

Temperature response function for leaf appearance rate in wheat and corn

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Jame, Y. W., Cutforth, H. W. and Ritchie, J. T. 1999. **Temperature response function for leaf appearance rate in wheat and corn.** Can. J. Plant Sci. **79**: 1–10. The ability to predict leaf appearance would enhance our capability of modeling plant development and the rate of leaf area expansion. Many crop models use the constant thermal time for successive leaf tip appearance (which is often termed a phyllochron) as one model parameter to predict total number of leaves and date of anthesis. However, many researchers have found that phyllochron is not constant, but is dependent upon environment. The problem could be related to the simplified assumption that the daily leaf appearance rate is linearly related to temperature (and hence, phyllochron is constant, independent of temperature). In reality, the temperature response function for the development of a biological system is nonlinear. Thus, we fitted daily leaf appearance rate–temperature relationships obtained from growth room studies for both wheat (*Triticum aestivum*) and corn (*Zea mays* L.) to a nonlinear beta function with 0°C as the base temperature and 42°C as the upper critical temperature. The function described the relationships very well over the full range of temperatures for plant development. Other variables that are used to describe the duration and rate of leaf appearance, such as calendar days, phyllochron, and thermal rate of leaf appearance, are related to the daily leaf appearance rate, eliminating the need to develop various mathematical functions to independently describe the response of these variables to temperature. Because of the nonlinear nature of the temperature response function, we demonstrated that more accurate determinations of daily leaf appearance rates can be achieved by calculating rates over relatively short periods (i.e., hourly) and summing these to get the mean daily rate. Many environmental factors other than temperature also affect leaf appearance rate. However, once the proper temperature response function for leaf appearance rate is determined, it is much easier to determine when and how other factors are involved to modify the leaf appearance rate under a given environment.

Key words: Temperature, leaf appearance rate, phyllochron, wheat, corn, beta function

Jame, Y. W., Cutforth, H. W. et Ritchie, J. T. 1999. **Rôle de la température dans le rythme d'apparition des feuilles.** Can. J. Plant Sci. **79**: 1–10. La possibilité de prédire l'apparition des feuilles rendrait plus facile la modélisation du développement des plantes ainsi que du rythme d'expansion de la surface foliaire. Entre autres paramètres, beaucoup de modèles cultureux utilisent les sommes de chaleur constantes requises pour l'apparition des boutons foliaires successifs, ce que l'on désigne souvent du terme de phyllochrone, pour prédire le nombre total de feuilles et la date de l'anthèse. Toutefois, de nombreux chercheurs ont constaté que le phyllochrone n'est pas une donnée constante, mais qu'il est fonction des conditions du milieu. Le problème se rattache à l'hypothèse simplifiée selon laquelle le rythme quotidien d'apparition des feuilles serait en fonction linéaire de la température (et que, par conséquent, le phyllochrone demeure constant, indépendamment de la température). En fait, la fonction de réponse à la température pour le développement des systèmes biologiques n'est pas linéaire. Nous avons donc ajuster les rapports rythme quotidien d'apparition des feuilles/température obtenus dans des études en chambre de végétation sur le blé (*Triticum aestivum* L.) et sur le maïs (*Zea mays* L.) à une fonction bêta non linéaire, utilisant 0° comme seuil et 42° comme plafond thermique. Cette fonction décrivait parfaitement les rapports dans tout l'écart des températures requises pour le développement de la plante. Les autres variables utilisées pour décrire la durée et le rythme d'apparition des feuilles, c.-à-d. le nombre de jour, le phyllochrone et le rythme thermique d'apparition des feuilles, sont toutes reliées au rythme quotidien d'apparition des feuilles ce qui dispense de construire des fonctions mathématiques distinctes pour décrire la réponse de ces variables à la température. Du fait de la non-linéarité de la fonction de réponse à la température, nous démontrons qu'on obtiendrait des prédictions plus exactes des rythmes quotidiens d'apparition des feuilles en calculant ces rythmes par périodes relativement courtes (par exemple en heures) puis en les additionnant pour obtenir le rythme quotidien moyen. À part la température plusieurs autres facteurs environnementaux jouent sur le rythme d'apparition des feuilles. Cependant, une fois déterminée la fonction exacte de réponse à la température pour le rythme, il est beaucoup plus facile de déterminer quand et comment les autres facteurs interviennent pour le modifier dans une situation environnementale donnée.

Mots clés: Température, rythme d'apparition des feuilles, phyllochrone, blé, maïs, fonction bêta

A common way of describing wheat phenology during the leaf development stage is by counting the number of leaves on the main stem (Haun 1973; Zadoks et al. 1974; Klepper et al. 1982). The ability to predict the timing of successive leaf appearance is important because it impacts not only the timing of certain developmental stages of the plant but also

Abbreviations: CALDAY, chronological time (days) between the appearance of successive leaves on the main stem; DLAR, daily leaf (day⁻¹) appearance rate; PHYLLOCHRON, thermal time (°Cd) between the appearance of successive leaves; TLAR, thermal rate (°C d⁻¹) of leaf appearance; TT, thermal time

the rate of leaf area expansion. Thus, many crop models nowadays include phyllochron as one of the model parameters to predict leaf appearance on the main stem and date of anthesis (Kiniry et al. 1991). In most cases, phyllochron is cultivar specific and is assumed to be constant, independent of temperature. However, many researchers have found that phyllochron is not constant but is dependent upon environment. Environmental and genetic factors that influence the relationship between leaf appearance and whole plant development were discussed in detail in eight scientific papers presented as part of a special symposium *Understanding Development and Growth in Grasses: Role of the Phyllochron Concept* at the Crop Science Society of America meeting in Cincinnati, OH, on 10 November 1993 (Frank and Bauer 1995; Kirby 1995; McMaster and Wilhelm 1995; Moore and Moser 1995; Nemoto et al. 1995; Rickman and Klepper 1995; Skinner and Nelson 1995; Wilhelm and McMaster 1995). Temperature and daylength are recognized as the two most important factors affecting leaf appearance rate (Kirby 1995; McMaster 1997). However, both Kirby (1995) and McMaster and Wilhelm (1995) have critically evaluated several existing models describing the interaction of temperature and daylength on leaf appearance rate and concluded that none of the models provided adequate prediction for all data set examined. They emphasized the need for further research in this area. The purpose of this paper is to put forward a means of describing a nonlinear temperature response function for leaf appearance rate that may answer some of the questions raised in their papers. In a separate paper (Jame et al. 1998a), we discussed how this nonlinear temperature function can be used to determine the combined action of temperature and daylength on leaf appearance rate. As well, we demonstrated and discussed the proposed nonlinear leaf appearance model in two separate papers (Jame et al. 1998b, 1999), in which models predictions were compared to observed data from field-grown crops.

TERMINOLOGY USED TO EXPRESS DURATION AND RATE OF LEAF APPEARANCE

An implicit dimension in expressing leaf appearance rate is time. We can express the time interval between the appearance of successive leaves on the main stem in chronological time (CALDAY – days). The inverse of CALDAY is the daily rate of leaf appearance (DLAR – day⁻¹). Temperature affects plants by altering the daily rate of metabolic processes. Thus, the main effect of temperature is on the daily rate of plant development as manifested, for example, by germination, the successive appearance of leaves, and the initiation of reproductive organs (Monteith 1981). For wheat, DLAR generally starts at temperatures slightly above a base temperature (T_b) close to 0°C (Gallagher 1979; Jones, 1983) and increases with increased temperature up to about 20–25°C (Cao and Moss 1989a; Ritchie and NeSmith 1991). Above this optimum temperature (T_o), DLAR declines, reaching zero at an upper critical temperature (T_c) somewhere around 40°C (Jones 1983; Ritchie and NeSmith 1991). For corn, DLAR increases from 8 to 34°C and then decreases to 0 at 44°C (Kiniry 1991).

Because CALDAY was non-linearly related to temperature, as early as 1735, Reaumur (Wang 1960) suggested that the time required for plants to complete a phase of their development could be more accurately estimated from the sum of daily mean air temperatures than from calendar days. Since then, this approach has been widely used. The prediction of plant growth duration by the summation of temperature is generally referred to as the thermal time (Gallagher 1979; Jones 1983). Thermal time has the unit of degree-days (°C d) and is defined as:

$$TT = \sum_{i=1}^n (T - T_b) \quad (1)$$

where T is the daily mean air temperature, T_b is the base temperature at which development stops, and n is the number of days of temperature observations used in the summation. The daily mean temperature is usually calculated by averaging the daily maximum and minimum temperatures. For thermal time to be an appropriate predictor (i.e., constant thermal time for a particular developmental stage), the selection of T_b is a crucial step in calculating degree-days. Conventionally, T_b is defined as the temperature at which DLAR equals zero when determined by linear regression analysis of experimental data. Scientists have used numerous statistical methods to find a value of T_b that gives the least variation in TT for a given developmental phase across years and sites. The assumption that DLAR is linearly related to temperature implies that a crop has a constant thermal time for a particular developmental phase. For instance, a particular cultivar of wheat may need 500°Cd to reach maturity after anthesis; therefore, we accumulate daily thermal time over the number of days required to attain 500°Cd. For years, this thermal time approach has been used to predict the completion of a particular development phase of a crop.

The phyllochron is the thermal time between the appearance of successive leaves on the main stem (Kiniry 1991; Wilhelm and McMaster 1995) and is a time unit used to quantify the orderly coordinated developmental stages of a crop (Rickman and Klepper 1995). The recommended base temperature to calculate thermal time for leaf appearance is 0°C for wheat (Gallagher 1979) and 8°C for corn (Kiniry 1991; Ritchie and NeSmith 1991). Phyllochron can be determined by documenting the time of appearance of successive leaves on the main stem. In practice, the Haun scale (Haun 1973) is often used to determine phyllochron during the leaf development stage. Growth room studies (Klepper et al. 1982) as well as some field experiments (Baker et al. 1986) have shown that each leaf on the wheat plant required about the same thermal time to develop. The slope determined from this linear regression analysis is the thermal rate of leaf appearance (TLAR – °C d⁻¹). The inverse of TLAR is the phyllochron.

For small grain cereals, phyllochron varies among cultivars (Bauer et al. 1984; Baker et al. 1986; Kirby and Perry 1987; Kirby 1995). In the CERES model, the phyllochron is a genetic coefficient that is cultivar specific and is required as an input to run the model for that particular cultivar (Tsuji et al. 1994).

FACTORS AFFECTING LEAF APPEARANCE

Phyllochron is not constant but is dependent upon the environment. Several seeding date experiments conducted in the United Kingdom (Baker et al. 1980) and in western Australia (Kirby and Perry 1987) have indicated that phyllochron was correlated with the rate of daylength change at emergence. This concept has been incorporated in some wheat simulation models (Weir et al. 1984; Wilhelm et al. 1993; Rickman et al. 1996). However, more recently, researchers have found this correlation did not exist in growth rooms (Cao and Moss 1989b; Hay and Delecolle 1989) or in the field (Baker et al. 1986; Hotsonyame and Hunt 1997). If the correlation between phyllochron and change in daylength at seedling emergence existed at certain locations, it may be an environmental cue that we can determine from correlation analysis but is not the actual cause determining phyllochron shortly after emergence (Hay and Delecolle 1989; Jamieson et al. 1995; McMaster 1997).

Temperature and light (quantity and quality) are the two most important factors affecting the leaf appearance rate (McMaster 1997). Cao and Moss (1989a) studied the effect of constant temperatures ranging from 7.5 to 25°C on phyllochron and found the best fit equations were exponential; phyllochron was about 60°Cd at 7.5°C and about 120°Cd at 24°C. Cutforth et al. (1992) conducted growth room experiments to determine phyllochron in five day/night temperature regimes with mean temperatures ranging from 5 to 28°C. They also reported that phyllochron was curvilinearly related to temperature and increased as temperature increased. They obtained the best fit of their data with a cubic equation.

Cao and Moss (1989b) also found that daylength affected leaf emergence. They conducted experiments to determine the leaf appearance rate at 8, 10, 12, 14, 16, 18, 21 and 24-h daylength in growth chambers that had a constant day/night temperature of 15°C and the light intensity during the "day" of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Their results clearly indicated that as daylength increased, DLAR increased and phyllochron decreased, both curvilinearly. They proposed a linear relationship of phyllochron to the thermo/photo ratio to quantify the combined effects of temperature and daylength on the leaf appearance (Cao and Moss 1989c).

Other environmental factors affecting leaf appearance include water (Baker et al. 1986; Krenzer et al. 1991; Cutforth et al. 1992), nutrients (Dale and Wilson 1978; Longnecker et al. 1993), salinity (Mass and Grieve 1990), CO_2 (LeCain et al. 1992), light intensity (Friend et al. 1962; Barnes and Bugbee 1991), seed size (Peterson et al. 1989), planting depth (Kirby 1993) and soil strength (Masle and Passioura 1987). Another factor that may affect the leaf appearance rate of wheat is ontogeny; the rate is determined by the timing of leaf initiation at the stem apex and the duration of leaf tip elongation through the whorl of the mature sheaths (Migletta 1991).

The effects of environmental factors other than temperature on leaf appearance rate are contentious. For example, some investigators reported that water and nutrient stresses (Bauer et al. 1984; Hotsonyame and Hunt 1997) had little effect on the leaf appearance rate. However, others have

shown that water and nitrogen stresses can either increase (Baker et al. 1986) or decrease the leaf appearance rate (Cutforth et al. 1992; Longnecker et al. 1993). Apparently, there are confounding effects of temperature and other environmental factors on the leaf appearance rate. For example, phyllochron is usually determined based on air temperature; however, until stem elongation begins, the apical meristem is under the soil surface so that leaf appearance rate will be controlled by soil temperature. Soil temperature can differ substantially from air temperature, especially when the canopy is sparse (Brooking and McPherson 1989). Once stem elongation has started, leaf development rate depends on the canopy temperature, which is seldom equal to air temperature. The difference between air temperature and canopy temperature depends upon several factors. The canopy tends to be warmer than the air during conditions that keep the canopy sparse (e.g. nitrogen stress) or that limit transpiration (e.g. water stress), while it tends to be cooler than the air when the crop is well supplied with water (transpirational cooling). The effect of water stress on canopy temperature was used by Baker et al. (1986) to explain the increase in the leaf appearance rate of drought-stressed plants. Jamieson et al. (1995) reported that a model of leaf appearance based on estimates of near-surface temperature and canopy temperature gave superior predictions than others based on air temperature alone or modified by the rate of change of daylength. Thus, it appears that the conflicting results for factors other than temperature influencing leaf appearance can only be reconciled by first determining the temperature effect and then determining when and how other factors are involved to modify the leaf appearance rate.

TEMPERATURE RESPONSE FUNCTION OF DLAR

The concept of constant phyllochron in respect to temperature is based on the assumption that DLAR is a linear function of temperature. In reality, the response of the development rate of plants to temperature is nonlinear. Shaykewich (1995) stressed the importance of choosing a correct biological function to analyze the plant development rate and suggested that plant development rate should be expressed as a logistic curve or a complex logarithmic curve. In fact, numerous nonlinear temperature response functions for plant development have been proposed (Tollenaar et al. 1979; Jones 1983; Warrington and Kanemasu 1983; Cao and Moss 1989a; Shaykewich 1995). However, most of the functions either contain an unwieldy number of coefficients or are not flexible enough to describe the plant development rate over the full range of temperatures for plant development. We suggest that the most appropriate expression of the temperature response function of DLAR is the beta function (Abramowitz and Stegun 1965):

$$\text{DLAR} = \text{EXP}(\mu) \times (T - T_b)^\alpha \times (T_c - T)^\beta \quad (2)$$

where T is temperature in °C ($T_b < T < T_c$), T_b and T_c are base and critical temperatures, respectively, where DLAR = 0,

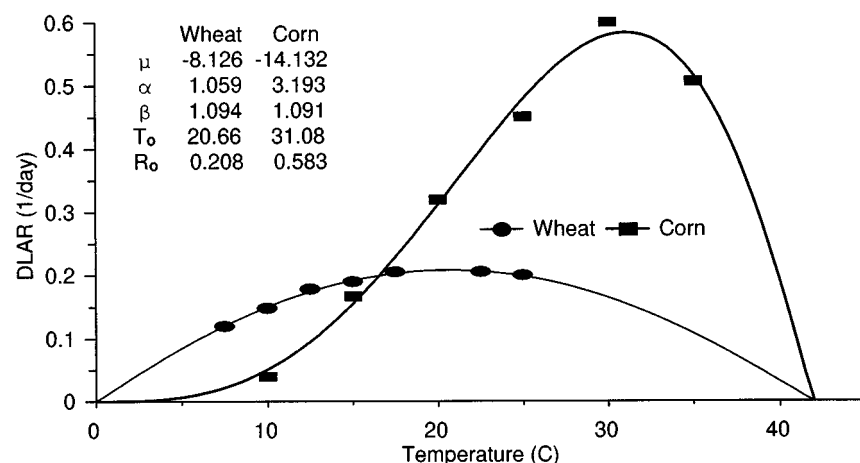


Fig. 1. The beta function describing the relationship between daily leaf appearance rate (DLAR) and temperature for winter wheat (cv. Stephens, data from Cao and Moss 1989a) and corn (data from Tollenaar et al. [1979]).

and μ , α and β are the model parameters. The optimum temperature (T_o) and the optimum value of DLAR at T_o (R_o) can be calculated from the five model parameters T_b , T_c , α , β and μ (Yin et al. 1995):

$$T_o = (\alpha \times T_c + \beta \times T_b) / (\alpha + \beta) \quad (3)$$

$$R_o = \text{EXP}(\mu) \times \alpha^\alpha \times \beta^\beta \times ((T_c - T_b) / (\alpha + \beta))^{(\alpha + \beta)} \quad (4)$$

The beta function is commonly used to describe a flexible family of nonsymmetric functions which allow points of inflection on either side of the mode. Parameter α determines the curvature of the relationship for the temperature range between T_b and T_o , whereas parameter β determines the curvature of the relationship for the temperature range between T_o and T_c . An inflection occurs in the temperature range between T_b and T_o only if $\alpha > 1$, and occurs in the temperature range between T_o and T_c only if $\beta > 1$. The beta function becomes a simple linear curve if $\alpha = 1$ and $\beta = 0$, a power function if $\beta = 0$, a quadratic function if $\alpha = \beta = 1$, and a general symmetric function if $\alpha = \beta$. The temperatures at which the inflexions occur can be calculated as:

$$T_{f1} = [(\alpha \times T_c + \beta \times T_b) / (\alpha + \beta)] - \{[(T_c - T_b) / (\alpha + \beta)] \times [(\alpha \times \beta) / (\alpha + \beta - 1)]^{1/2}\} \quad (5)$$

$$T_{f2} = [(\alpha \times T_c + \beta \times T_b) / (\alpha + \beta)] + \{[(T_c - T_b) / (\alpha + \beta)] \times [(\alpha \times \beta) / (\alpha + \beta - 1)]^{1/2}\} \quad (6)$$

where T_{f1} and T_{f2} are the temperatures at the inflection points located between T_b and T_o , and T_o and T_c , respectively.

Nonlinear curve fitting techniques (SAS Institute, Inc. 1988) can be used to determine the model parameters whether or not values of T_b and T_c are known. However, the values of T_b and T_c determined from curve fitting can be affected significantly by the nature of the data set used in a given analysis. Ideally, the parameters used in the function should be determined from data collected over the full range of temperatures expected to influence development. In reality, there are few studies that have determined development

rate at very low (near 0°C) or very high (above 35°C) temperatures. To our knowledge, most crops do not grow at temperature below 0°C nor above 40–45°C (Jones 1983; Kiniry 1991; Ritchie and NeSmith 1991). Thus, we selected $T_b = 0^\circ\text{C}$ and $T_c = 42^\circ\text{C}$ when we fitted the beta function to the data of Cao and Moss (1989a) for wheat and of Tollenaar et al. (1979) for corn (Fig. 1). Cao and Moss (1989a) grew wheat (cultivar Stephens) under constant day/night temperatures, ranging from 7.5 to 25°C in 2.5°C increments with a 14-h daylength, and Tollenaar et al. (1979) grew corn (six hybrids, namely, Stewart 2300, Trojan TX 68, United 106, PAG SX42, Pioneer 3911 and United 132) under constant day/night temperatures, ranging from 10 to 35°C in 5°C increments with a 15-h daylength. Tollenaar et al. (1979) reported the means of DLAR for the six hybrids with the corresponding temperatures. The beta function fits both wheat and corn data sets very well. The temperature response curve of DLAR for wheat is almost symmetric with $T_o = 21^\circ\text{C}$. For corn, the response curve is nonsymmetric with $T_o = 31^\circ\text{C}$ and a point of inflection at 21.2°C. At T_o , DLAR is much higher for corn than for wheat (i.e., 0.583 vs. 0.208 d⁻¹).

Cao and Moss (1989a) determined the effect of temperature on the leaf appearance rate for the first four leaves on the main stem of four winter wheat cultivars. Fitting the beta function to the DLAR-temperature data resulted in $R^2 > 0.98$ for all cultivars (Fig. 2). Although all cultivars had similarly shaped temperature response curves for DLAR, T_o and R_o varied among cultivars: Tres and Nugaines winter wheats had higher optimum temperatures (24.4 and 23.0°C) than Yamhill and Stephens winter wheats (20.9 and 20.7°C). The leaf appearance rate at T_o was slightly higher (0.22 d⁻¹) for Nugaines than for the other cultivars (0.21 d⁻¹). Thus, to develop a realistic wheat phenology model, the genotypic difference in the response of leaf appearance rate to temperature needs to be included in the model.

Slafer and Rawson (1995) studied the effect of temperature on leaf appearance rate for four Austrian wheat cultivars grown at six constant temperature regimes of 10, 13,

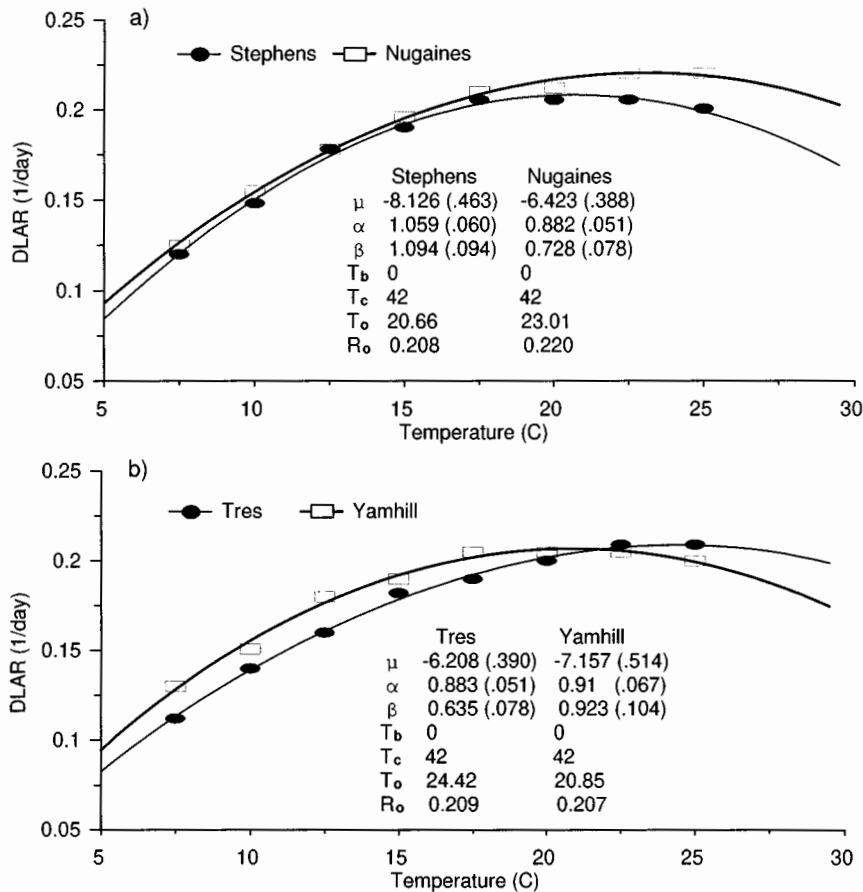


Fig. 2. The beta function describing the relationship between daily leaf appearance rate (DLAR) and temperature for four winter wheat cultivars — a) Stephens and Nugaines, and b) Tres and Yamhill — from Cao and Moss (1989a). Also listed are the coefficients (with standard errors) and cardinal temperatures, as well as the optimum temperature (T_o) and rate (R_o), for each beta function.

16, 19, 22 and 25°C. In contrast to Cao and Moss (1989a), they calculated rates of leaf appearance using all leaves on the main stem of their cultivars and found, for a given cultivar, no change in phyllochron during the course of plant development. However, they used the linear relationship to analyze the temperature response of leaf appearance rate (excluding 25°C) and found that both the slopes of the relationships (ranging from 0.0076 to 0.0092°C d⁻¹) and T_b (ranging from -1.9 to -5.9°C) differed between cultivars. We re-analyzed the data from Slafer and Rawson (1995) with the beta function (including 25°C) and found that the function described the relationship between DLAR and temperature very well over the full temperature range (Fig. 3). T_o for the four cultivars varied between 22.1 and 23.9°C and the maximum DLAR varied between 0.188 and 0.203 d⁻¹. Those values correspond closely to T_o (20.7–24.4°C) and R_o (0.207–0.220 d⁻¹) for the four cultivars used in Cao and Moss's experiment (Fig. 2). However, the measured values of DLAR at 10°C and 13°C for cultivars used in Cao and Moss's experiment were much higher (0.14–0.15 d⁻¹ at 10°C and 0.16–0.18 d⁻¹ at 12.5°C) than for those cultivars used in Slafer and Rawson's experiment (0.112–0.125 d⁻¹ at 10°C and 0.116–0.138 d⁻¹ at 13°C). Thus, α values were higher (1.44 to 1.61 vs. 0.88 to 1.06) and μ values were lower (-9.44 to -10.42 vs. -6.21 to -8.13) in Slafer and

Rawson's experiment. These differences may be due to genetics (cultivar differences) or differences in experimental techniques. In Slafer and Rawson's experiment, the plants were sown and retained at room temperature for 1 day and then transferred to a 4°C room for 50 d under 8 h low-intensity fluorescent lamps (150 $\mu\text{mol m}^{-2} \text{s}^{-1}$) before being transferred to the differential temperature chambers in the phytotron. In those chambers, the total light period was 18 h: 9 h of natural radiation that was artificially extended a further 9 h with low-intensity incandescent lamps of about 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. As mentioned previously, in Cao and Moss's experiment they used a 14 h daylength with a PPFD of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Because the DLAR is strongly affected by the interaction between temperature and daylength, it is difficult to compare temperature treatments of Cao and Moss (1989a) and Slafer and Rawson (1995). This also stresses the importance that, when applying DLAR derived from experiments conducted under a set of controlled environments to field conditions, adjustment may be needed to account for the effect of different environments on DLAR. The comparison of the relationships derived from growth room studies discussed in this paper and those obtained from conditions with the high light intensity and wide range of temperature in the field was presented in a separate paper (Jame et al. 1989b).

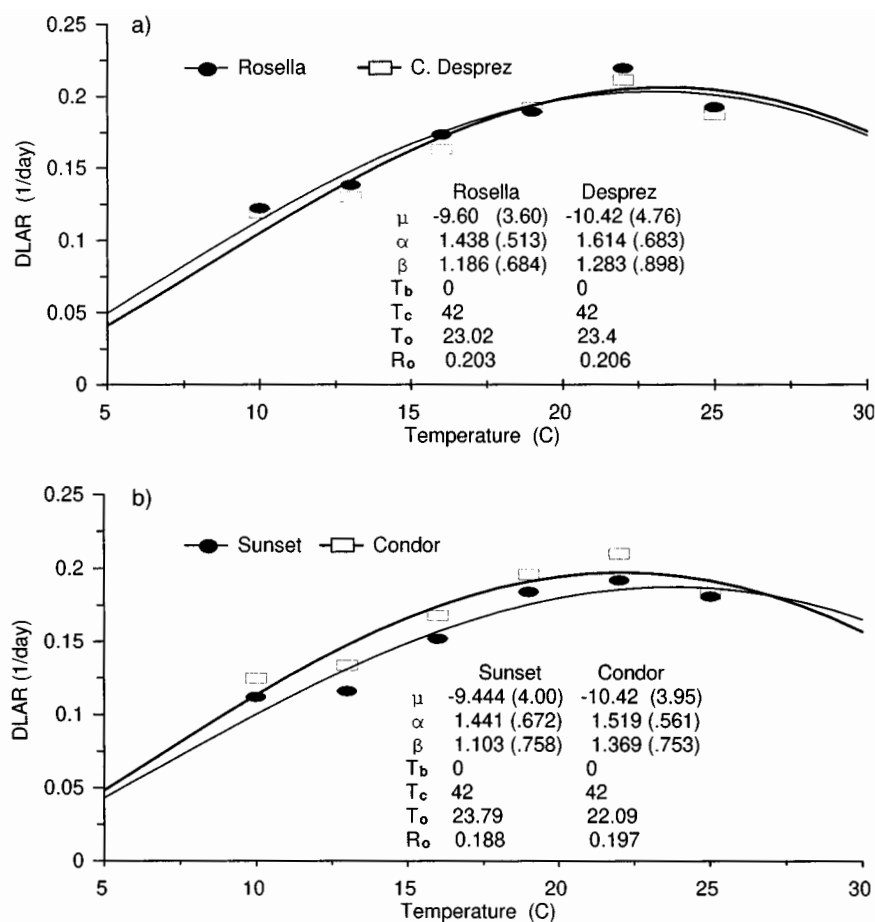


Fig. 3. The beta function describing the relationship between daily leaf appearance rate (DLAR) and temperature for four wheat cultivars — a) Rosella and Capelle Desprez, and b) Sunset and Condor — from Slafer and Rawson (1995). Also listed are the coefficients (with standard errors) and cardinal temperatures, as well as the optimum temperature (T_o) and rate (R_o), for each beta function.

RELATIONSHIPS BETWEEN DLAR, CALDAY, PHYLLOCHRON AND TLAR

The daily development rate of a biological system is a non-linear function of temperature (Shaykewich 1995). Using linear functions to analyze nonlinear relationships ensures that T_b is a function of the temperature range of the data set. As a result, conflicting views of the value of T_b have appeared in many scientific publications (Gallagher 1979; Monteith 1981; Ritchie and Nesmith 1991; Slafer and Rawson 1995). As well, scientists have used various mathematical functions to describe the nonlinear temperature response of leaf appearance. For example, Cao and Moss (1989a) used quadratic polynomials to fit the temperature response curves of DLAR and used exponential equations to fit the temperature response function of PHYLLOCHRON.

The four variables used to describe the duration and the rate of leaf appearance, i.e., DLAR, CALDAY, PHYLLOCHRON and TLAR, are related. Thus, once the temperature response function of DLAR (i.e., Eq. 2) is determined, the temperature functions for CALDAY, PHYLLOCHRON and TLAR can be obtained accordingly, i.e.,

$$\text{CALDAY} = 1/\text{DLAR} \quad (7)$$

$$\text{PHYLLOCHRON} = (1/\text{DLAR}) \times (T - T_b) \quad (8)$$

$$\text{and TLAR} = (1/\text{PHYLLOCHRON}) \quad (9)$$

Because most plant species stop growing at 0°C , we set $T_b = 0^\circ\text{C}$ and used the beta function to describe the nonlinear relationship between DLAR and temperature (Fig. 1). We then determined the relationships of CALDAY, PHYLLOCHRON, and TLAR to temperature using Eqs. 7, 8, and 9, respectively for wheat and corn (Fig. 4a, b, c).

When $T_b = 0^\circ\text{C}$ and the temperature response function of DLAR is described by the beta function, the chronological time (days) required for successive leaf appearance is fairly constant when the daily temperature is between 15 and 25°C for wheat (5 d) and between 25 and 35°C for corn (1.7 d) (Fig. 4a). The chronological time required for successive leaf appearance increased exponentially as temperature either decreased or increased below and above these temperature ranges, respectively.

Calculating thermal time with $T_b = 0^\circ\text{C}$, phyllochron is not constant with respect to temperature. Between 5 and 35°C , phyllochron for wheat increases non-linearly from about 60°Cd at 5°C to 125°Cd at 25°C (Fig. 4b). For corn, phyllochron was approximately constant (about 50°Cd) between 25 and 32°C . Phyllochron increased exponentially either as temperature decreased below 25°C or increased above 32°C .

The thermal rate of leaf appearance for wheat decreased almost linearly from $\text{TLAR} = 0.0165^\circ\text{C d}^{-1}$ at 5°C , to TLAR

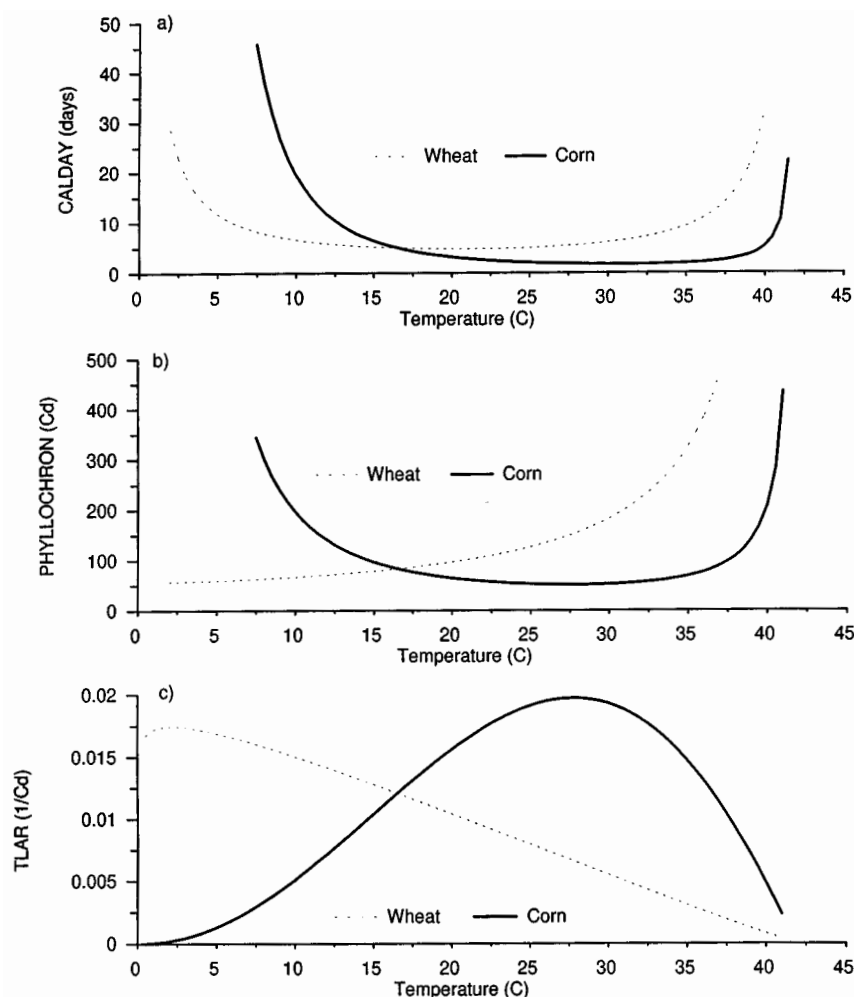


Fig. 4. Temperature response functions for: a) CALDAY, b) PHYLLOCHRON, and c) TLAR.

$= 0.003^{\circ}\text{C d}^{-1}$ at 35°C (Fig. 4c). Thus, for wheat, a cool season crop, the thermal rate of development is higher at low than at high temperatures. For corn, a warm season crop, the relationship between TLAR and temperature is nonlinear with optimum thermal rate of development occurring at 28°C .

The advantage of expressing the leaf appearance in either chronological time or thermal time is the convenience for facilitating easy and simple calculation of leaf appearance when plants are grown in a constant temperature environment. However, when modeling the crop development with daily time steps, because of the large variability in daily temperature and the nature of nonlinear temperature response of leaf appearance, we have to use the daily rate of leaf appearance to accurately predict when a new leaf will appear. Thus, in crop modeling, we predict the timing of leaf appearance by summing daily DLARs calculated using daily temperatures: when the summation of DLAR is equal to 1, a new leaf appears.

DLAR FOR DIURNAL VARIATION IN TEMPERATURE

Because plant development rate is not a linear function of temperature, averaging the daily maximum and minimum

temperatures to estimate development will result in error (Shaykewich 1995). Warrington and Kanemasu (1983) showed that for various day/night temperature ranges about the same mean, DLAR was dependent upon the size of the range. When they summed the contributions of both day and night temperatures to development, the development rate under the diurnal temperature cycle could be estimated quite well. Thus, accurate modeling of leaf appearance requires consideration of the temperature variation throughout the day. This can be done by separating the day into 1-h segments, calculating development rates over 24-h periods and summing these rates to obtain the appropriate mean daily rate.

Air temperature generally exhibits a characteristic daily cycle with a minimum near sunrise and a maximum at 13–14 h (solar time). Deviations from this pattern can occur as a result of, for example, the passage of a cold front. However, on average, the daily cycle can be described reasonably well when the minimum and maximum temperatures are known. The best representation of diurnal variation in temperature is to use a sinusoidal progression during the daytime and a decreasing exponential curve at night (Parton and Logan 1981; Goudriaan and van Laar 1994). The transition from one curve to the next takes place at sunrise and sunset.

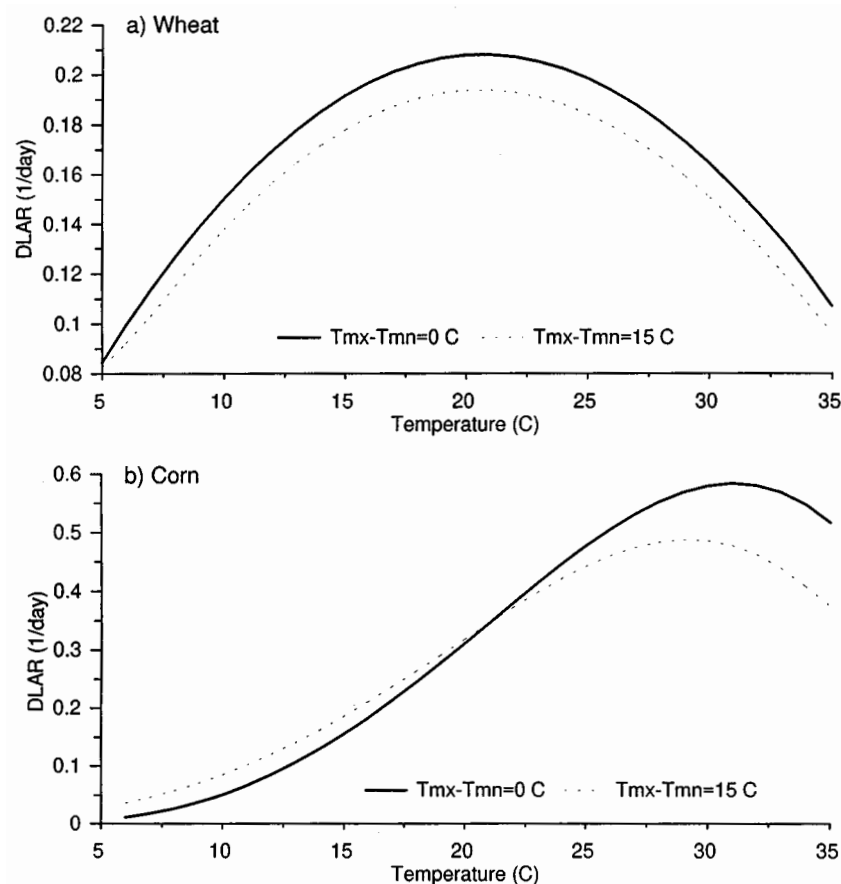


Fig. 5. Effects of diurnal variation in temperature on daily leaf appearance rate for a) wheat and b) corn.

Daily leaf appearance rates under a temperature regime with $T_{mx} - T_{mn} = 15^{\circ}\text{C}$ were calculated on a hourly basis and the results compared to DLAR determined for constant temperature conditions (i.e., $T_{mx} - T_{mn} = 0^{\circ}\text{C}$) for wheat (Fig. 5a) and for corn (Fig. 5b); for both cases, daily mean temperatures were the same. The diurnal temperature curve was constructed using procedures described by Goudriaan and van Laar (1994) with a fixed daylength of 15 h and the values of DLAR under constant temperature were determined using the beta function and parameters listed in Fig. 1. The results showed that for temperatures between 5 and 35°C , DLAR for wheat was slightly lower under the differential day/night temperature regime than under constant temperatures (Fig. 5a). At $T_o = 20.5^{\circ}\text{C}$, DLAR for the differential day/night temperature treatment was about 7% lower than for the constant temperature treatment. Contrarily, Slafer and Rawson (1995) found that the magnitude of diurnal temperature variation was of little consequence to the rate of leaf appearance in wheat. They found that the diurnal temperature cycle varying between 0 and 14°C around a common mean of 19°C did not change rates of leaf appearance. The small differences in DLAR between the differential day/night temperature regimes and constant temperature conditions may not be detectable due to experimental error.

For corn, when temperature regimes had means lower than 20°C , the leaf appearance rates were slightly higher under the differential day/night temperatures than under

constant temperature conditions (Fig. 5b). Above 20°C , the pattern was reversed with the rates for differential day/night temperature regimes lower than under constant temperature conditions. At $T_o = 31^{\circ}\text{C}$, DLAR for the differential temperature treatment was about 17% lower than for constant temperature conditions. Similarly, Warrington and Kanemasu (1983) showed that if the mean temperature was lower than the inflection point, DLAR for the differential temperature regimes was higher than for constant temperature conditions, whereas, above the inflection point, DLAR was lower for differential temperature regimes compared to constant temperature conditions.

The implication of our work is that DLAR determined from constant temperature conditions can be extrapolated to differential day/night temperature regimes with confidence if DLAR is properly adjusted by calculating development rate over relatively short periods and summing these rates to get a mean daily rate.

CONCLUSIONS

Based on our analysis, we conclude:

1. The relationship between DLAR and temperature is non-linear. Assuming that the relationship is linear, and that phyllochron is independent of temperature is not accurate and leads to confusion, with derivation of several T_b that only apply to conditions similar to these under which each T_b was developed.

2. The temperature response function for DLAR over the full temperature range for plant development can be properly described by a nonlinear Beta function with 0°C as the base temperature.

3. The four variables (i.e., DLAR, CALDAY, PHYLLOCHRON, and TLAR) that express the duration and the rate of leaf appearance are related. Once the temperature response function for DLAR is determined, the temperature response functions for CALDAY, PHYLLOCHRON, and TLAR can be obtained accordingly. Thus, there is no need to independently develop various mathematic functions to describe these variables.

4. Of the many factors influencing the leaf appearance rate, temperature is the most important. Thus, once the proper temperature response function for leaf appearance rate is determined, it is much easier to determine when and how other factors are involved to modify the leaf appearance rate under a given environment.

5. Because of the large diurnal variation in temperature and the nonlinear nature of the response of DLAR to temperature, the timing of successive leaf appearance will be more accurately modeled when daily DLAR is determined using hourly temperature rather than daily mean temperature.

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