

## Chapter 4

# **PREDICTING DAYLENGTH EFFECTS ON PHENOLOGICAL PROCESSES**

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## I. INTRODUCTION

In this chapter we make three points concerning the relationship between daylength and phenological events. The first is that the phenological response to daylength has evolved as a tool to maximize the survival of the species. The second point is that with some notable exceptions, the phenological responses to temperature and daylength are independent. The final point is that the genetic control of the phenological response to daylength controls adaptation, but the seasonal progression toward maturity is mainly determined by temperature. Our general approach in this chapter is to stress similarities of response among species and genotypes within species but confined mainly to crops of agricultural significance. As with all fields of endeavor, there are many ways of investigating the same problem. We hope to illustrate the strengths of the various approaches that are most commonly used. Where possible we demonstrate the similarities in results among the methods and attempt to clarify terminology.

The predominant bias in this chapter, however, lies in our philosophy that the similarities among species and genotypes are more important than the differences. When one considers the vast quantity of literature that is available for the various methods of studying daylength effects on about 50 crop species, it is difficult to visualize a distillation of the theories into a unified model. Biological variability and experimental error further complicate the search for a universal understanding of the problem. This is made even more difficult when we add our own personal and perhaps even cultural biases. By complementing the other chapters in this book we hope to present, to the extent possible, a unified perspective on the daylength response.

## II. RESEARCH PHILOSOPHIES IN DAYLENGTH RESEARCH

### A. EARLY RESEARCH

General acceptance that daylength controlled phenological events arrived in 1920 when Garner and Allard<sup>1</sup> showed that daylength changed the phenology of soybeans. Much of the research in the next 30 years was conducted at the USDA station in Beltsville, MD.

The multicollinearity of temperature and daylength is probably the factor that has made it so difficult to assign a definite role to daylength. In the temperate regions, daylength and mean air temperature follow a sinusoidal pattern but the maximum temperature occurs about 1 month after the solstice.<sup>2</sup> Added to this complexity is the fact that the natural daylength is always changing. Early daylength studies involved transferring potted plants between a greenhouse and rooms which shortened or extended the daylengths.<sup>3</sup> Another method was to study serial planting dates in a greenhouse in which the annual mean temperature was relatively constant.<sup>4</sup> Throughout the succeeding years there has been a succession of planting date studies with and without temperature control which have enhanced our knowledge of the daylength response.<sup>5</sup>

Simultaneous with the field and greenhouse studies was the search to explain daylength effects at the cellular level. Obviously, a continually changing day/night rhythm has to be explained in terms of circadian rhythms.<sup>6</sup>

In the 1950s phytochrome, the photoreversible pigment located in cell membranes, was discovered. One of the two forms predominates depending on light conditions. This probably controls membrane permeability and also may be responsible for stomatal opening through its control of ATP pumps and the inter-/intracellular potassium balance.<sup>7</sup>

Extrapolation from a circadian rhythm to a sudden change in the apical meristem is difficult but the search continues.<sup>8</sup> This has led to the concept of the flowering hormone, florigen, which has yet to be identified. One current hypothesis is that florigen may simply be a balance of gibberellin and kinetin or some other hormones.<sup>9</sup>

Regardless of how circadian phytochrome rhythms translate into phenological changes, two important points need to be made. The first is that the timing of events is remarkably constant.

A single genotype seeded on the same date will flower within a few days of the same calendar date every year. The other point is that all higher plants seem to have evolved with daylength responsivity. There are many instances of varietal insensitivity, but there are as yet no examples of an entire species being daylength insensitive. Thus we conclude that daylength insensitivity does not imply a lack of circadian rhythms but simply that the genetic control of the phenological process is not responsive to daylength.

The advent of controlled environment cabinets or growth chambers allowed the separate study of daylength and temperature. However, one difficulty with early growth chamber research was related to inadequate experimental replication. Growth chambers represent a large capital expenditure and are large energy consumers. Consequently, it was not uncommon to use the same growth chamber for an entire experiment or, in daylength/temperature experiments, to have all daylengths for a given temperature in the same growth chamber. Consequently, a 1°C temperature difference between chambers turns out to be a 10% error if the temperature is 20°C and the base for summation of temperatures is 10°C. Another error is that there are usually three or more mechanical clocks, typically with 5 to 15 min gradations, controlling the lighting in a growth chamber. These clocks are subject to losing or gaining about 0.5 h every 50 d, so it is possible that the daylength might be 1 h longer at the end of the experiment than it was at the beginning. New electronic controls have resolved this problem, but the temperature bias still has to be eliminated through accurate calibration and appropriate replication.

In spite of these problems, growth chamber studies have been the key to increasing our knowledge of the daylength response. It was in growth chamber manipulations of the day/night rhythm beyond 24 h that we found that the length of the night rather than the daylength actually controls the phenological response in short-day plants. However, since in nature the 24 h rhythm prevails, so too do the terms daylength and photoperiod.

## B. ABSOLUTE VS. QUANTITATIVE DESCRIPTORS

Garner and Allard<sup>10</sup> realized that annual crop species fall into two categories, long-day plants or short-day plants. A short-day plant completes its development in less time in short daylengths, and a long-day plant takes less time in long daylengths. The response is not linear, however, and as a result there have been various designations for the various types of responses.

One approach, which we have chosen to call absolute, separates cultivars or species according to whether they are obligate or facultative. In fact, Salisbury<sup>11</sup> developed a scheme in which examples are given for 777 classifications ranging from a simple description such as "day-neutral, no causative temperature effect" to more complicated descriptions such as "long-day plants; no causative effect of temperature; critical dark period inversely proportional to temperature". Unfortunately, using this scheme, genotypes of a given species fall into many different categories and the information is of limited value in computer modeling of the daylength response.

Although some controversy may still exist, it is likely that the temperate cereal grains — wheat, barley, oat, and rye — are all long-day species,<sup>12,13</sup> and maize, sorghum, rice, and soybeans are short-day species.<sup>12,14-16</sup>

In the quantitative approach, an attempt is made to express the daylength response in terms of parameters of a mathematical model. There are many methods of doing this, some combining temperature and photoperiod,<sup>17,18</sup> and one that even includes a term for water stress.<sup>19</sup> In general, two methods are used to relate development to photoperiod when all other environmental factors are held constant, and they are discussed in detail in Sections III.B and III.C of this chapter. The difference in these two methods is that one relates the duration between events to daylength and the other relates rate of development, calculated by inverting the duration, to daylength. The value of the quantitative response approach is that the model parameters can be used in computer models to predict the date of phenological events.

### C. TIME INTERVAL BETWEEN EVENTS VS. DURATION OF EVENTS

The scope of daylength response studies is based either on prediction of the date of an event, such as anthesis, or on the duration of an event, such as the reproductive phase and the amount of leaves or florets that are initiated during the interval.

The simpler of the two is to model the onset of the phenological event. Theoretical models based on growth chamber data<sup>20</sup> or empirical models usually based on field data<sup>21,22</sup> have been used. When these development models are coupled with yield or photosynthesis models they have tremendous value for monitoring condition and yields of important crops. Input for the development portion of the model usually requires only air temperature and daylength and an estimate of seeding date.

Depending on the model, a genetic component for the daylength parameters also might be included. A refinement of the models described is to relate daylength to plastochron or phyllochron so that the leaf number and position are also known at the time of the phenological event. The plastochron is the time interval between periodic events and in crop development the periodic event usually has been assumed to be the initiation of new leaf primordia.<sup>23</sup> The term phyllochron refers to the time interval between the appearance of new leaves and was coined to differentiate the two.<sup>24</sup> The reason for differentiating the two terms is that the appearance of a leaf tip is not the same as the initiation of new primordia. After the first flower is initiated, the total number of florets initiated or the duration of flower initiation is also influenced by daylength.

## III. PHENOLOGY AS AN EVOLUTIONARY PROCESS

### A. MAXIMIZING SEED PRODUCTION THROUGH FLOWERING DATE

Daylength provides plants with a consistent environmental variable for controlling date of flowering. At a given latitude, photoperiodism ensures that plants will flower near the same day of year every year. It is not surprising that daylength-controlled mechanisms have evolved for maximizing seed production and quality to aid survival of plant species. Such consistency in flowering date is important in temperate regions and tropical regions for two different survival strategies. In a temperate climate, seed production must be completed before immature embryos or seeds are killed by autumn frosts. Conversely, premature senescence results in low seed production and also may result in deterioration of seed exposed to long periods of warm moist conditions. Thus, species have survived which optimize their seed production depending on when they emerged as seedlings.

Planting date studies demonstrate this optimization of flowering date very well. Plantings at various dates will often flower on the same or nearly the same date.<sup>25</sup> While low temperatures during early development contribute to the delay in flowering for early plantings in temperate regions, photoperiodism is also important. Floral initiation of long-day plants is delayed until the daylength is sufficiently long.<sup>26</sup>

In order to understand the importance of the sensitivity of short-day plants to daylength, one must look at their regions of origin. Sorghum and maize, both short-day plants, are of tropical origin. Their sensitivity is important for inducing flowering during the most productive season relative to rain, as discussed previously. Breeding programs for producing maize and sorghum cultivars for temperate regions have included reduction or elimination of photoperiod sensitivity. In more northern environments, reduced photoperiod sensitivity, along with reduction of the basic vegetative phase, has provided hybrids that mature in very short growing seasons. Thus, one concludes that daylength effects play an important role in determining the region of adaptation.<sup>27</sup> However, during the growth cycle, daylength effects are less important than temperature effects.

### B. PHASES OF DEVELOPMENT

Many phases have been devised to describe crop species in terms of their progression toward

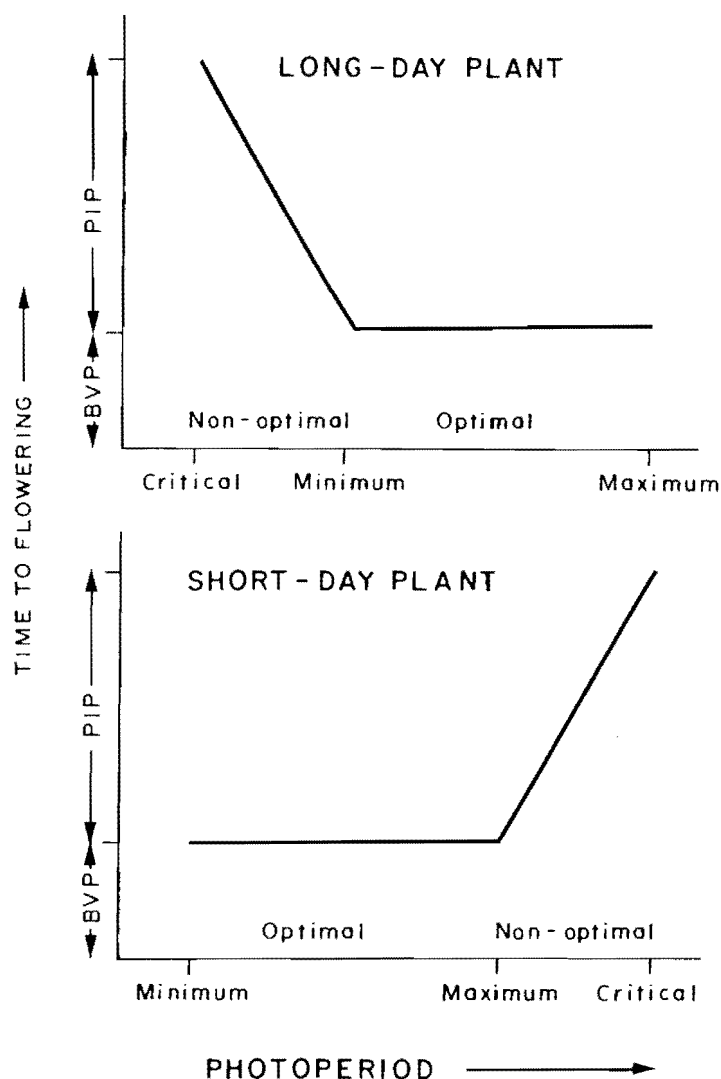


FIGURE 1. Responses of long- and short-day plants to photoperiod. PIP = photoperiod-induced phase; BVP = basic vegetative phase.

maturity. They generally fall into the qualitative and quantitative types. The sorghum and rice examples are ideal because (1) the number of phases is only three, (2) the transition to each phase is marked by an easily identifiable stage,<sup>28,29</sup> and (3) each phase is identifiable regardless of environmental conditions. The phases include the vegetative phase ending with panicle initiation, the reproductive phase ending with anthesis, and the ripening phase ending at maturity.<sup>30</sup> The disadvantage of these phase designations is that they do not provide any information with respect to plant size or leaf number as do the wheat, maize, rape, sorghum, or soybean growth stage schemes.<sup>31-35</sup> These types of staging scales become complicated when used to describe a range of cultivars because of variability in total leaf numbers.

### C. ANALYSIS OF DAYS OR THERMAL TIME VS. DAYLENGTH

Daylength effects are most often apparent on the length of the vegetative phase. In this chapter most of the discussion is directed to this phase.

Major<sup>20</sup> developed a system of describing daylength responses that is universally applicable, is amenable to genotypic and species differences, and provides useful criteria for computer modelers (Figure 1). While originally developed for rice by Vergara and Chang<sup>30</sup> the system has been applied to a wide range of crop species, with modifications in terminology. In this system

the vegetative phase is broken down into a juvenile phase and a photoperiod-induced phase (PIP). The juvenile phase is independent of daylength but can be of variable length depending on genetic control. The minimum duration from seedling emergence to floral initiation, termed the basic vegetative phase (BVP), is the sum of the juvenile phase and the PIP in optimum daylengths.

The length of the PIP is controlled by daylength. Under optimum daylength conditions duration of the PIP is a constant, minimal number of days. Nonoptimal daylengths increase the length of the PIP. The maximum optimal photoperiod for short-day plants, or minimum optimal photoperiod for long-day plants, is the threshold between optimal and nonoptimal daylengths. These thresholds are, for convenience, designated MOP.

Nonoptimal photoperiods increase the duration of the PIP in proportion to the genetically controlled photoperiod sensitivity. This sensitivity can be described in units of days delay per hour of increase in daylength. For long-day plants photoperiod sensitivity is negative. Maize plants are only directly sensitive to photoperiod in the days just prior to tassel initiation. This interval is 4 to 5 d long for plants growing in daylengths shorter than 12.5 h but is longer with photoperiod-sensitive cultivars in longer daylengths.<sup>36</sup> Most common soybean cultivars apparently lack a juvenile phase and are sensitive to photoperiod immediately after seedling emergence. Wilkerson et al.<sup>37</sup> found, however, that soybean genotypes which have a long juvenile phase can be identified. The length of the PIP in optimum daylengths is constant across genotypes, with flowering occurring in the same number of days for all genotypes under such conditions.<sup>37</sup> The PIP lasted until 6 to 9 d before the first flower. As with soybeans, sorghum cultivars apparently all have a BVP of about 20 d.<sup>28</sup> Thus, panicle initiation will occur 20 d after seedling emergence in short daylengths. Rice, on the other hand, exhibits a wide range of values of the BVP,<sup>30</sup> as does maize<sup>38</sup> and mungbean.<sup>39</sup>

Research is required to determine if the variability in MOP is independent of photoperiod sensitivity. This question arises because relatively small errors in the estimation of photoperiod sensitivity can cause large errors in estimating the MOP. The results of Criswell and Hume<sup>40</sup> suggest that variability in MOP might be the main source of variation in soybean photoperiodic response, although variability for photoperiod sensitivity is indicated when a wider range of maturity is considered.<sup>27,41</sup> Most other crops exhibit little if any variability for this character. MOP was not included in the original photoperiod description of Vergara and Chang so one must interpret their graphic presentations of rice results. From the data presented in the Appendix of the bulletin prepared by Vergara and Chang,<sup>30</sup> it is reasonable to assume that rice cultivars have MOPs that vary from less than 10 to more than 13 h. The MOP is consistently 12.5 h for maize<sup>38,42</sup> and  $12 \pm 1$  h for sorghum of several maturity types.<sup>43</sup> Mungbeans have an MOP that varies from 12 to more than 14 h.<sup>44</sup> The mean MOP for a number of long-day crops, including wheat, barley, oat, rye, flax, and rape, is 17.7 h and appeared to not vary among species or cultivars.<sup>20</sup> The MOP for 10 oilseed rape cultivars also did not vary and the mean value was 17.1 h.<sup>45</sup>

Photoperiod sensitivity expressed as days delay of flowering or floral initiation per hour increase of daylength almost always varies among cultivars within a species. In rice it varies from 0 for cultivar Tainan 3<sup>30</sup> to about 200 d/h for cultivars such as Skrivimankoti.<sup>46</sup> Maize photoperiod sensitivity varies from 0 to more than 2 d/h<sup>36,47</sup> or from 0 to 2 leaves/hour.<sup>38</sup> In an analysis of Garner and Allard's<sup>10</sup> data, Major<sup>26</sup> found that photoperiod sensitivity varied from 2.5 d/h for "Mandarin" soybeans to 147 d/h for "Biloxi". Byth,<sup>48</sup> Cregan and Hartwig,<sup>27</sup> and Jones et al.<sup>41</sup> found differences in soybean photoperiod sensitivity. Sorghum photoperiod sensitivity apparently varies from 0 for the lines containing the Ma<sub>3</sub> allele from Ryer<sup>43</sup> to over 40.5 d/h.<sup>49</sup> In long-day species, the only reported differences are between the conventional northern wheats (–15 d/h) and the semidwarf, the latter being less sensitive (–5 d/h).<sup>20</sup> King and Kondra<sup>45</sup> found no differences among rape cultivars with a mean of about –2.7 d/h. Major<sup>20</sup> found a mean value for 4 rape cultivars of –6.8 d/h. The range of values used in the CERES-wheat model is –100 to –500 GDD<sub>0</sub>, which would translate to –4 to –20 d/h at 25°C.

In the originally proposed model there sometimes appeared to be a critical daylength which defined either the beginning of a response plateau for extreme nonoptimum daylengths or the most extreme nonoptimum daylength at which flowering will occur. Thus, when the daylength is longer than the critical photoperiod for short-day plants or shorter than the critical photoperiod for long-day plants, floral initiation occurs in the same number of days regardless of daylength, or it never occurs. This implies that there is a basic rate of development even if daylength is longer than the critical photoperiod for short-day plants. This has been occasionally observed for soybeans<sup>48,50</sup> and for maize.<sup>47</sup> Roberts et al.<sup>18</sup> describe this as the "ceiling photoperiod".

#### D. ANALYSIS OF RATE OF DEVELOPMENT VS. DAYLENGTH

While the daylength response often has been expressed with duration of an interval as a segmented function of photoperiod, there is evidence that rate of development as a function of photoperiod may be more appropriate. Rate, or inverse of duration, is more consistent with enzyme kinetics<sup>51</sup> and basic plant physiology. However, while rate may be more appealing mechanistically, from an applications viewpoint either approach is adequate. One argument for using rate is that the apparent nonlinear or segmented response function with duration becomes linear when rate is used.<sup>52</sup> A similar situation exists with duration of grain-filling of cereals as a function of temperature.<sup>53,54</sup> However, even rate of development can show a segmented or nonlinear response to photoperiod in some cases.<sup>18</sup> In addition, variability in measured data is often too great to justify choosing one approach over another.

#### E. THE REPRODUCTIVE PHASE

In this chapter, we use the term "reproductive phase" as originally proposed by Vergara and Chang,<sup>30</sup> although it may be more aptly referred to as the preanthesis phase. The daylength response of the interval from floral initiation to anthesis appears to differ among species. It is important to differentiate direct sensitivity to daylength during this interval from the secondary response of anthesis delays due to increased number of leaf primordia initiated when floral initiation is delayed by nonoptimum daylengths. Maize provides an example in which long daylengths increase the duration of the reproductive phase without the plants being directly sensitive to daylength in this interval. Each unit delay in floral initiation results in a 1.2 to 1.4 unit increase in the interval from floral initiation to anthesis.<sup>42,55-57</sup> However, daylength switching treatments indicate that, for maize, direct sensitivity to daylength ends at tassel initiation.<sup>36</sup> Thus, the delay in tassel emergence appears to be due to an increased number of initiated leaves. This lack of daylength sensitivity following floral initiation does not appear to be general among crop species, however. Panicle emergence of rice can be prevented by long daylengths after floral initiation,<sup>58,59</sup> and the reproductive primordia can revert to vegetative primordia if photoinduction is incomplete.<sup>60</sup>

Likewise, the increase in the interval between floral initiation and anthesis of wheat, barley, and oats observed in noninductive daylengths<sup>61-64</sup> also may be a direct response to daylength. Spike emergence of barley has an absolute long daylength requirement even though spike initiation does not.<sup>13</sup> Unfavorable daylength conditions can result in development of abnormal floral structures in wheat.<sup>65</sup> Long daylengths after floral initiation of Biloxi soybeans can delay development of flower buds.<sup>37,66</sup>

In spite of the daylength sensitivity after floral initiation in some crops, the most critical sensitivity for cereal crops is during the interval from seedling emergence to floral initiation. Duration of this interval determines total number of leaves initiated and thus the number which must emerge prior to flower appearance. In addition, winter annual cereals reach floral initiation in periods of increasing daylength. Thus short, noninductive daylengths will not occur between floral initiation and anthesis. Spring-sown short-day crops in temperate regions could experience longer, less optimum daylengths in the period between floral initiation and anthesis than prior to floral initiation.

With this in mind, daylength sensitivity for some crop species, particularly cereals, need only

be considered when predicting date of floral initiation. Delays in floral initiation due to maturity type or nonoptimum daylengths can then be related directly to duration of the interval ending at anthesis. For example, Kiniry et al.<sup>36</sup> found a good relationship between growing degree days (GDD) from emergence to tassel initiation of maize and GDD from emergence to anthesis. There was an intercept of  $-25.9$  and a slope of  $0.46$ . GDD in this chapter are defined as the mean of the maximum and minimum temperatures minus a base temperature with the condition that if either temperature is less than the base it is set equal to the base temperature. Unless indicated by a subscript, the base temperature is  $10^{\circ}\text{C}$ . Others<sup>55-57</sup> plotted leaf numbers at tassel initiation on the abscissa and final leaf numbers on the ordinate for various daylengths and temperatures and obtained a good relationship with a slope of  $0.42$  to  $0.44$  and intercept ranging from  $-1.95$  to  $-2.30$  leaves. The remarkably similar slopes from these independent studies are also similar to the ratio of  $0.54$  for  $\text{GDD}_8$  per leaf primordia divided by  $\text{GDD}_8$  per leaf tip found by Kiniry and Ritchie.<sup>67</sup> In addition, the negative intercepts of these relationships can be accounted for by the six-leaf primordia present in the maize seedling at emergence.<sup>67,68</sup> These results suggest that the longer the interval from emergence to tassel initiation, the longer the interval from tassel initiation to anthesis.

A relationship also exists for sorghum based on data from Quinby and Karper<sup>69</sup> and Castleberry<sup>70</sup> in which the slope is  $1.01 \text{ GDD}_8(\text{em-pi})/\text{GDD}_8(\text{em-an})$  and the intercept is  $626 \text{ GDD}_8(\text{em-an})$ . This differs from maize, however, in that a constant  $626 \text{ GDD}_8$  are required from panicle initiation to anthesis.

The slope of the relationship for rice, based on combined data of Sircar and Sen,<sup>71</sup> Velasco and Manuel,<sup>72</sup> Tang and Liu,<sup>73</sup> Sen and Roy,<sup>74</sup> and Misra and Khan,<sup>75</sup> is  $1.37 \text{ d}$  (from sowing to panicle emergence) per day (from sowing to panicle initiation) with an intercept of almost  $0$ .

The comparable relationship for wheat from Riddell et al.<sup>76</sup> has a slope of  $1.97 \text{ GDD}_0$  from emergence to floral initiation per  $\text{GDD}_0$  from emergence to anthesis.

These relationships are useful and valuable in computer modeling of crops and in the interpretation of data from various types of studies.

Thus, in most cereal crops, the reproductive phase is related to the time between seedling emergence and floral initiation. Consequently, the time from emergence to anthesis is proportional to the time from emergence to floral initiation or terminal spikelet. However, the time from anthesis to physiological maturity fails to show a strong relationship to duration of earlier phases.

## F. THE MATURATION PHASE

The period between flowering and maturing was called the maturation phase by Vergara and Chang.<sup>30</sup> The growth habit plays a critical role in the environmental response of the duration of the maturation phase.<sup>77</sup> Indeterminate species such as soybeans or cotton produce flowers over a long period of time if the environment is favorable. Graminae crop species show differences of only a few days in dates of maturity of florets within the inflorescence.

While the period from sowing to anthesis has been shown to be correlated sometimes with the duration from anthesis to maturity for different maize cultivars,<sup>78,79</sup> there are differences in duration from the anthesis to maturity among cultivars of the same maturity.<sup>78-81</sup> In addition, there is no evidence that photoperiodic delays in the reproductive phase alter the duration of the maturation phase.

This interval for wheat and barley is probably also independent of daylength, although Guitard<sup>61</sup> reported a decreased number of days from heading to maturity for barley when daylength increased in growth chambers, and an iterative regression procedure using field data of wheat indicated a daylength response for the interval.<sup>21</sup> However, Marcellos and Single<sup>2</sup> found that the development rate after flowering of wheat was independent of daylength.

Soybean represents an indeterminate species for which maturity can be delayed by long daylengths. Using Robertson's<sup>21</sup> iterative regression technique, Major et al.<sup>22</sup> found that the



anthesis to maturity interval was related to daylength. Other studies<sup>25,41,82-84</sup> also indicated that long daylengths can delay postflowering development of soybean. Even some cultivars that are insensitive to daylength in preflowering stages can have delayed maturity in long daylengths.<sup>85</sup>

#### IV. INTERACTION OF DAYLENGTH AND TEMPERATURE

Identification of interactions between daylength response and temperature response in the field are difficult because of the seasonal trends of both environmental variables. As daylength increases in the spring, temperature also increases. Simple descriptions of daylength responses in terms of days have led to numerous reports of such interactions. Low night temperatures hasten flowering of rice in short days but not in long days.<sup>86</sup> Temperature during the night was more important for soybean development than temperature during the day.<sup>3,87</sup> Similarly, shorter daylengths were required for flowering of soybeans with cooler night temperatures.<sup>88</sup> A single maturity gene of sorghum ( $Ma_2$ ) has even been identified as apparently mediating a temperature  $\times$  daylength interaction.<sup>43</sup>

It has been suggested that decreased daylength sensitivity leads to increased thermosensitivity. Rice cultivars that were least sensitive to daylength have been reported to be the most sensitive to temperature.<sup>89,90</sup> However, the results of Vergara et al.<sup>91</sup> indicated that the most daylength-sensitive rice cultivars were also the most sensitive to temperature. Similarly, Kuriyama,<sup>92</sup> studying rice cultivars of diverse origin, concluded that cultivar differences existed for both daylength and temperature sensitivity but that there was no relationship between daylength response or temperature response. Temperature effects on field-grown soybeans have been reported to be apparent only when daylengths were short and temperatures were cool.<sup>5</sup>

The description of daylength sensitivity in units of thermal time may eliminate much of the temperature  $\times$  daylength interaction evident when units are days. There is increasing evidence that plant responses to daylength and temperature are independent when each is adequately described.<sup>50,84</sup> Kuriyama<sup>92</sup> failed to detect any effect of temperature on the optimum daylengths or daylength sensitivity of rice.

Application of a thermal-time system requires accurate expression of the development rate response to temperature. The commonly used GDD represents a crude approximation of a complex biological response. Each error in estimation of thermal time is cumulative and can easily exceed 10%. For this reason, the choice of the thermal-time scale for expressing duration or rate of development as a function of daylength is important.

##### A. SCALES USED FOR DAYLENGTH RESPONSE

Three scales can be used to measure phenological time: calendar days, thermal time, and leaf number. These vary in complexity and in dependence on temperature. There are advantages and disadvantages to each scale.

Calendar days represent the oldest and most easily applied system. Obviously, temperature differences will alter the magnitude of the daylength response parameters. This scale is most useful for describing results when the temperature is held constant.

The thermal-time or physiological-day scale is designed to quantify development rate responses to temperature. The physiological day is obtained by dividing the thermal unit accumulation by a value representative of a day when temperature is optimum all day. To be completely independent of temperature, the function must exactly duplicate the thermal response. The temperature response may vary among genotypes and among stages of development. This scale is widely used, particularly for field experiments with variable temperatures.

The leaf number scale is feasible for determinate species because leaves on the main stem are initiated at a temperature-dependent rate. Final leaf number is sometimes influenced by temperature, but this effect is slight. The practical problem with leaf number is accounting for lower leaves that are lost prior to flowering. Steps must be taken to account for such leaves.

## B. EXTREME INTERACTIONS

Using the thermal-time scale or leaf numbers generally demonstrates that the temperature and daylength responses are independent. However, extreme values for either environmental variable may result in dramatic interactions.

Historically, vernalization has been a common candidate for such temperature  $\times$  daylength interactions. In wheat, vernalization was reported to reduce the requirement for long days.<sup>93-95</sup> The effect of cold temperature has been reported to be more effective in inducing barley flowering when accompanied by short daylengths.<sup>18</sup> Such interaction between vernalization and daylength responses is not universally accepted, however.

Two independent sets of genes control the vernalization and daylength responses.<sup>96-98</sup> In addition, other researchers have found that vernalization does not reduce the daylength sensitivity.<sup>99-103</sup> It appears that vernalization alters the duration of the juvenile phase and daylength acts independently on the succeeding PIP. Sorghum and maize development in the tropics represents additional cases of daylength  $\times$  temperature interactions. Short winter daylengths at tropical locations result in delays in panicle emergence of sorghum<sup>49</sup> and silking of maize.<sup>104</sup>

Milo lines have more leaves at 30°C than at 25 or 20°C in nonoptimal daylengths.<sup>43</sup> It may be that these interactions are due to deficiencies in photosynthate availability caused by short days, with insufficient quantities of solar radiation to meet the energy requirements of the plant.

## V. EFFECT OF DAYLENGTH RESPONSE ON ADAPTATION

### A. EFFECT OF LATITUDE

While daylength varies consistently with latitude, large scale climatic differences alter the seasonal temperature profile at different longitudes. Thus, genotypes are not adapted to all longitudes. Surveys of genotypes and their region of adaptation suggest that the effect of a decreasing latitude is that genetically adapted plants tend to have a longer juvenile phase and decreased daylength sensitivity. For an adapted short-day plant, the juvenile phase also increases as the latitude decreases but the daylength sensitivity increases.

As latitude decreases, the adapted long-day plant changes from spring to winter habit and it is grown in shorter and shorter daylengths. The onset of rapid growth is controlled by temperature.<sup>105</sup> Thus, the southern-adapted cereal such as Pitic wheat has a lower daylength sensitivity than the northern cultivar such as Thatcher or Park<sup>20,106</sup> but, in the southern latitudes, it is affected more by daylength because it is growing in winter during nonoptimal daylengths. Thus, a Canadian wheat takes longer to mature in a winter nursery in California than a California cultivar, but the Canadian wheat is earlier when it is grown as a spring cereal in Canada.

### B. EFFECT OF PLANTING DATE

For most short-day plants, adapted genotypes exhibit a 1-d delay in flowering for every 2 d delay in planting. The effect is similar for spring-seeded long-day plants in cool temperate climates. For winter-habitat long-day plants, the effects are somewhat more muted, depending on the severity of winter.

Major<sup>26</sup> applied the basic flowering model to 9 species of greenhouse-grown plants seeded fortnightly at 49° latitude. The model works for both short- and long-day plants and so provides an idea of how daylength influences development in the field. Since temperatures usually peak 1 month after the solstice, short-day plants are likely affected to some degree by the long daylength, regardless of seeding date. Late-seeded short-day plants, such as soybeans planted after winter wheat, will be exposed to warm temperatures and rapidly decreasing daylengths.

Short-day plants seeded in late April and May are subjected to lower spring temperatures and nonoptimum daylengths so that flower initiation is delayed by cool temperatures and long daylengths. In spring, the winter annual long-day plants are delayed by cool temperatures and

short daylengths, but as summer approaches, the increasing temperatures and daylengths work together to hasten development.

### C. GENETIC VARIABILITY OF DAYLENGTH RESPONSES

In the past decade, a picture of the type of variability that exists for the daylength responses has emerged. Rice has been the most extensively studied in this respect and, not surprisingly, shows variability for BVP, MOP, and daylength sensitivity. Studies of North American cultivars have revealed lower variability. A study by Criswell and Hume<sup>40</sup> suggested that in early maturing soybeans, the only variability was in the MOP, with BVP and daylength sensitivity essentially the same for all U.S. cultivars. In sorghum the BVP and MOP appear to be constant, with daylength sensitivity changing and additional variability coming from temperature sensitivity. Maize seems to have a constant MOP but the BVP varies among maturity types. Wheat appears to be relatively constant in terms of MOP but varies in BVP and daylength sensitivity. There is also variability for vernalization.

Some studies suggest that inheritance of the BVP is dominant in wheat and maize and that daylength sensitivity is also dominant. This gives rise to the interesting situation in which lateness and earliness are both dominant characteristics and helps explain how relatively few genes can control a seemingly complex response. Control of the MOP may or may not be linked to daylength sensitivity. Correlations between the MOP and daylength sensitivity generally suggest that they are associated, but it should be remembered that this could be an artifact if the same regression technique was used to calculate both parameters.

## VI. CONCLUSIONS

There is agreement in principle on the response characteristics of a wide range of crop plants. Whether expressed as time or as the inverse of time (rate), there appears to be a juvenile phase, which is independent of daylength, and a daylength-sensitive phase, which controls the initiation of the reproductive structures. There is an increased awareness of the effects of temperature on phenology, but a feeling that actual temperature-daylength interactions exist but are modifiers of the response. There is also a general acceptance that we need to catalog the genetic differences for the various phases. A benefit of crop modeling has been the encouragement of mathematically based phenology models, resulting in more quantitative descriptors and providing indirect proof that the growth chamber-based models are realistic. Perhaps, most importantly, there is a growing consensus among scientists that daylength research is moving in the right direction.

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