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ABSTRACT

Phenological development affects canopy structure, radiation interception, and dry matter production; most crop simulation models therefore incorporate leaf emergence rate as a basic parameter. A recent study examined leaf emergence rate as a function of temperature and daylength among wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) cultivars. Leaf emergence rate and phyllochron were modeled as functions of temperature alone, daylength alone, and the interaction between temperature and daylength. The resulting equations contained an unwieldy number of constants. Here we simplify by reducing the constants by >70%, and show leaf emergence rate as a single response surface with temperature and daylength. In addition, we incorporate the effect of photosynthetic photon flux into the model. Generic fits for wheat and barley show cultivar differences less than $\pm 5\%$ for wheat and less than $\pm 10\%$ for barley. Barley is more sensitive to daylength changes than wheat for common environmental values of daylength, which may be related to the difference in sensitivity to daylength between spring and winter cultivars. Differences in leaf emergence rate between cultivars can be incorporated into the model by means of a single, nondimensional factor for each cultivar.

IN A SERIES of three papers (Cao and Moss, 1989a,b,c; hereafter C&M-a, C&M-b, and C&M-c), Cao and Moss computed the leaf emergence rate (LER, leaves d^{-1}) for wheat and barley by counting the number of leaves on the main stem as a function of time. The slope of leaves vs. time was used to estimate the emergence rate. They found a linear relationship; i.e., LER is constant for a given environment from the time of seedling emergence and up to 20 d, or approximately the third leaf. They also were concerned with a related quantity, the phyllochron (P in degree-days leaf $^{-1}$), which is the thermal time required for the emergence of each leaf. As they stated, these quantities are important in many dynamic simulation models and need refinement.

They conducted experiments using four soft-white winter wheat cultivars and four spring barley genotypes. Temperature and daylight hours were varied to determine the effect on LER and P . Temperature (T) varied from 7.5 to 25 °C. Daylight hours (D), with a photosynthetic photon flux density of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, varied from 6 to 24 h.

Cao and Moss fit curves for LER and P as functions of T (C&M-a), as functions of D (C&M-b), and as functions of a synthetic quantity they called the thermal-photo ratio, TD^{-1} , in degree-days per hour (C&M-c). Their equations are useful, but have important inconsistencies. Our objective was to combine their findings into a single equation for LER that will sim-

plify the application in larger models. For symbols and variables used, see Table 1.

RESULTS FROM CAO AND MOSS

Temperature Effects

The results of an experiment to isolate temperature effects were reported in C&M-a. With $D = 14$ h, T was varied between 7.5 and 25 °C at intervals of 2.5 °C. Data points for LER and P fell along smooth curves. They fit LER and P with the following equations:

$$\text{LER} = c_1 + c_2T - c_3T^2 \quad [1a]$$

$$P = c_4 \exp(c_5T) \quad [1b]$$

The constants, c_1 to c_5 , were fit for each of the eight cultivars of wheat and barley.

Daylength Effects

Photoperiod effects were examined in C&M-b. With $T = 15$ °C, D was varied at 8, 10, 12, 14, 16, 18, 21, and 24 h. As with the T variation, the resulting LER and P were smooth curves. They fit these data with the following equations:

$$\text{LER} = \frac{D}{c_6 + c_7D} \quad [1c]$$

$$P = \frac{c_8 + c_9D}{D} \quad [1d]$$

These equations require four new constants. Note that $c_6 \neq c_8$ and $c_7 \neq c_9$, because, as explained more fully below, P and LER vary by a factor that must include T .

Temperature and Daylength Interactions

In C&M-c, Cao and Moss examined the value for the phyllochron in experiments in which $T = 10, 15,$ and 20 °C, and $D = 6, 10, 14,$ and 18 h. When these 12 points were plotted against a thermo-photo ratio, a term proposed by Cao and Moss with the units of degree-days per hour of photoperiod (TD^{-1}), there was a linear correlation. The following equation was used to fit this data:

$$P = c_{10} + c_{11} \frac{T}{D} \quad [1e]$$

Since C&M-c emphasized the phyllochron, the data and potential models for LER were not shown.

Choices among Models

There are several inconsistencies in the results reported by Cao and Moss. For example, consider Eq. [1a] and [1b]. Presumably, a modeler could select either Eq. [1a] for LER or Eq. [1b] for P , depending on the needs of the model. However, P is usually defined as a function of LER, T , and a constant base temperature (T_b):

$$P = \frac{T - T_b}{\text{LER}} \quad [2]$$

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Table 1. List of symbols used in modeling light and temperature effects on leaf emergence in wheat and barley.

Symbol	Name	Units
D	daylength, photoperiod	h
T	temperature	°C
LER	leaf emergence rate	leaves d ⁻¹
P	phylochron	degree-days leaf ⁻¹
PPF	photosynthetic photon flux	mol m ⁻² d ⁻¹
PPF ₀	value for PPF where LER = 0	mol m ⁻² d ⁻¹
PPF _{hr}	PPF half-saturation constant	mol m ⁻² d ⁻¹
c_i	constants in Eq. [1a-e]	various dimensions
D_{hr}	photoperiod half-saturation constant	h
T_{max}	temperature at maximum LER	°C
a_i	constants in Eq. [3a]	various dimensions
a	rate constant in Eq. [3b]	leaves d ⁻¹
b	maximum LER in Eq. [3c]	leaves d ⁻¹
d	maximum LER in Eq. [5a]	leaves d ⁻¹
r	rate constant in improved model, Eq. [4]	leaves d ⁻¹
f	factor to account for PPF effect on LER	nondimensional

Using this definition, a modeler could select either Eq. [1a] or Eq. [1b] and calculate both LER and P . Note that Eq. [1a] and [1b], taken as a pair, do not satisfy the relation of definition between P and LER in Eq. [2], and therefore present an inconsistency.

A similar choice confronts the modeler computing LER and P for a specified daylength. Again, two equations, Eq. [1c] and [1d], functionally could be reduced to one by using the definition in Eq. [2].

Most growth models require knowledge of LER as a function of both T and D . C&M-c presents a potential solution to the interaction between T and D in Eq. [1e]; however, a model for the interaction of T and D should indicate how T varies with constant D and how D varies with constant T . If so, then Eq. [1e] with D equal to a constant should be identical (in the structure of its variables and constants) to Eq. [1b]. This is not the case here: Eq. [1e] with D equal to a constant shows P to be a linear function of T , while in Eq. [1b] P varies exponentially with T . The different solutions shown by Cao and Moss present difficulties for the modeler who must select, perhaps arbitrarily, from among several possibilities.

THE IMPROVED MODEL

Temperature and Daylength Effects

It appears that smooth curves for LER and P as a function of D in Eq. [1c] and [1d] could alternatively have been fit with either parabolic or exponential curves, like those used in Eq. [1a] and [1b]. Cao and Moss did not explain why they chose their functions.

We develop a single model that is simple and physiologically meaningful. First, we suggest deriving an equation either for LER or for P , and then consistently calculating the other, if required, using Eq. [2]. We select LER as the fundamental property of the plant, because it is a rate. Also, the phylochron definition is not universal; it can also be defined as days per leaf.

For the effect of temperature alone we select a parabolic form. A parabola accounts for both positive and negative effects of T on LER. When T is close to the baseline temperature, an increase in T increases development, which increases LER. As T becomes large, negative effects begin to dominate; e.g., protein den-

aturation rates increase with temperature (Morowitz, 1975), which slows the development. This is similar to the idea behind the logistic equation (see Causton and Venus, 1981, for a review of its applications), with a positive first-order term and a negative second-order term.

A parabola was one form used in C&M-a; see Eq. [1a]. We eliminate the additive constant c_1 for the following reasons. Since the data for wheat and barley (C&M-a) showed a base temperature of 0.02 °C, Cao and Moss used 0 °C as the base temperature to compute the degree-days for P ; in other words, $T_b = 0$ °C in Eq. [2]. For consistency, this demands that $c_1 = 0$ in Eq. [1a]. Therefore, an equation for LER as a function of T alone is:

$$\text{at constant } D, \text{ LER} = a_1 T - a_2 T^2 \quad [3a]$$

Eq. [3a] describes a parabolic curve where $\partial \text{LER} / \partial T = 0$ at $T = T_{max}$. T_{max} is a useful concept—for example, Cao and Moss compared T_{max} across cultivars—and we use it to recast Eq. [3a]:

$$\text{at constant } D, \text{ LER} = a \left[\frac{T}{T_{max}} \left(2 - \frac{T}{T_{max}} \right) \right] \quad [3b]$$

In Eq. [3b] there are still two fitting parameters, a and T_{max} . The term inside the square brackets equals 1 when $T = T_{max}$, and thus a is the maximum leaf emergence rate.

Our equation for photoperiod dynamics is similar to Eq. [1c], but is expressed in the more traditional form of the Michaelis-Menton equation:

$$\text{at constant } T, \text{ LER} = \frac{b D}{D_{hr} + D} \quad [3c]$$

Eq. [3c] has two fitting parameters, b and D_{hr} . The term b is the maximum development rate, for as D becomes large, LER approaches the value of b . In our case, D is constrained to a maximum of 24 h, and thus the actual maximum value of LER may be significantly less than the mathematical maximum b . The term D_{hr} is the half-saturation constant, and when $D = D_{hr}$, LER is exactly half of its maximum value b . This equation is commonly used in growth dynamics, where growth increases as a function of some parameter, then levels off to an asymptotic maximum.

Response Surface with Temperature and Daylength

The LER is a function of T at constant D in Eq. [3b] and a function of D at constant T in Eq. [3c]. Equations [3b] and [3c] should be the functional forms for LER that can be derived from a response surface for LER, where the dependent LER results from independent variation of both T and D . This is possible by forming a surface from the product of the right sides of Eq. [3b] and [3c]. Performing this multiplication, and letting $r = ab$, we obtain:

$$\text{LER} = r \left[\frac{T}{T_{max}} \left(2 - \frac{T}{T_{max}} \right) \right] \left[\frac{D}{D_{hr} + D} \right] \quad [4]$$

In Eq. [4], both terms in brackets are nondimensional and therefore r has the same units as LER, or leaves per day. This is a simple system: a rate is multiplied by two nondimensional terms that are functions of only T and only D , respectively. There are only three free parameters, compared to eleven in Eq. [1a-1e]. Furthermore, the three free parameters (r , T_{\max} , and D_{hr}) are relevant to plant growth: a rate, an optimal temperature, and a photoperiod. Computing the phyllochron does not add any additional parameters, because P can be computed from its definition in Eq. [2].

Daily Photosynthetic Photon Flux in the Response Surface

Temperature and photoperiod are the dominant factors influencing LER, but the total daily PPF can be important at low light levels, when there is insufficient photosynthate for normal cell division and expansion, or when comparing equal day lengths with instantaneously varying values of flux density. Friend et al. (1962) found that LER decreased by 30% as PPF was decreased from 43 mol m⁻² d⁻¹ (typical summer daily integral) to 3 mol m⁻² d⁻¹ (near the light compensation point), and this result was recently confirmed by Barnes and Bugbee (1991) (Fig. 1). Bugbee and Salisbury (1988) examined the effect of high PPF levels on development rate and found that days to anthesis (a sensitive indicator of developmental rate) was not affected by 23 to 92 mol m⁻² d⁻¹. This finding is not consistent with Friend et al., who found that LER continued to increase from 30 to 43 mol m⁻² d⁻¹. Some of the effect of PPF on LER in the Friend et al. study may have been due to temperature. Rickman et al. (1985) found that the temperature of the stem base (leaf growing point) increased with increasing PPF, and that almost all of the effect of PPF on LER was explained by the temperature change. It is extremely difficult to maintain a constant plant temperature with increasing radiation unless chilled water baths are installed below the lamps. Water baths were used by both Barnes and Bugbee (1991) and Bugbee and Salisbury (1988), but not by Friend et al. (1962). The effect of PPF is probably negligible above 30 mol m⁻²

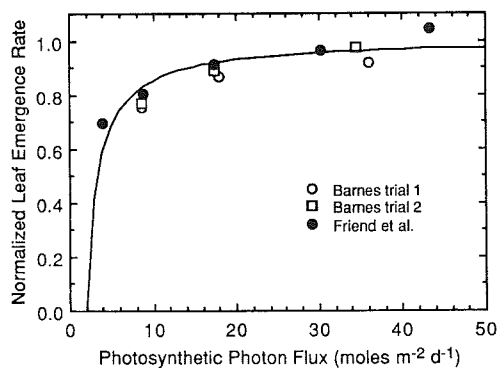


Fig. 1. Fit to data of Barnes and Bugbee (1991) and Friend et al. (1962) using Eq. [5a] with $d = 1$. Data have been normalized and combined using procedure described in text, and assuming minimal photosynthetic photon flux required to balance maintenance respiration (PPF_0) = 2 mol m⁻² d⁻¹. Best fit yields half-saturation $\text{PPF}_{\text{hr}} = 3.4$ mol m⁻² d⁻¹.

d⁻¹ and this parameter could therefore be ignored in most field studies.

The effects of PPF cannot be ignored, however, in studies below 30 mol m⁻² d⁻¹, which is the case for some of the Cao and Moss values. We account for the effects of PPF on leaf emergence rate by specifying the following conditions: (i) a minimum value of PPF required to balance maintenance respiration (PPF_0); (ii) a positive correlation between PPF and LER at relatively low levels of PPF; and (iii) relatively little effect of PPF due to saturation at increasingly higher levels of PPF. These conditions can be satisfied by a modified Michaelis-Menton equation, and we write:

at constant T and D ,

$$\text{LER} = d \frac{\text{PPF} - \text{PPF}_0}{(\text{PPF}_{\text{hr}} - \text{PPF}_0) + (\text{PPF} - \text{PPF}_0)} \quad [5a]$$

In Eq. [5a], two constants, PPF_{hr} and PPF_0 , are introduced, and the difference $\text{PPF}_{\text{hr}} - \text{PPF}_0$ is similar in meaning to D_{hr} in Eq. [3c]. The overall shape of the

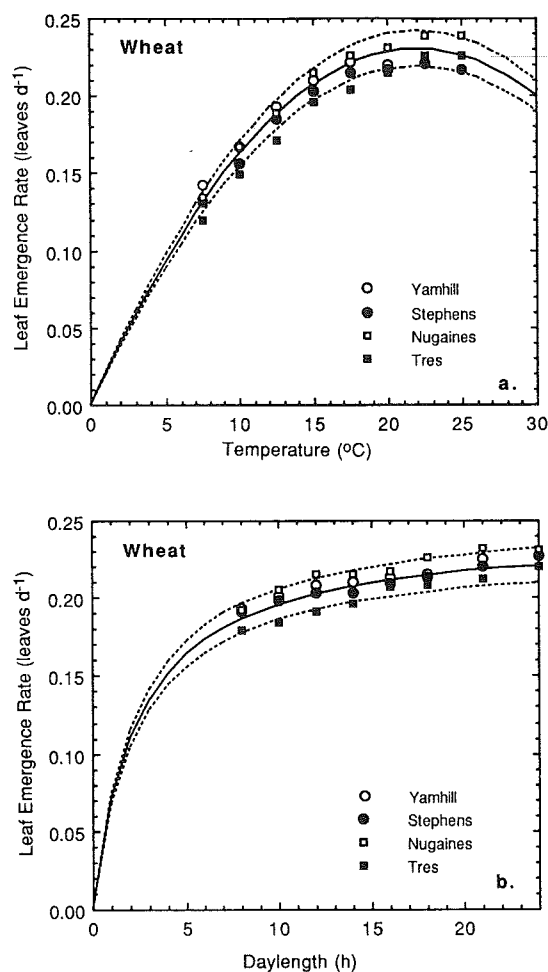


Fig. 2. Model curves generated from Eq. [4] at various conditions of (a) constant daylength $D = 14$ h and (b) constant temperature $T = 15$ °C for comparison with data for wheat genotypes from Cao and Moss (1989a,b). Model plots (solid lines) use rate $r = 0.27$ leaves d⁻¹, half-saturation daylength $D_{\text{hr}} = 2.4$ h, $T_{\max} = 22$ °C. Effect of increasing and decreasing r by 5% shown by dotted lines. Cao and Moss data has been corrected for PPF using Eq. [5b] and Fig. 1, as described in the text.

function derives from the differences between the terms PPF and PPF_0 and between PPF_{hr} and PPF_0 . The constant d is a rate with the same units as LER.

It is possible to incorporate the effect of PPF on LER by multiplying the right hand side of Eq. [4] by the right hand side of Eq. [5a] and eliminate d by subsuming it in the term r . This would add two additional constants to the response surface, making a total of five. However, because PPF is important only in low light, we propose using the inverse of Eq. [5a] to adjust LER so that the effect of PPF can be eliminated before using Eq. [4].

We define a coefficient (f) that can be used to adjust the data for LER from Cao and Moss to eliminate the effect of PPF, as follows:

$$f = \frac{(PPF_{hr} - PPF_0) + (PPF - PPF_0)}{PPF - PPF_0} \quad [5b]$$

The function f is computed using data from Barnes and Bugbee (1991) and Friend et al. (1962) using a

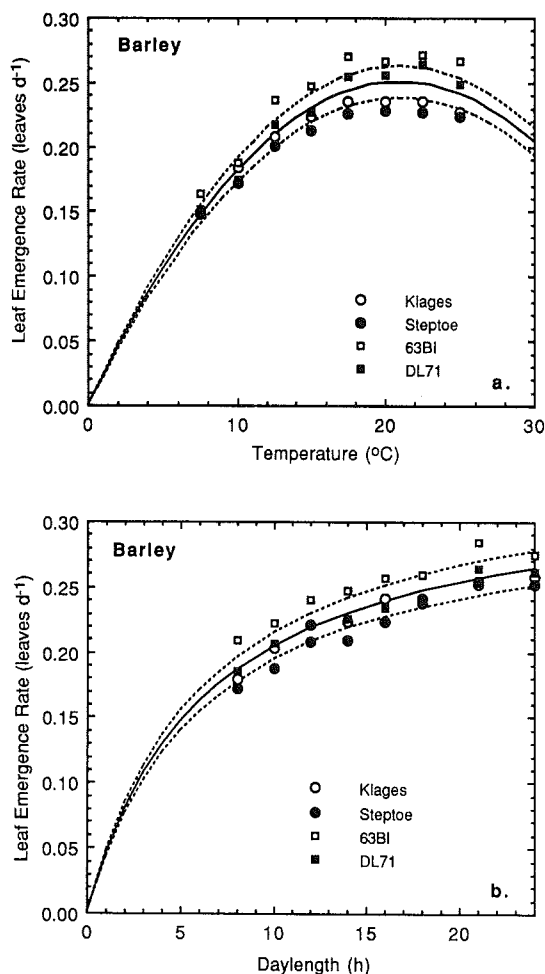


Fig. 3. Model curves generated from Eq. [4] at various conditions of (a) constant daylength $D = 14$ h and (b) constant temperature $T = 15$ °C for comparison with data for barley genotypes from Cao and Moss (1989a,b). Model plots shown use rate $r = 0.36$ leaves d^{-1} , half-saturation daylength $D_{hr} = 6.3$ h, $T_{max} = 21$ °C. Effect of increasing and decreasing r by 5% shown by dotted lines. Cao and Moss data has been corrected for PPF using Eq. [5b] and Fig. 1, as described in the text.

two-step fitting procedure. First, we separately fit the two data sets using Eq. [5a] to derive a different PPF_{hr} and d for each. Each value for LER from the two data sets is then normalized by dividing by the respective fitted d s, which allows the two sets of data to be combined into a single, normalized set (Fig. 1). Finally, this combined set is fit to derive a single value of PPF_{hr} . In the normalized combined set, d is equal to unity. We assume $PPF_0 = 2$ mol $m^{-2} d^{-1}$. Changing this across a reasonable range (0–5 mol $m^{-2} d^{-1}$) of values produces only small effects ($\approx 1\%$) on the calculated correction factors.

With PPF_0 and the fitted PPF_{hr} , Eq. [5b] is used to multiply each value for LER in the Cao and Moss data set by f . Lacking additional data, we assume that LER for barley can be modified to remove the effect of PPF by the same function that we have derived for wheat. For Cao and Moss's lowest values of PPF (8 h light at 400 $\mu\text{mol} m^{-2} s^{-1}$, or ≈ 11.5 mol $m^{-2} d^{-1}$), f is ≈ 1.15 . With 24 h of daylength, f is ≈ 1.04 in the Cao and Moss experiments. The lower end of PPF in the Bugbee and Salisbury (1988) experiments is approximately the higher end of PPF in the Cao and Moss experiments; Bugbee and Salisbury thus noted no significant effect because the effect of PPF was close to saturation.

Response Surface Compared to Data

The data of Cao and Moss were fit using Eq. [4], after modification for the effect of PPF as just explained. If either D or T are assumed to be constant, then Eq. [4] is equivalent to two of Cao and Moss's original equations (here, Eqs. [1a] and [1c], with $c_1 = 0$ in Eq. [1a]). Cao and Moss proved that such formulations will fit the data for individual cultivars with a high correlation coefficient ($r^2 > 0.97$ in all cases, and usually > 0.99).

Comparisons among the wheat cultivars considered as a group, and among the barley cultivars considered as a group, could emphasize either the differences or the similarities. To examine these issues, we have combined into groups the four cultivars of wheat and the four of barley for fitting with our model.

The results for wheat and barley are shown in Fig. 2 and 3, respectively. Model fits using Eq. [4] are dis-

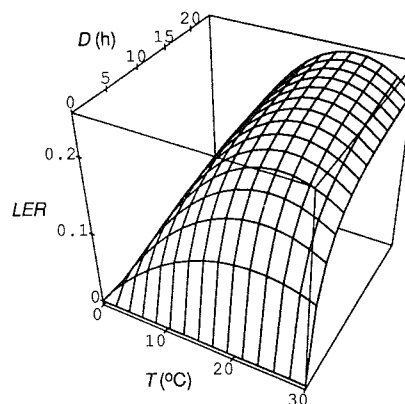


Fig. 4. Three-dimensional response surface for wheat LER (leaf emergence rate) as a function of T and D , using Eq. [4] with the constants identical to those in Fig. 2 (rate $r = 0.27$ leaves d^{-1} , $T_{max} = 22$ °C, and half-saturation daylength $D_{hr} = 2.4$ h).

played for the two two-dimensional sections where the most data were taken by Cao and Moss, varying T at constant $D = 14$ h and varying D at constant $T = 15$ °C.

For a conceptual picture of the response surface, LER for wheat as a function of T and D in three dimensions is shown in Fig. 4. For a numerical picture of the response surface, contour plots of LER for wheat and barley as a function of T and D are shown in Fig. 5. It is evident from the contour plots that LER has little sensitivity to D at low values of T and little sensitivity to T at low values of D . Low values of either environmental factor limit the potential variation in LER due to the other factor.

Our model provides a unified interpretation of the forcing processes. In contrast, the thermo-photo ratio sometimes used (C&M-c being one example) needs to be critically examined. Our model in Eq. [4] is not equivalent to Eq. [1e]. When the systems of Eq. [2] and [4] are used to plot P vs. TD^{-1} (for comparison with the analogous plot in C&M-c) the generated points are scattered across a field, rather than along a single line. In contrast, with our model, temperature, photoperiod, and leaf emergence rate can be expressed

as a parsimonious three-dimensional response surface, as shown in Fig. 4. The thermo-photo ratio does not represent the behavior of the system, and we recommend Eq. [4] as the model for the interaction of T and D .

Figures 2 and 3 exhibit differences among cultivars. In our opinion, these differences are relatively small; the wheat cultivars fall within $\approx 5\%$ of the group fit; the corresponding value for barley is somewhat larger, $\leq 10\%$. These data should be weighed into the modeling objectives to determine the utility of working toward separate coefficients for each cultivar against the streamlining possible with a single generic set of coefficients that could apply to all cultivars.

There are strong similarities in shapes among the grouped cultivars. Specifically, Fig. 2 and 3 show that usually the LER for any particular cultivar is consistently above or below the generic fit. This observation can be incorporated easily into the model by modifying the rate multiplier r in Eq. [4] by a nondimensional cultivar factor. Table 2 lists the cultivar factors which give the least-squares fits for the wheat and barley cultivars. They range from 0.97 to 1.04 for the

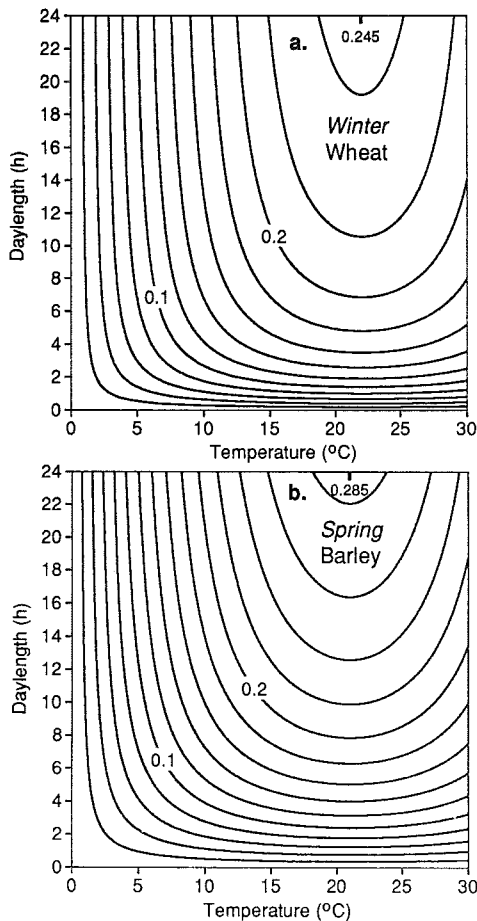


Fig. 5. Contour plots of the response surface for LER (leaf emergence rate) as a function of temperature T and daylength D . (a) Wheat. Constants identical to those in Fig. 2 (rate $r = 0.27$ levels d^{-1} , $T_{max} = 22$ °C, and half-saturation daylength $D_{hr} = 2.4$ h). (b) Barley. Constants identical to those in Fig. 3 ($r = 0.36$ leaves d^{-1} , $T_{max} = 21$ °C, and $D_{hr} = 6.3$ h).

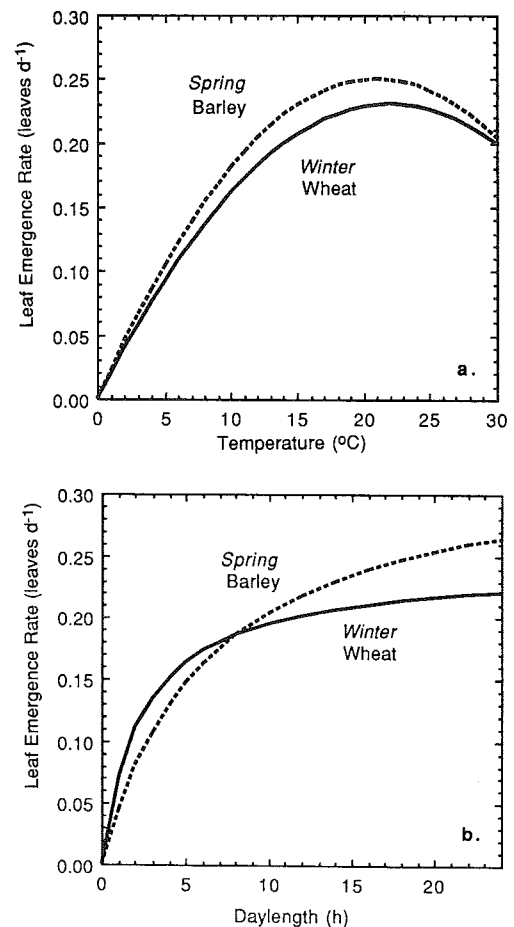


Fig. 6. The fits from Fig. 2 and 3 combined to compare and contrast wheat and barley. (a) The temperature curves are for daylengths of 14 h. (b) The daylength curves are for temperatures of 15 °C. Since all wheat cultivars are winter and all barley cultivars are spring, similarities in temperature response and differences in daylength response may be due to behaviors inherent in spring and winter cultivars.

wheat cultivars, and from 0.94 to 1.08 for the barley cultivars. The importance of small cultivar differences should not be ignored, because seemingly minor changes during early growth can have important effects on yield. We therefore suggest applying cultivar factors when necessary, and furthermore that the values for T_{\max} and D_{hf} listed in Fig. 2 and 3 for wheat ($T_{\max} = 22^{\circ}\text{C}$, $D_{\text{hf}} = 2.4$ h) and barley ($T_{\max} = 21^{\circ}\text{C}$, $D_{\text{hf}} = 6.3$ h), may be considered as species properties. In our analysis, the variation among cultivars then occurs among the rates but not the shapes.

In this context, it is useful to compare the average fit to the wheat cultivars with the average fit to the barley cultivars (Fig. 6). We see that because the difference in the value of T_{\max} between wheat and barley is so small, the difference in LER between any particular wheat and barley cultivar remains nearly a constant fraction as temperature is varied.

When daylength is varied, a substantial difference in shape occurs between wheat and barley (Fig. 6). Compared to barley, wheat saturates at very low daylengths. The barley cultivars are more sensitive to daylength than the wheat cultivars. In this study, all the barley cultivars were spring and the wheat cultivars winter. The difference in photoperiod sensitivity may be because of inherent differences between wheat and barley, or it may be an inherent difference between spring and winter cultivars.

Both spring and winter cultivars would be planted at about the same photoperiod (12 h; spring or fall equinox, respectively), but 30 d after planting, the daylength would be 3 or 4 h longer in the spring than in the fall (depending on latitude). It may be advantageous for spring cultivars to be more sensitive to daylength than winter cultivars. If spring planting were delayed, it would be useful to have a cultivar that develops rapidly, so that anthesis occurs before the onset of high temperatures. Conversely, if spring planting was early, the LER of the main culm should be slow, to maximize tillering and yield potential.

CONCLUSIONS

This paper presents a model for LER in wheat and barley that is simple and represents temperature and daylength responses. Many questions remain. This model is based on data from constant day-night temperatures. Night temperatures are almost always lower than day temperatures in a natural environment. It may not be appropriate to use an average daily temperature in this model, because temperature responses are typically parabolic and the leaf emergence rate at a constant daily temperature might not be the same as the average leaf emergence rate with diurnal fluctuations in temperature (Erwin and Heins, 1990). In some crops, however, diurnal temperature fluctuations do not affect development rate (Yourstone and Wallace, 1990).

Bauer et al. (1984) found that N and water supply did not alter the rate of wheat development of the main stem within certain bounds. Longnecker et al. (1990), however, found that N deficiency reduced LER. The effect of N on LER may be similar to that of PPF; development is somewhat affected only after

Table 2. Factors for modification of r in Eq. [4] to fit individual cultivars (Fig. 2 and 3).

Cultivar	Cultivar factor
<u>Wheat</u>	
Yamhill	1.01
Stephens	0.99
Nugaines	1.04
Tres	0.97
<u>Barley</u>	
Klages	0.98
Steptoe	0.94
63BI	1.08
DL97	1.01

growth is severely reduced. Other factors that have large effects on growth have the potential to alter development. The two variables in this study (temperature and photoperiod) almost completely control the rate of development in wheat (Bauer et al., 1984), but leaf area and yield are affected by many other variables. One could also quantify possible differences between wheat and barley in their response to changing PPF.

Our model is based on data from plants in early vegetative growth stages. Temperature and photoperiod also seem to control developmental rate during reproductive development in wheat (Porter, 1984). Photoperiod is less important than temperature in determining the length of the grain-fill period, so perhaps the photoperiod half-saturation constant (D_{hf}) shifts. The general structure of this model may be applicable to other growth stages of small grains, but with appropriate changes for T_{\max} and D_{hf} to these other stages. During seed fill, for example, D_{hf} may shift to very low values, nearly eliminating the photoperiod contribution to grain fill.

Other environmental parameters may be useful in refining the model. For example, the temperature at the stem base ($\approx 1-2$ cm below the soil surface) should be more useful in predicting LER than air temperature (Rickman et al., 1985). Although there are statistically significant differences among cultivars, refining experimental data and the model for separate cultivars may not be necessary. When such refinement is desired, we recommend multiplying the generic leaf emergence rate by a single cultivar factor, as shown in Table 2.

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