

Chapter 5

PREDICTING LEAF DEVELOPMENT OF CROP PLANTS**J. R. Kiniry, W. D. Rosenthal, B. S. Jackson, and G. Hoogenboom****TABLE OF CONTENTS**

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I. INTRODUCTION

Leaf development is strongly interrelated with phenology in a number of ways. The total number of leaves of a given shoot (and often of the entire plant) is related to the duration of the development interval to floral initiation, as well as to the rate of leaf primordia initiation. The total number of leaves and rate of appearance directly relate to the development of the plant toward anthesis. Once final leaf number is determined, these leaves emerge before the flower becomes visible and anthesis occurs. In some conditions, such as in cases of drought stress with maize, the anthers actually dehisce prior to emergence of the male flower. However, these situations are rare.

Efforts to simulate leaf area in relation to phenology have resulted in models of varying complexity. In its simplest form, potential leaf area per plant or leaf area index (LAI) is modeled as a direct function of total number of leaves or duration of the period of vegetative growth.^{1,2} A more complex modeling approach in common use involves modeling areas of individual leaves.³⁻⁶ In this approach, leaf initiation, leaf tip appearance, leaf expansion, and leaf senescence are all simulated. Finally, some models are intermediate in complexity between these two.⁷ Such models may describe leaf initiation and tip appearance in an effort to predict total number of leaves and date of anthesis. In such cases, leaf area development may be simulated only on a whole-plant basis.

Leaf development is visible and easily measured prior to anthesis. Thus, it is easy to understand the attractiveness of this subject for researchers interested in vegetative stage development. Aitken⁸ discussed both the interval between initiation of formation of successive leaf primordia (plastochron) and the interval between the opening of two successive leaves (phyllochron) for wheat, barley, oat, and rye. For the following discussion, phyllochron refers to the interval between appearance of successive leaf tips or trifoliolate tips outside of the leaf whorl, rather than to the opening of leaves. This definition is essentially identical to the other for plants with only one leaf expanding at a time. However, for species such as maize, in which as many as four not-fully-expanded leaf tips may be outside the leaf whorl at one time, the definition using leaf tip appearance is more useful. The degree days (base 8°C) between emergence of successive leaf tips of maize is fairly constant on a plant after the second leaf. However, differences in the duration of the tip emergence and the collaring interval among leaves on a plant cause the degree days between appearance of leaf ligules to vary greatly.

In this chapter we investigate the three major processes involved in leaf development which relate to phenology: (1) leaf primordia initiation, (2) leaf tip appearance, and (3) leaf expansion. Values for the base temperature for each development rate, the cumulative degree days required per leaf event, and the effects of stress and cultivar on the rate will be discussed for various crop species.

A. IDEAL LEAF DEVELOPMENT SCHEME

When modeling complex systems such as the development of leaves, it is often valuable to develop a simple system, derive constants for the crop species of interest, and test on field data before more complex approaches are attempted. Growing degree days (GDD) calculation represents one such approach. For this chapter, GDD_{t_b} for 1 d are calculated with the same form as the "heat stress" equations of Gilmore and Rogers,⁹ with development rate increasing linearly above a base temperature (t_b in Figure 1) up to an optimum temperature (t_{opt}) and thereafter decreasing linearly to zero rate at a maximum temperature (t_{max}).

In addition to simplicity of derivation and application, there are three other reasons why this form could be preferable to the nonlinear systems often described. First, development rates which have been used to derive nonlinear equations are often based on either split day/night temperature data or temperatures too low for long-term plant viability. A split day/night temperature treatment should have a development rate similar to the rate in a constant temperature treatment with the same mean only if the day and night temperatures both are

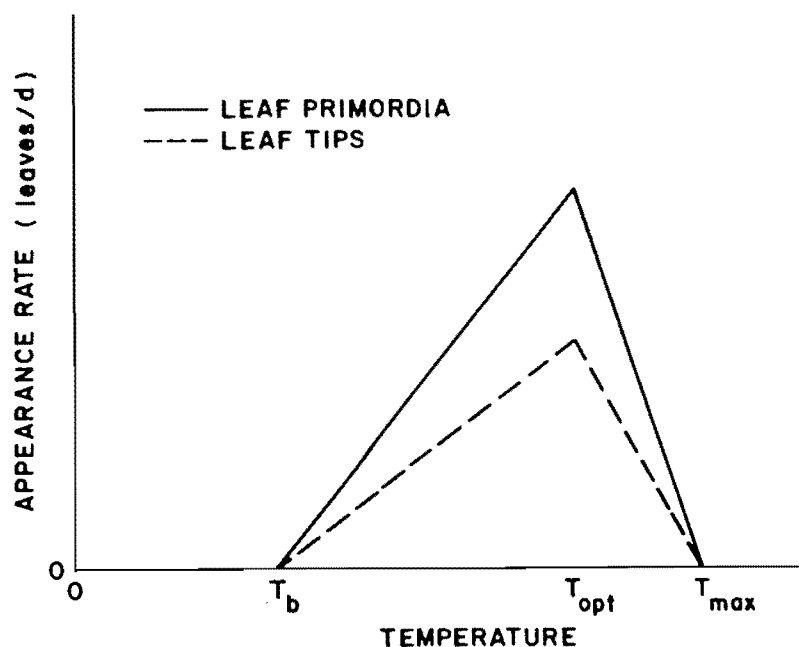


FIGURE 1. Idealized leaf development rate response to temperature. The three cardinal temperature variables are base temperature (t_b), optimal temperature (t_{opt}), and maximum temperature (t_{max}).

between t_b and t_{opt} or both are between t_{opt} and t_{max} . If the day temperature is greater than t_{opt} and the night temperature less than t_{opt} , the rate of development should be less than for the constant temperature treatment with the same mean temperature, thus making the rate appear curvilinear when actually a two-step approach as described here may be more appropriate. From an application standpoint, when daily maximum or minimum temperature falls outside the t_b to t_{opt} range, sine wave interpolations similar to those of Fry,¹⁰ as described in Jones and Kiniry,⁷ can be used to compute several rates for a day and the mean rate thus calculated.

A second justification for use of this GDD system is that errors in predicting development rate at temperatures near t_b are often negligible when predicting development with field data. Development rate predictions are at their lowest near t_b and such GDD values comprise only a small percentage of the total.

Finally, attempts at prediction in the field using curvilinear equations for rate as a function of temperature have failed to prove superior to GDD equations and in many cases have been inferior. Prediction of development stages of maize was attempted with a curvilinear equation,^{9,11} and such systems proved to be less accurate than GDD equations.

Thus, for this chapter, the "heat stress" GDD system will be used to describe leaf development. This does not preclude future application of nonlinear temperature response functions, but it does suggest that such approaches be examined very critically before they are accepted.

The relationship between the interval between initiation of leaf primordia (plastochron interval) and the phyllochron interval, both in degree days, is closely related to the relationship between the seedling emergence to floral initiation interval and the seedling emergence to anthesis interval, again both in degree days (Figure 2). Delays in floral initiation, whether due to maturity genotype or photoperiod, allow formation of additional leaf primordia, thus providing additional leaf tips which must emerge prior to anthesis.

Degree days, with a decrease in rate of accumulation when temperatures exceed the optimum, provide a useful means of describing both plastochron and phyllochron intervals. Both rates of leaf primordia initiation and leaf tip appearance increase with increased temperature above a base temperature, up to an optimum. For maize, analysis of data for both plastochron¹² and phyllochron¹³ indicated the base temperature is 8°C and the optimum 34°C.¹⁴

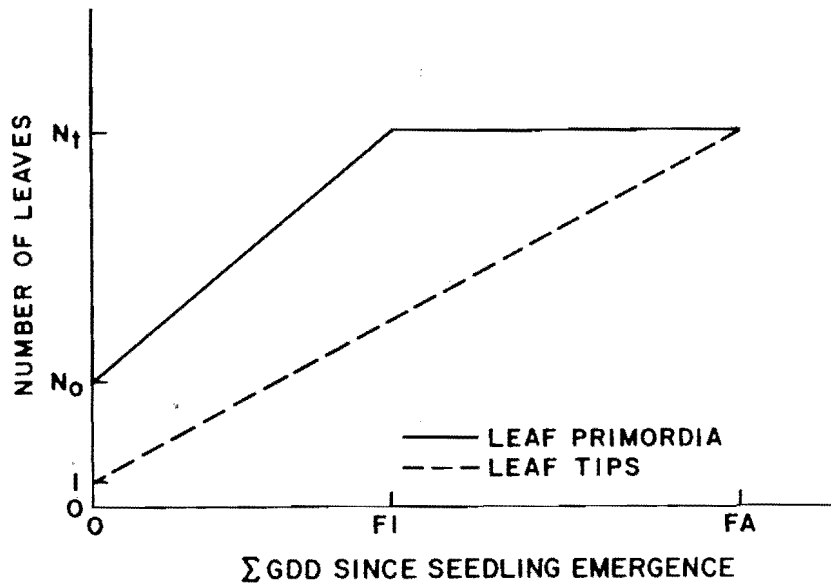


FIGURE 2. Idealized scheme for leaf development. Leaf primordia initiation begins at seedling emergence with a species-specific number of primordia (N_0) already present and stops at floral initiation (FI) at which time the total number of leaves (N_{total}) have been initiated. Leaf tip appearance begins with one at seedling emergence and concludes at anthesis (FA).

GDD sums to predict the number of leaf primordia initiated or the number of leaf tips emerged are also needed for this leaf development system. Assuming the parameters of t_b , t_{opt} , and t_{max} are correct, the simplest scheme would be a given GDD sum required for initiation of each primordium and appearance of each leaf tip. This assumes the leaf development rates are independent of leaf position, as has been shown to be true for maize.¹⁴ The number of leaf primordia present at seedling emergence (N_0) can be determined by linear extrapolation of counts back to summed GDD = 0, as was done by Warrington and Kanemasu.¹² The summed GDD at floral initiation (FI) can be a function of cultivar, photoperiod, and, for winter cereals, vernalization. Total number of leaves (N_{total}) is easily calculated by:

$$N_{total} = FI/Plastochron + N_0 \quad (1)$$

The total GDD from seedling emergence to flower appearance (FA) is calculated by

$$FA = (N_{total} - 1) * Phyllochron \quad (2)$$

More rapid appearance of the first two or three leaves can cause an error which should be corrected with some plant species. However, for the purposes of this chapter such effects will be ignored.

With this system, the interaction of leaf development with phenology can be described without involving duration of expansion of individual leaves. However, determination of duration of expansion is valuable when modeling leaf area. As is seen with maize,¹⁴ duration of expansion is more complex than tip appearance or primordia initiation, as it varies with leaf position. Leaf duration of expansion is strongly correlated to final areas of each leaf, as the largest leaves on a maize plant require the greatest time to expand. For simplicity, the GDD system described previously will be used for duration, with the GDD required being a function of leaf position.

TABLE 1
Sources of Data and Functions for Leaf Development

Plant species	Ref.
Maize (<i>Zea mays</i> L.)	14,66,67
Sorghum (<i>Sorghum bicolor</i> L. Moench)	3,68,69
Pearl millet (<i>Pennisetum typhoides</i> S. & H.)	69,70
Wheat (<i>Triticum aestivum</i> L.)	24,31,58,71-73
Barley (<i>Hordeum vulgare</i> L.)	44,73
Rice (<i>Oryza sativa</i> L.)	69,74,75
Cotton (<i>Gossypium hirsutum</i> L.)	65,76-80
Soybean (<i>Glycine max</i> (L.) Merrill)	48,81-85
Sunflower (<i>Helianthus annuus</i> L.)	45,86-88
Cowpeas (<i>Vigna unguiculata</i>)	89
English peas (<i>Pisum sativum</i> L.)	8,86
Faba bean (<i>Vicia faba</i> Maris Bead)	46
Sugarbeet (<i>Beta vulgaris</i> L.)	90-92
Subterranean clover (<i>Tricolum subterraneum</i> L.)	8
Velvet leaf (<i>Abutilon theophrasti</i>), Lambsquarter (<i>Chenopodium album</i> agg.), Pigweed (<i>Amaranthus hybridis</i>), and Cocklebur (<i>Xanthium canadense</i>)	86
Cocklebur (<i>Xanthium pennsylvanicum</i> Wallr.)	93
Banana (<i>Musa</i> sp.)	55

II. RESULTS

A. LEAF APPEARANCE RATE

Due to the scarcity of data (Table 1) related to leaf initiation rates, only comparisons of leaf appearance rates will be made in the following discussion. However, the initiation rate data are provided for future reference (Table 2).

The results for base temperature for the major warm-season grain and oil crops are strikingly similar (Table 2). It appears that a base temperature of 7 to 9°C could be used for maize, sorghum, pearl millet, rice, soybean, and sunflower. The greatest differences among species appears to be

TABLE 2
Parameters for Leaf Development for Various Crop Species (Data Sources with Drastically Different Base Temperature within a Species are Identified)

Plant	t_b	t_{opt}	t_{max}	GDD/ primordium	GDD/ leaf tip	N_o	N_{total}
Leaves		°C					
Maize	8	32	42	20	39	6	8—48
Sorghum a ^{1,68}	8	26	—	—	48	4	—
b ⁶⁹	8	—	—	—	44	—	—
Pearl millet c ⁷⁰	12	28+	—	24	26	—	—
b ⁶⁹	7	—	—	—	43	—	—
Wheat	0	25	—	—	99	—	—
Barley	1	—	—	—	75	—	—
Rice d ⁷³	5	—	—	—	90	—	—
b ⁶⁹	7	—	—	—	76	—	—
e ⁷⁰	7	—	—	—	—	—	—
Cotton	12	32+	—	—	37—41	—	—
Soybean f ⁸¹	7	—	—	—	54	—	—
g ⁸²	9	—	—	—	55	—	—
h ⁸⁵	7	—	—	—	70	—	—
i ⁸³	9	—	—	—	55	—	—
j ⁸⁴	10	—	—	—	—	—	—
k ⁴⁸	10	—	—	—	52	—	—
l ⁸⁶	4	—	—	—	52	—	—
Sunflower l ⁸⁶ ,m ⁸⁷	9	—	—	12	29	—	22—29
n ⁸⁸	0	—	—	—	38	—	—
Cowpeas	16	—	—	—	30	—	—
English peas l ⁸⁶	9	—	—	—	38	—	—
o ⁸	3	25	64	—	41	—	—
Faba bean	1	—	—	—	44	—	—
Sugarbeet p ⁹⁰	2	—	—	—	30	—	—
q(early trifoliolates only) ⁹¹	1	—	—	—	31	—	—
r ⁹²	5	—	—	—	29	—	—
Subterranean clover	2	22	42	—	80	—	—
Lambsquarter	15	—	—	—	15	—	—
Pigweed	10	—	—	—	12	—	—
Velvetleaf	8	—	—	—	24	—	—
Cocklebur	6	—	—	—	50	—	—
Banana	8	27	—	—	196	—	—

TABLE 3
Functions for Duration of Expansion of Individual Leaves

Plant species	Function
Maize	Duration (in GDD ₁₀ for temp. > 20 and in GDD ₇ for temp. < 20) = $37.58 * N - 1.576 * N^{**2}$, where N is the leaf number ¹⁵ Rate of leaf extension for 15 < temp. < 35 has a tbase of 7°C and t _{opt} of 35 and was nonlinear for temp. < 15°C ⁹⁴
Sorghum	DUR = LFNO * 16.7 ³
Wheat	t _b for leaf extension = 6°C and t _{opt} = 28°C, ⁷² or t _b for leaf extension = 0°C and linear to at least 20°C ²⁴
Sugarbeet	t _b for leaf expansion rate = 7°C ⁹⁰ t _b for leaf expansion rate = 3°C ⁹¹
Soybean	Duration of expansion of a primary leaf = 70 GDD ₁₅ with temperature set equal to 23°C if it exceeds 23°C ⁸⁸
Faba bean	1/[duration of expansion(d)] = 0.0057 (temp - 1.0) ⁴⁶
Cowpea	t _b for leaf expansion = 20°C ⁸⁹

the GDD required per leaf tip. Rice had the slowest leaf appearance rates, with 76 GDD₇ per leaf. Sunflower had the fastest rate of appearance, with only 29 GDD₉ per leaf. The others, in increasing order of GDD required per leaf, were maize, pearl millet, and sorghum. These three had 39 GDD₈, 43 GDD₇, and 46 GDD₈ per leaf, respectively.

Cotton and cowpea had greater base temperatures with values of 12 and 16°C, respectively. The GDD per trifoliate for cotton was similar to the grain crops, ranging from 37 to 41 GDD₁₂ per leaf. The value for cowpea was lower at 30 GDD₁₆ per leaf.

English pea and sugarbeet generally had lower base temperatures than the grain crops. Mean values were 6 and 3.5°C, respectively. The GDD per leaf ranged from 38 to 41 for English pea and from 29 to 30 for sugarbeet at these base temperatures.

A base temperature near 0°C was reported not only for the two winter cereals as expected, but also for faba bean and subterranean clover. The base was 0°C for wheat, 1°C for barley and faba bean, and 2°C for subterranean clover. GDD per leaf was noticeably smaller for the faba bean with 44. Wheat required 99 GDD per leaf, barley required 75, and finally, subterranean clover required 80.

Of the four weed species included, two had high base temperatures, similar to cotton, and two had base temperatures close to 7°C. The two with high base temperatures, lambsquarter and pigweed, required only 12 to 15 GDD per leaf. Velvetleaf and cocklebur required 24 GDD₈ and 50 GDD₆ per leaf, respectively.

B. DURATION OF LEAF EXPANSION

Duration of leaf expansion is strongly related to leaf number for maize^{14,15} and sorghum³ (Table 3). The larger the final leaf area of a leaf, the greater the duration of expansion. Like leaf tip appearance rate, leaf expansion duration has also been shown to be dependent on temperature for several species.

After describing the thermal response of the three systems, leaf primordia initiation, leaf tip appearance, and leaf duration of expansion, it is of interest to know what other factors, such as water or nutrients, can alter these processes. A better appreciation of the effects of such factors should aid in interpretation of errors or model improvement when predicting leaf development in variable field environments.

C. EFFECTS OF DROUGHT STRESS

Moisture stress, either excess or drought, reduces the rate of leaf extension of maize,¹⁶⁻¹⁸ sorghum,^{19,20} sunflower,^{21,22} soybean,^{21,23} and wheat.²⁴ However, moisture stress effects on the three processes of leaf development have not been as thoroughly investigated.

The effect of moisture stress on leaf primordia initiation is critical in that altered initiation could change the total number of leaves of a plant and thus the duration of the vegetative phase. Moisture stress prior to panicle initiation has been shown to decrease²⁵ or increase²⁰ the final number of sorghum leaves by one to two leaves. Leaf initiation is very sensitive to moisture stress in *Lupinus alba*,²⁶ barley,²⁷ and sunflower.²⁸ Rate of initiation can be halted if drought stress is sufficiently severe.

The effect of drought on rate of leaf tip appearance differs among crop species. Drought has been shown to slow down or stop leaf tip appearance of sorghum,²⁵ tobacco,²⁹ and cassava.³⁰ However, leaf appearance of wheat was 10% faster with dryland treatment than with irrigation.³¹ Likewise, leaf appearance of maize can show a short-term delay due to drought, but the effect largely disappears with silking.^{32,33} Similarly, drought severe enough to limit leaf area of sunflower to one third of the value of the control had no effect on leaf appearance.³⁴

Duration of leaf growth also responds to drought differently depending on crop species. Drought did not alter duration of expansion of wheat.²⁴ In contrast duration of leaf expansion of sunflower decreased 11 to 22% when drought stress occurred.³⁴

D. PHOTOPERIOD, RATE OF CHANGE OF PHOTOPERIOD, AND SOLAR RADIATION

In field environments, associations between photoperiod, cumulative solar radiation, temperature, and a variety of other environmental factors make actual cause and effect relationships difficult to distinguish from spurious correlations. This is especially true for developmental response to photoperiod and amount of solar radiation. However, determination of the true environmental stimulus — photoperiod or amount of solar radiation — causing the plant response is critical for developing models which are general across temperate and tropical regions. For this reason, it is often most appropriate to develop relationships with data from controlled environment growth chambers and validate such relationships with data from field environments. In growth chambers, photoperiods can be extended with low light, thus increasing the accumulated solar radiation only a negligible amount. Likewise, rate of change of photoperiod can be altered without simultaneous changes in cumulative daily solar radiation or changes in temperature as are experienced in the field. Such carefully derived response functions should then be tested for reasonability and accuracy using field data. This aids in avoiding errors in response functions due to artifacts of the growth chamber facility or experimental design.

Another important consideration in deriving relationships between environmental variables and plant developmental processes is the pertinent range for such variables in the field. Care should be taken to ensure that an excessive amount of research effort not be invested in studying plant response to a variable in a range not normally experienced in the field. Photoperiods outside the 10 to 17.5 h range seldom if ever occur in the field environment at times when crop plants are sensitive to photoperiod. Likewise, in temperate regions, daily values for PAR below 3.8 MJ/m²/d for extended periods only occur in winter periods when temperatures are too low for any measurable development. Typical clear-day values for March to September at latitudes of 30 to 50N are 8 to 15 MJ/m²/d.³⁵ At latitudes under 30, clear-day values range from 7 to 15 MJ/m²/d throughout the year. Developmental response functions derived from data with unrealistically low PAR are of limited value for application-oriented plant models.

E. LEAF INITIATION WITH DIFFERENT PHOTOPERIODS AND SOLAR RADIATION

Leaf initiation rate of maize has been shown to have a variable response to photoperiod. In

a 10 h photoperiod with 2.6 MJ PAR/m²/d, rate was 15 to 19% greater than in a 20 h photoperiod at similar daily PAR.³⁶ In a similar study, maize leaf initiation rates were 11% smaller in a 12 h photoperiod with 8.7 MJ/m²/d PAR than in a 16 h photoperiod with 11.5 MJ/m²/d PAR.¹²

In a study with very low PAR, leaf initiation rate of cucumber (*Cucumis sativus*) showed no response to incident PAR from 1.2 to 2.3 MJ/m²/d.³⁷ Only when values for PAR decreased below 1.2 MJ/m²/d was the rate of leaf initiation decreased.

F. LEAF APPEARANCE AND DURATION OF EXPANSION WITH DIFFERENT PHOTOPERIODS AND SOLAR RADIATION

Leaf appearance rate and duration of leaf expansion are more easily measured than leaf initiation rate, and thus have been more frequently studied. Treatments which have been investigated include differences in cumulative daily solar radiation, different photoperiods, and different rates of change of photoperiod. The first two types of treatments will be discussed here, while rate of change of photoperiod will be discussed in a later section.

For maize, the response of leaf appearance rate to photoperiod has varied according to the methods of imposing the treatments. Serial sowings in a greenhouse³⁸ failed to show a consistent relationship between photoperiod and rate of leaf appearance when PAR exceeded 3.8 MJ/m²/d. In growth chambers,¹² rate of leaf collar appearance in a 12 h photoperiod and with a total PAR of 8.7 MJ/m²/d was 16 to 20% lower than rate in a 16 h photoperiod with a total PAR of 11.5 MJ/m²/d, when temperature was 18°C. However, when temperature was 28°C, there was no significant difference in appearance rate among the photoperiod treatments. Finally, when using field data from several latitudes,³⁹ leaf tip appearance rate was positively correlated with photoperiod. The mean GDD₅ per leaf when photoperiods were less than 12.5 h was 27% greater than with photoperiods of 15.7 to 16.0 h.

Results with wheat and barley, like those with maize, indicate that the methods of imposing the treatments alter the response of leaf appearance rate. Rate of leaf appearance of barley in growth chambers is constant over a wide range of radiation flux density.⁴⁰ Even when flux density treatments were 6-fold different, rate of leaf appearance differed by only 15%. Photoperiod treatments of 8 and 16 h in growth chambers, with nearly identical total light energy, produced little difference in rate of leaf appearance of wheat.⁴¹ However, decreasing illuminance with the same photoperiods caused a systematic decrease in rate of leaf appearance of wheat in growth chambers.⁴² Likewise, growth chamber treatments with both greater photoperiod and greater total PAR per day caused an increase in rate of leaf appearance of wheat.⁴³ Furthermore, results with serial sowings of wheat in Wales showed a strong positive relationship between the photoperiod at seedling emergence and the rate of leaf appearance of barley.⁴⁴

Field results with sunflower indicate that the rate of leaf appearance is sensitive to radiation flux density, but duration of leaf expansion is not.⁴⁵ Shading of 50% caused a 11% reduction in rate of leaf appearance. An 80% shading treatment caused a 21% reduction in rate of leaf appearance. Duration of expansion of individual leaves was not affected by these treatments.

Results with faba bean and soybean indicate that the rate of leaf appearance in the former is not sensitive to radiation level, while the latter can be sensitive to either photoperiod or radiation level. In the field, reduction of solar radiation by 56% did not alter rate of leaf appearance or duration of leaf expansion of faba bean.⁴⁶ For soybeans in the field, rate of leaf appearance differed by 12% among treatments differing in the radiation level of the artificial photoperiod extension.⁴⁷ Likewise, for soybeans in growth chambers,⁴⁸ leaf appearance was 14 to 33% slower in a 10 h photoperiod with total PAR of 3.9 MJ/m²/d than in a 16 h photoperiod with total PAR of 6.3 MJ/m²/d. In the same study, leaf appearance in an 8 h photoperiod with total PAR of 3.1 MJ/m²/d was 9% slower than in an 8 h photoperiod with 6.3 MJ/m²/d.

Responses of leaf appearance of forages to increasing photoperiod include decreased rate, no effect, and increased rate, depending on the species. Leaves of tall fescue (*Festuca arundinacea* Schreb.) appeared more rapidly in 8 h than in 16 h photoperiods when both treatments had nearly

the same total cumulative radiation.⁴⁹ Increases in the natural photoperiod from 8 to 16 h had little influence on rate of leaf appearance of ryegrass (*Lolium perenne* L.), but decreased rates of leaf appearance of orchardgrass (*Dactylis glomerata* L.) and meadow fescue (*Festuca elatior* L.) by 13%.⁵⁰ In the same study, low light extensions of an 8 h natural daylength with 4 h of low light at each end of the natural photoperiod reduced the rate of leaf appearance of the three species by 12 to 19%. In growth chambers, rate of leaf appearance of orchardgrass and ryegrass were 24 and 8% lower in longer photoperiods of equal energy supply.⁵¹ However, leaf appearance rate of meadow fescue was not sensitive to photoperiod. Rate of leaf appearance of ryegrass, orchardgrass, browntop (*Panicum fasciculatum* Swartz) and paspalum (*Paspalum dilatatum* Poir.) increased in response to an increase in photoperiod from 8 to 16 h along with a concomitant doubling of total light energy.⁵² Rate of leaf appearance of rye (*Secale cereale* L.)⁵³ and ryegrass⁵⁴ showed no response to the cumulative radiation or photoperiod.

Leaf appearance of cucumber was slower when PAR was below 1.2 MJ/m²/d.³⁷ Similar to leaf initiation for this species, there was no noticeable change in rate of leaf tip appearance from 1.2 to 2.3 MJ/m²/d.

In several field data sets with bananas (*Musa* sp.), leaf appearance rate in a 14 h natural photoperiod was 25% faster than the rate in a 10 h natural photoperiod.⁵⁵

G. LEAF APPEARANCE WITH DIFFERENT RATES OF CHANGE IN PHOTOPERIOD

Rate of change of photoperiod has been found to be correlated with leaf appearance rate of wheat and barley in the field.⁵⁶⁻⁵⁸ However, controlled environment research has failed to support this as a cause and effect relationship. An experiment in controlled-temperature growth chambers indicated that rates of change of photoperiods of +5 min/d, -5 min/d or no change had no effect on leaf appearance rates of two wheat cultivars and two maize hybrids.⁵⁹

H. NUTRIENTS

Nitrogen stress for the most part does not seem to alter rate of leaf appearance of forages. The general conclusion in a review on leaf appearance rate of grass species was that there was no noticeable response of leaf appearance rate to mineral nutrition.⁶⁰ Rate of leaf appearance of timothy (*Phleum pratense* L.) was not influenced by the level of nitrate in the culture solution used.⁶¹ Different levels of nitrogen nutrition in the culture solution did not alter rate of leaf appearance on the main shoot of rye plants.⁵³ Nitrogen deficiency sufficiently severe to stop tiller formation of ryegrass had no effect on the rate of appearance of the leaves.⁵⁴

However, for some crops it appears that nitrogen stress can alter leaf appearance. When the radiation intensity was sufficiently great, the leaf appearance rate of wheat was decreased 29% by nitrogen stress.⁶² Likewise, leaf appearance rate of soybean fertilized with only 3 mM of N in solution was 13% below the rate of soybean fertilized with 18 mM of N in solution.⁴⁸

I. WITHIN-SPECIES CULTIVAR DIFFERENCES

In any modeling effort, when attempting to simulate a crop species across a wide range of latitudes and regions, cultivar differences should be investigated. Such differences for leaf appearance rates exist in some common crop species. Leaf initiation rate of maize cultivars has been found to differ by as much as 12 to 16% from the mean value.⁶³ Likewise, rates of leaf appearance of different maize cultivars could vary by as much as 12 to 16% from the mean.⁶⁴ The GDD per leaf of some cotton cultivars can be as much as 6 to 8% different from the mean.⁶⁵ Leaf appearance rate of soybean cultivars can vary by as much as 28%.⁴⁸

III. SUMMARY

The majority of plant species in this chapter can be categorized into three groups depending

on their base temperatures for leaf development. The most extensive group has base temperatures of 7 to 9°C. These species include maize, sorghum, pearl millet, rice, soybean, sunflower, English peas, velvet leaf, and banana. From an application viewpoint, GDD with a base temperature of 8°C could be used for all of these. The second group, with base temperatures of 0 to 2°C, includes the winter cereals wheat and barley, as well as faba bean, sugarbeet, and subterranean clover. As with the first group, a single base temperature value should be adequate. The intermediate value of 1°C is the obvious choice. Finally, the group with base temperatures of 12 to 16°C includes cotton, cowpeas, and lambsquarter. The average base temperature for these is 14°C.

The impact of environmental factors other than temperature on leaf appearance is unresolved and appears to vary with species. Drought retards leaf appearance of sorghum, tobacco, and cassava, but such an effect is not evident for wheat, maize, and sunflower. Radiation flux density appears to have no effect on leaf appearance of maize, barley, and faba bean. In contrast, decreases in flux density slowed leaf appearance of soybeans and sunflower. Reported effects due to photoperiod and rate of change of photoperiod are difficult to verify at this time due to frequent confounding by temperature and total daily PAR. Likewise, while a range of genotypes within a species can often be chosen which will demonstrate within-species variability in leaf development, future research may show that the majority of commercial cultivars within each crop species can be simulated with a single GDD system.

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