Research and Information Center at the University of California, Davis (www.fruitsandnuts.ucdavis.edu), which were calculated using all three models. Chilling requirements of different cultivars can be

found at the same web site. Average chilling requirements of different species rank as follows: apples > cherries > peaches. But new cultivars have been developed that have much lower chilling requirements than the traditional cultivars of a species. For example, Fuji and Gala cultivars of apple are commercially successful in warm subtropical zones such as near Bakersfield, California (Figure 10.3), whereas traditional apple cultivars are successful in temperate zones such as the Yakima Valley of Washington (Figure 5.6) and in England (Figure 10.14).

Winter-type cereals (e.g., winter wheat) are sown in the fall in temperate zones, because they require several weeks of chilling (vernalization) if they are to produce flowers in the spring, whereas spring wheat does not require any chilling. It should be noted that, in some cases, there is confusion in the labeling of wheat cultivars in that some that are labeled as being "winter wheats" do not have a chilling requirement.

Some biennials, such as sugar beet, carrots, and celery, have a chilling requirement for flowering. Sugar beet is sown as seed in the first year and, in appropriate commercial production environments, it produces a storage root that is harvested and sent to factories for the extraction of sucrose. If the root is left in the ground and experiences chilling during the winter, it will produce a flowering stem as the days become longer in the following spring. Sometimes, there is a problem in fields where sugar beet is being grown to produce roots for sucrose if plants experience too much chilling during the seedling stage. In this case, some plants produce both a storage root and a flowering stem (bolting) during the first year. This is a problem, because the hard, woody, flowering stem interferes with harvesting machinery. A solution to this problem is to breed sugar beet cultivars that have a higher chilling requirement such that they do not bolt during the first season when they are producing a storage root. In temperate zones (e.g., Figure 10.14), sugar beet cultivars with resistance to bolting can be sown earlier and thus reach full canopy development sooner in the season and have a more optimal phenology (Bunting, 1975).

Chilling during the winter season can be beneficial for orange production in that it results in fruit having more of the carotenoids and less of the chlorophylls such that they have a bright orange color that is favored on the fresh market. In contrast, oranges produced in warmer more tropical environments can have a yellow/green appearance, and those not sold on local markets are mainly sold on commercial juice markets, which have much lower prices than fresh fruit markets. Sometimes, mature Valencia oranges are kept on trees in California into the summer while waiting for a suitable market. During this period, chlorophyll returns to the rind, and carotenoid content decreases, changing fruit color from a bright orange to a more yellowish green, which reduces their appeal to consumers. Another advantage of chilling during the winter season is that it induces a quasi-dormancy, which results in a concentrated spring bloom and thus a short period when there are many mature fruit on the trees, which facilitates picking. In contrast, in more tropical environments, oranges tend to be ever-bearing, producing small amounts of fruit during different periods of the year. This ever-bearing is good for trees used for home consumption but is not suited to commercial production, because it requires substantial labor for harvesting. Information on the extent of chilling in different parts of California is provided at the following web site: www.ipm.ucdavis.edu.

PLANT DEVELOPMENTAL RESPONSES TO PHOTOPERIOD

Some developmental responses of some cultivars of some species are influenced by photoperiod. This usually is considered as a response to day length, although the mechanism appears to involve the length of the night. Where photoperiod determines the date of flowering, it also determines the node at which flowering first occurs. These photoperiod-sensitive cultivars can begin flowering at different nodes, depending on their date of sowing and the prevailing photoperiods. In contrast, the development of cultivars that are insensitive to photoperiod (day-neutral cultivars) is determined by heat units. For all cultivars, the rate at which nodes appear is positively correlated with the average temperature (above a baseline temperature), and day-neutral cultivars produce their first flowers at the same node even with different temperatures and photoperiods.

Effective day length is defined as the period between sunrise and sunset plus twilight of about 26 minutes, because the twilight does influence plant photoperiod responses. Effective day length changes with season and latitude. More extreme latitudes have longer days in summer and shorter days in winter (Figure 6.2). In the northern hemisphere, the longest day occurs at the summer solstice, on about June 22nd (day 173), and the shortest day occurs on the winter solstice on about December 22nd (day 356). Effective day length is about 12.5 hours on the equinoxes [about March 21 (day 80) and September 24 (day 267)] and year round at the equator.

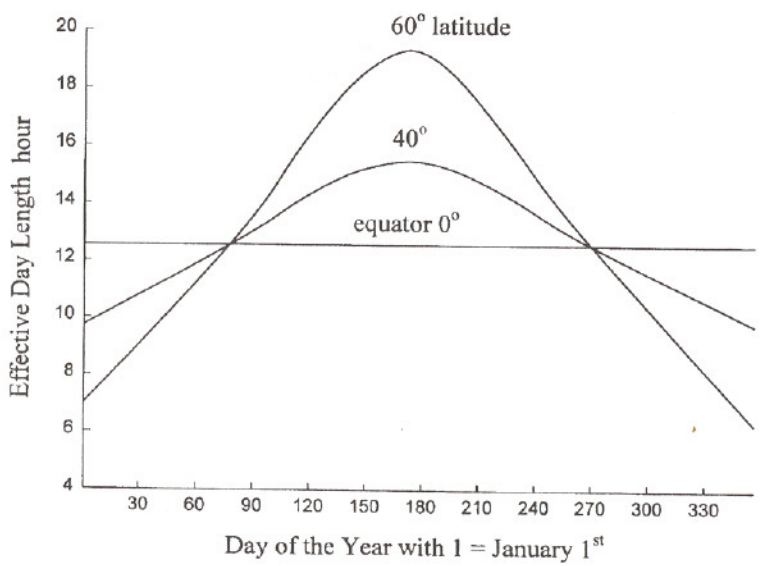

FIGURE 6.2 Day length in hours between sunrise and sunset plus 26 minutes of twilight for the equator and two locations with different latitudes in the northern hemisphere at different days of the year.

Generally, there are larger seasonal changes in both photoperiod and temperature at more extreme latitudes, which led some scientists to believe that plant responses to photoperiod may be more prevalent at extreme latitudes. However, adaptively significant responses to photoperiod occur with some cultivars of sorghum at latitudes not far from the equator (e.g., 10°), where the changes in day length are small (Bunting, 1975).

The aspect of photoperiod that determines the first flowering of different types of crops may be understood by considering the annual cycle of cropping in a subtropical zone at 34°N latitude (Figure 6.3). A photoperiod-sensitive cool-season annual that is sown in early winter would be induced to flower during the lengthening days of spring. In contrast, a photoperiod-sensitive warm-season annual that is sown in late spring would be induced to flower during the shortening days in the late summer. This leads to the following definitions.

- *Cool-season annuals* that are sensitive to photoperiod begin flowering when photoperiods become longer than a critical value. They are called LD (longer day) plants and include some wheat cultivars.
- *Warm-season annuals* that are sensitive to photoperiod begin flowering when photoperiods become shorter than a critical value. They are called SD (shorter day) plants and include most soybean cultivars and some tropical cowpea, sorghum, and rice cultivars.

The strength of the photoperiod effect varies among cultivars. For some cultivars, the photoperiod effect is *obligate*, and the plant will remain vegetative until it receives the appropriate photoperiod. For most photoperiod-sensitive cultivars, the photoperiod effect is *quantitative*, in that the plant will flower under noninductive photoperiods, but it begins flowering later. In this case, the photoperiod trigger can cause flowering to occur earlier.

In addition to flowering, several other developmental processes are influenced by photoperiod including: tuber formation, bulb formation, runner formation, and the formation of dormant buds in deciduous trees that occurs in the fall.

Day-neutral annuals exhibit no effect of photoperiod on the time at which flowering occurs. They begin flowering at a fixed nodal position, and their time of flowering is determined by heat units. This group includes many important agricultural crops: virtually all cultivars of cucumber, sweet corn, tomato, and pea; modern cultivars of cotton, maize, and spring wheat; and some cultivars of rice, sorghum, and cowpea that are grown in subtropical zones.

The photoperiod-induced developmental responses have some adaptive significance. For cool-season annuals in a Mediterranean climate (Figures 10.4 and 10.6) the LD trigger results in seed maturation prior to the hot and dry weather of the early summer. In contrast, for warm-season annuals, such as soybean, in temperate (Figure 5.5) or subtropical (Figure 5.4) climatic zones, the SD trigger results in seed maturation prior to cold weather in the fall. For warm-season annuals in tropical semi-arid zones (Figure 10.8), the SD trigger can result in seed maturation prior to the extreme droughts of the dry season. These responses are less important in agriculture than in natural conditions. When using day-neutral cultivars, farmers can

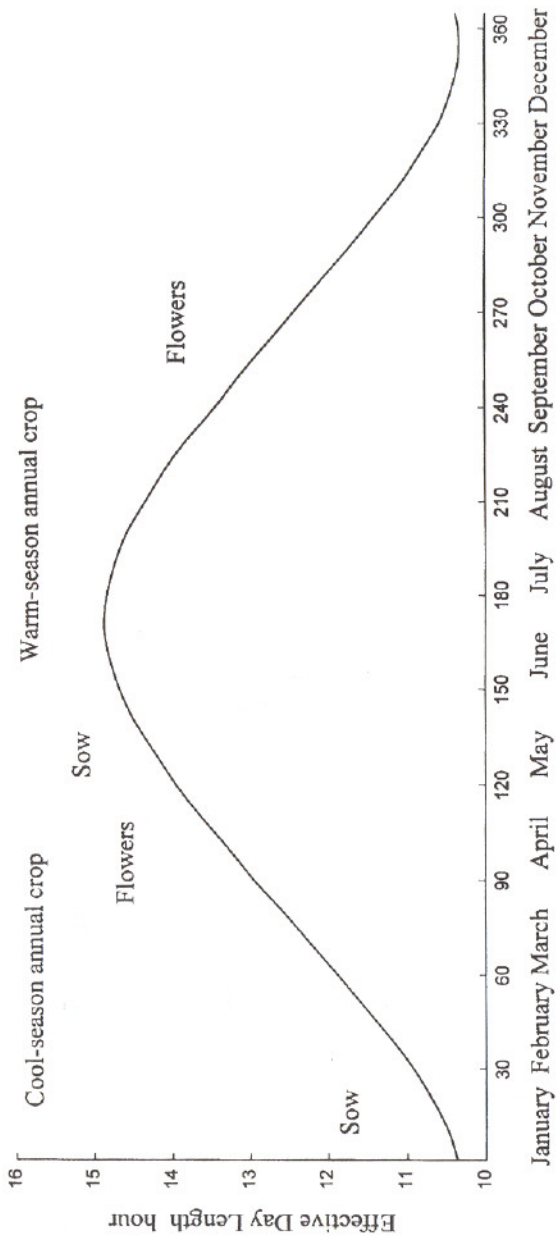

FIGURE 6.3 Effective day length throughout the year at Riverside, California, U.S.A. (location 33°58'N, 117°21'W). Dates of sowing and first flowering are indicated for a cool-season annual crop and a warm-season annual crop.

control the date of flowering simply by either varying the sowing date or choosing a cultivar with a different heat-unit requirement. For some deciduous trees, such as those being grown in temperate zones (Figures 5.6 and 10.14), an SD response in the fall can result in the formation of dormant buds that have substantial resistance to the cold weather of the winter. Some types of outdoor artificial lighting can disturb this response and reduce the adaptation of the trees.

Photoperiod-sensitive cultivars of annual crops often are adapted to only a narrow range of latitudes. With changes in latitude, day lengths change, and seasonal temperatures change in a manner that does not favor broad adaptation of a single photoperiod-sensitive cultivar. There are different types of solution to this problem. Traditional cultivars of maize were SD types that were adapted to the low latitudes found in Central America. They were not well adapted to some environments in the United States, because they flowered too late and were damaged by chilling during the grain production stage. The same problem occurs with SD cultivars of cowpea and grain sorghum from tropical Africa when they are grown in the Central Valley of California. The solution in these cases involved the development of day-neutral cultivars with relatively low heat-unit requirements for flowering so that they mature before the onset of cool weather in the fall. Cool-season annuals with a LD requirement also can exhibit narrow adaptation. For example, some wheat cultivars have a LD requirement for flowering that confers adaptation in climatic zones around the Mediterranean Sea. At high elevations near the equator, temperature conditions are suitable for growing wheat, but cultivars with an obligate LD requirement do not flower. In this case also, the solution involved the development of day-neutral cultivars.

In contrast, modern soybean cultivars have an SD requirement for flowering. Individual cultivars flower at similar dates when they are sown at different dates, and they are adapted to a narrow range of latitudes. At more extreme latitudes, they tend to flower too late and become damaged by chilling temperatures during grain development. When grown near the equator, they can be triggered to flower too early by the short days, and the plants are too small when entering the reproductive stage and produce small grain yields. The solution to this problem involved the development of many different types of soybean cultivars with different photoperiod responses for commercial production in regions with different latitudes. The problem with this solution is that it has required a substantial investment by society in soybean breeding programs. Large investments are now being required as genetic engineering is being used to incorporate genes to confer traits, such as herbicide resistance and resistance to insect pests, because it must be done with many different types of soybean cultivars. A potential advantage of the large numbers of cultivars is that the soybean crop may be less likely to suffer large-scale damaging effects from disease epidemics than crop species where a few cultivars with similar genetic background are grown over very large areas. For example, the maize crop in the United States in 1970 suffered from an epidemic caused by a "new" strain of the fungi that causes corn leaf blight, which reduced grain yield by about 50% in some southern states and 15% nationwide. At that time, most of the cultivars of maize used in the United States had the same "Texas" cytoplasm that had been used to confer male sterility that facilitated the breeding of hybrid cultivars. All cultivars

with the "Texas" cytoplasm were susceptible to the "new" fungal strain that causes corn leaf blight.

Multiple seasons of cropping are possible with warm-season annuals in the tropics because of the year-round warm to hot temperatures. Traditional tropical cultivars of rice were only grown in the rainy season and were SD types. With the availability of irrigation, it became possible to grow three crops of rice per year on the same field. In some cases, this required the development of day-neutral cultivars of rice for growing in the dry season. Growing the same crop species season after season or year after year on the same field usually is not sustainable because of the buildup of soil pests and diseases and specific weeds. For rice, this practice may be effective (Dobermann et al., 2000) and may be needed in those areas where the density of the human population is too high in relation to the area of arable land that is available for producing food.

There are cases where flowering causes agronomic problems and must be prevented. One case is where annual legumes are grown as green manure or forage crops. Cultivars of cowpea are being developed for use as green manure crops in the United States. They have extreme sensitivity to photoperiod (they are SD types) and, when sown in June, they grow actively, without flowering, until September, when they are incorporated to enrich the fertility of the soil. The advantage of this phenology is that the plants abundantly fix atmospheric nitrogen for a longer period compared with cowpea cultivars that initiate reproductive activity early, because nitrogen fixation rate decreases when plants produce many pods. Commercial supplies of seed of these SD cowpea cultivars can be produced by sowing them in mid August in a location with a hot fall season, such as the Coachella Valley in California, which has a similar climate as the location in Figure 10.2. In this valley, day lengths become shorter than the critical photoperiod in late September and trigger flowering, and the temperatures are warm enough until mid November to enable the crop to produce adequate yields of seed.

Another case where flowering can be detrimental is where sugar cane is being grown for commercial sucrose production. Some cultivars of sugar cane tend to begin flowering if grown for two years in some locations, such as Hawaii. This is undesirable, because flowering causes decreases in sucrose concentration in the cane. These sugar cane cultivars are SD types. The first method used to prevent flowering was to install large lights in the field and turn them on to lengthen the day. This was effective but used too much electricity. The next method used was based on the idea that it is the length of the night not the length of the day that determines the photoperiod response. This method consisted of turning the search lights on for a period in the middle of the night. This also was effective and used less electricity. Subsequently, effective results were obtained using sprays of a herbicide that destroys the apical meristem and prevents flowering and its detrimental effects. The most effective solution is to breed sugar cane cultivars that do not flower in the commercial production regions.

Floriculturists, plant breeders, and scientists often wish to achieve year-round production of flowers by annual plants growing in greenhouses. For day-neutral plants, it is simply necessary to maintain optimal temperatures in the greenhouses. For photoperiod-sensitive plants, special procedures must be used. I will provide an

example of procedures that can be effective with an SD annual plant. First, it is necessary to achieve a vegetative period of adequate duration. If the day lengths are longer than the critical value, this will happen naturally. If the day lengths are shorter than the critical value, the plants may begin flowering too soon when they are very small. In this case, supplemental lighting must be used to either lengthen the day or, more practically, to shorten the night with night-break lighting. This consists of providing 2 to 5 hours of low intensity light [5 to 50 watts (input electricity) per m^2 of bench]. It also is necessary to induce flowering at appropriate times. If the day length is shorter than the critical value, this will occur naturally. If the day length is longer than the critical value, it will be necessary to shorten the day, which can be done by enclosing the plants with opaque curtains for a few hours or minutes prior to sunset.

Phenological responses such as flowering can be complex, depending on both photoperiod and temperature, and they vary among cultivars as well as species. When working with a crop species, it is important to learn the specific developmental responses to photoperiod and temperature of the major cultivars within the species.

LIGHT QUALITY EFFECTS ON PLANT DEVELOPMENT

Photoperiod-sensitive plants detect and respond to variations in night length through a specific system involving the pigment phytochrome and circadian regulation. Several other phytochromes are present in plants that enable plants to detect changes in the quality of light and have different functions. The aspect of light quality that the phytochromes respond to is the red (660 ± 5 nm)/far red (730 ± 5 nm) quantum flux ratio. Some examples of developmental responses to variation in light quality obtained from the review of Smith (1995) are presented. Forest soils commonly contain large amounts of dormant seed of pioneer species, with much of the seed present on the soil surface. When a gap of sufficiently large size appears in the canopy, these seed banks generate many seedlings, some of which are successful and colonize the gap. The dormancy of the seed was due to the low R/FR ratio of the light beneath the canopy of the forest. Sunlight has an R/FR of about 1.2, but leaves absorb much red light and transmit and reflect most of the far red light so that the R/FR beneath the canopy is less than 1.2. When a gap occurs, the R/FR ratio of the light on the soil surface increases, approaching 1.2. The ability of plants to detect and respond to changes in R/FR also enables them to detect and respond to shading by leaves and potential competing plants. For example, the recumbent weed and pot herb, purslane, appears to be able to detect FR that is reflected from neighboring vegetation and respond by growing away from it. Similarly, cucumber seedlings, which are day-neutral with respect to flowering responses, exhibit this negative phototropism to neighboring vegetation and actively project new leaves into light gaps present in patchy canopy environments. The overall effect involves both proximity detection and shade-avoidance reactions through changes in development. It should be noted that competition in the aerial environment can be very strong in that, when one leaf shades another, the PFD falling on the shaded leaf can be reduced as much as 90% (Chapter 7), and the effect can be amplified. The plant receiving

more PFD has greater P_n and produces more carbohydrate and more leaves, thus shading the other plant to an even greater extent.

Plant responses to light quality can explain some of the effects on plants of crop management practices. Soybean and many other species grown on narrower row spacings at higher densities tend to be taller, with longer internodes and fewer branches. Kasperbauer (1987) hypothesized that this effect could be explained by the fact that stem regions of plants grown at higher densities are subjected to lower R/FR ratios than for plants grown on wider rows. He also observed that plants sown on north-south rows had slightly longer internodes, initiated fewer branches, and received light with slightly lower R/FR than plants sown on rows oriented east-west. With controlled environments, he demonstrated that plants subjected to low R/FR light at the end of the day had longer internodes and more biomass in stems and petioles but less biomass in roots than plants subjected to high R/FR light at the end of the day. He hypothesized that, since the R/FR ratio influences development, it also should influence partitioning of photosynthate with high R/FR benefitting root crops and low R/FR benefitting crops that produce shoot products. This hypothesis was tested by comparing crops grown under field conditions with either a black plastic mulch or a red plastic mulch that reflects more R but much more FR, resulting in low R/FR of the light reflected from the red mulch. Fruit yields of tomato (Kasperbauer and Hunt, 1998) and strawberry (Kasperbauer, 2000) were greater with the red plastic than the black plastic mulch. Refer to Chapter 7 for a discussion of the merits of the clear plastic mulches commonly used in California as compared with the black plastic mulches widely used elsewhere.

Artifacts can occur in controlled-environment studies due to the use of fluorescent lamp systems that have a much higher R/FR ratio than sunlight. Floral bud development of cowpea was inhibited by high night temperatures and long days in field conditions with sunlight having R/FR of 1.2, and in growth chambers with artificial light having R/FR of 1.3 to 1.6, but not in growth chambers with only fluorescent lamps that had a R/FR of 1.9 (Ahmed et al., 1993b). Many growth chambers mainly have fluorescent lamps and a very high R/FR and thus the potential to generate artifactual plant responses. Note that, in field conditions, the R/FR deep in the canopy is less than 1.2, due to the enhanced transmission and reflection of FR than R by leaves. Consequently, the extent of heat-induced suppression of floral buds may be influenced by factors that change the R/FR experienced by the buds, such as the row width and plant density. Several aspects of plant morphology can vary among plants growing in different growth chambers that have different lighting systems. These effects are mainly caused by differences in R/FR ratio, and it usually is advisable to use lighting systems in growth chambers that provide a R/FR ratio of 1.2 to 1.6. When fluorescent lamps are used to provide most of the PFD, a sufficient number and wattage of tungsten lamps also should be used to increase the FR component of the light to achieve the desired R/FR ratio. Note that the R/FR ratio of the lighting system will tend to change with time, primarily due to differential aging and changes in lamp output of the different types of lamps. Artifactual plant responses that have resulted from growing plants in controlled environments often have been caused by differences in light quality, level of PFD, or rooting volume compared with plants growing in field environments.

ADDITIONAL READING

Ahmed F. E., R. G. Mutters and A. E. Hall. 1993b. Interactive effects of high temperature and light quality on floral bud development in cowpea. *Austral. J. Plant Physiol.* 20: 661–667.

Bunting, A. H. 1975. Time, phenology and the yields of crops. *Weather* 30: 312–325.

Kasperbauer, M. J. 1987. Far-red light reflection from green leaves and effects on phytochrome-mediated assimilate partitioning under field conditions. *Plant Physiol.* 85: 350–354.

Kasperbauer, M. J. 2000. Strawberry yield over red versus black plastic mulch. *Crop Sci.* 40: 171–174.

Smith, H. 1995. Physiological and ecological function within the phytochrome family. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 46: 289–315.