

Review

Bases and limits to using ‘degree.day’ units**Raymond Bonhomme ****INRA Unité de Recherche en Bioclimatologie, 78850 Thiverval-Grignon, France*

Received 10 August 1999; received in revised form 3 February 2000; accepted 4 April 2000

Abstract

Degree.day units, for which there are also several synonymous terms, are often used in agronomy essentially to estimate or predict the lengths of the different phases of development. The physiological and mathematical bases upon which they are founded are, however, sometimes forgotten, resulting in questionable interpretations. Such is particularly the case for anything relating to variations in the temperature thresholds which enter into the calculation of these degree.day sums. Without seeking to draw up a synthesis of the extremely numerous works published in the field, this review article sets out to present the basic principles of the degree.day unit notion as well as the limits of its use. On this last point, we will particularly emphasise the influence of the non-linearity of the temperature response of the method used in determining the threshold temperature as well as the pertinence of the temperature taken into account in studying the phenomenon. Several practical conclusions are drawn from this review article. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Base temperature; Day-degrees; Growing degree-days; Heat sums; Heat units; Thermal time; Thermal units; Threshold temperature

1. Introduction

The effects of temperature on physiological phenomena are numerous. For example, in Johnson and Thornley (1985) one finds an attempt at developing a conceptual outline of the different action laws both at the level of the various chem-

ical reactions (Arrhenius' equation, Q_{10} factor, reactions with or without optimum temperature) or phenomena such as diffusion, viscosity and translocations, and at the level of the organ, the plant or the cultivation: effect of temperature on photosynthesis, respiration or rate of development.

In general, the effect of temperatures on plant functioning is brought about by the action on enzymatic activities. The conformation of enzymes is the essential step in the enzymatic reaction and this conformation depends on temperature. At too low a temperature the en-

* Tel.: + 33-130-815555; fax: + 33-130-815563.

E-mail address: bonhomme@bcgn.grignon.inra.fr (R. Bonhomme)

zyme protein is not flexible enough and therefore not in a position to carry out the conformation change required for the reaction; at too high a temperature the enzyme coagulates and the new structure thus obtained is not able to catalyze the reaction. Temperature action curves thus typically have two sides: a growth segment where thermal activation of the molecules increases the efficiency of the reactions and a diminishing segment where the high temperatures progressively inactivate certain enzymes. Between these two sides the curve reaches a peak corresponding to the optimal temperature (Bourdu, 1984). It is for this reason that we have a minimum, a maximum, and an optimum temperature for the temperature responses.

A large number of enzymes play a role in plant development and presumably enzymes providing photosynthates are very important. There is a great deal of difference between C-3 and C-4 species as far as the enzymes involved in photosynthate production are concerned. The pyruvate-phosphate dikinase, which provides the PEP and hence the CO₂ acceptor in C-4 species, is sensitive to low temperatures (Edwards, 1986) whereas the Rubisco found in the C-3 species is very efficient even at low temperatures. This difference is clearly expressed in the leaf development temperature response: Fig. 1 shows that the minimum and optimum temperatures for wheat (C-3 species) are respectively about 0 and 20–25°C whereas for

maize (C-4 species) they are respectively about 10 and 30–35°C.

The ‘degree-day’ unit stems mainly from the relationship between development rate and temperature. It was Réaumur (1735) who first laid the basis of this notion: ‘The same grains are harvested in very different climates; it would be interesting to compare the sums of heat degrees over the months during which wheat does most of its growing and reaches complete maturity in hot countries, like Spain or Africa ... in temperate countries, like France ... and in the colder countries of the North,’ (original text in Old French: Durand, 1969). Even if the exact vocabulary was not correct (what is a sum of heat degrees?), the concept of a relationship between the development rate of crops (here the sowing to maturity period) and temperature was born.

Hundreds of works have set about using, proving, or even disproving this idea. Several comments can be made:

We will limit ourselves to works on development rate, with ‘development’ taken in the sense of ‘the series of identifiable events resulting in a qualitative (germination, flowering, etc.) or quantitative (number of leaves, flowers, etc.) modification of plant structure.’ The relationships between growth rate and temperature have, however, also been the object of numerous studies: the most often quoted experimental result in studies dealing with the effect of temperature on plants is certainly the action law concerning the effect of temperature on the growth in length of maize coleoptiles (Lehenbauer, 1914). It is true that separating growth phenomena from developmental phenomena is a bit artificial, as the two are connected (for example, growth often implies the appearance of specific new tissues; Rageau, 1985). Moreover, it is interesting to note the similarity between the form of the temperature response for a developmental phenomenon (rate of leaf emergence, Tollenaar et al., 1979; Fig. 1: curve) and for a growth phenomenon (coleoptile elongation, Lehenbauer, 1914; Fig. 1: dots). This similarity is all the more noticeable when the maize genotypes change a lot between the two periods. It should be noted that the rate of leaf emergence is the inverse of the duration separating the appearance of two

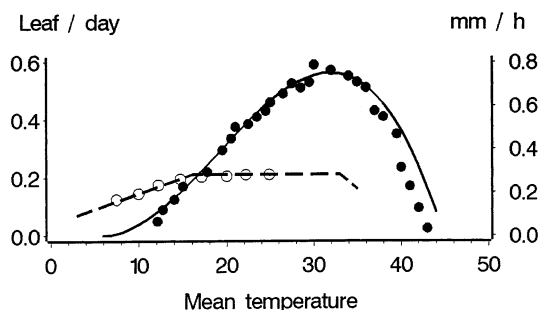


Fig. 1. Circles and segmented lines (left scale): wheat leaf appearance rate as a function of temperature (according to Ritchie and NeSmith, 1991). Curve (left scale): corn leaf appearance rate as a function of temperature (according to Tollenaar et al., 1979). Dots (right scale): elongation rate (mm h⁻¹) of maize coleoptiles as a function of temperature (according to Lehenbauer, 1914)

successive leaves, a period sometimes called ‘phyllochron’

From the moment that interest was turned to working on spring crops, which develop only under largely positive temperature conditions, or to using the Fahrenheit temperature scale ($0^{\circ}\text{C} = 32^{\circ}\text{F}$) it became necessary to introduce the threshold temperature concept (below which the rate of development is considered to be nil). Methods for determining this temperature threshold (to give a good prediction of a specific phase) as well as research into differences between species or between plants of a same species have given a large number of works.

It has often been found that the linearity between development rate and temperature is only valuable for a relatively limited range of temperatures. For example, the experimental curve in Fig. 1 shows that:

- Near threshold temperature the relationship is practically exponential, an observation explaining the use of Q_{10} sums within this range (Bidabé, 1967; Niquieux and Arnaud, 1967).
- The action law peaks then rapidly decreases. Determining the last part of this curve experimentally remains, however, very difficult due to the inevitable interactions with water stress at high temperatures. Even if the maximum position varies greatly between species and genotypes, there are very few biological phenomena occurring above 45°C .

2. Rate and path of development

If one considers:

- A time span $\Delta t = 1$ day
 - That development rate, R , is proportional to the daily temperature, T_d , reduced by a threshold temperature, T_l , then: $R = a(T_d - T_l)$
- this same daily growth rate R is the inverse of the total duration, in days, of the phase (for example, from sowing to flowering, from the emergence of leaf n to that of leaf $n + 1$, etc.), so:

$$R = \frac{1}{\sum_{d_1}^{d_2} \Delta t}$$

The path of development (rate \times time) for one day is, therefore:

$$R \cdot \Delta t = \left[\frac{1}{\sum_{d_1}^{d_2} \Delta t} \right] \cdot \Delta t$$

and the total path of development for the phase:

$$\sum_{d_1}^{d_2} (R \cdot \Delta t) = 1$$

$$\sum_{d_1}^{d_2} (R \cdot \Delta t) = a \cdot \sum_{d_1}^{d_2} (T_d - T_l) \cdot \Delta t$$

The $(T_d - T_l)$ sum from day d_1 at the beginning of the phase to day d_2 at the end of the phase is a degree.day sum which is, therefore, a constant equal to $1/a$.

To represent the example given in Fig. 1 in numerical form, by linearizing for the $10\text{--}30^{\circ}\text{C}$ interval, the temperature response of the foliar appearance, one obtains approximately:

$$R = a(T_d - 10) \text{ with } a = 0.033$$

with R in d^{-1} and a in $(\text{degree.day})^{-1}$. The fraction of development path obtained during 1 day with a temperature $T_d = 25^{\circ}\text{C}$ is 0.5 (at this constant temperature the development of one leaf in $1/0.5 = 2$ days). Should $T = 13^{\circ}\text{C}$, the fraction of development path becomes 0.1 (a leaf appears in 10 days). The total path of development for the appearance of a leaf in degree.day is $1/a$, hence 30 degree.day. Therefore, a 25°C day results in a sum of $(25 - 10) = 15$ degree.day (thus, at constant temperature, a leaf appears in $30/15 = 2$ days). At 13°C days the resulting leaf appearance in $30/(13 - 10) = 10$ days.

3. Examples of the use of degree.day units

The practical impact of using degree.day sums is considerable (Ritchie and NeSmith, 1991). To mention but a few examples, they can be used to:

- Classify plants for their flowering rate or length of cycle (Derieux and Bonhomme, 1982a,b).
- Estimate harvest maturity (Gilmore and Rogers, 1958, for maize).

- Schedule vegetable harvesting according to their level of tenderness (Katz, 1946, for peas).
- Predict the duration, under natural conditions, between two developmental stages for a parasite used in biological control (Bernal and Gonzalez, 1993).
- Anticipate insect development with a view to better phytosanitary control (Pruess, 1983).
- Assess sporulation intensity for a cereal fungus (Tyldesley, 1978), etc.

Still, this profusion of works using degree.day units sometimes results in the bases of the method being forgotten:

- Linearity between growing rate and temperature.
- Unequivocal relationship between growth rate and temperature.
- Obvious representational quality of temperature taken as a reference in relationship to the studied phenomenon.
- Absence of any other factor limiting development.

These different points will now be discussed.

4. Influence of non-linearity between development rate and temperature

Fig. 1 clearly shows that development rate can be considered as linearly proportional to temperature for only a short range of temperature variation. Using present-day calculation tools it is perfectly possible to calculate growth over a daily or even shorter time span using a more or less complicated development rate law. As examples taken from the case of maize (Bonhomme et al., 1994), let us cite a few non-linear methods used to estimate the daily development DD (always positive or nil), in function of minimum daily temperature, T_n , and maximum daily temperature, T_x :

$$DD = (Q_{10})^{(T/10)}, \text{ with } Q_{10} \text{ values close to } 2$$

$$DD = 0.0997 - 0.0360T + 0.00362T^2 - 0.0000639T^3,$$

according to Tollenaar et al. (1979)

$$DD = -2.80 + 0.59T - 0.046T^2 + 0.0019T^3 - 0.000027T^4,$$

according to Blacklow (1972). In these three formulae DD equals the average obtained using $T = T_n$ and $T = T_x$.

$$DD = 0.5[3.33(T_x - 10) - 0.084(T_x - 10)^2 + 1.85(T_n - 4.4)],$$

Ontario Corn Unit Method (Brown, 1975).

The increased calculation complexity brought about by using these formulae often results in quite minor improvements in the prediction of phase length (Bonhomme et al., 1994). It is, therefore, common to keep the simple calculation of development in degree.day sums while taking into account the fact that non-linearity will have several types of influence:

4.1. Depending on the temperature range at which linearization is carried out

An initial graphical estimate as to this effect can be seen in Fig. 1. Under relatively low temperature conditions the temperature threshold estimated by linearization of the curve over a specific range of temperatures will be lower than that estimated over warmer situations. Here one finds the explanation to the polemic concerning the superiority of the 'French method' of calculating degree.day sums (with 6–7°C temperature thresholds; Bloc and Gouet, 1977) over the 'American methods' (with temperature thresholds around 10°C). The difference lies simply in the fact that maize cultivation temperatures are, on an average, higher in the USA than in France!

Sinclair (1994) gives an analytical presentation of this effect for temperatures quite close to threshold level. A system's reaction rate can, hence, be described by a temperature exponential function (Arrhenius' equation):

$$R = B \exp(-A/CT)$$

where A is the system's activation energy (J mol^{-1}), C the gas constant ($8.31 \text{ J mol}^{-1} \text{ K}^{-1}$), T the temperature (K) and B a constant. Reaction rate can be presented in correspondence to a reference temperature, T_{ref} :

$$R/R_{\text{ref}} = \exp\left[\frac{A}{C}\left(\frac{T - T_{\text{ref}}}{T \cdot T_{\text{ref}}}\right)\right]$$

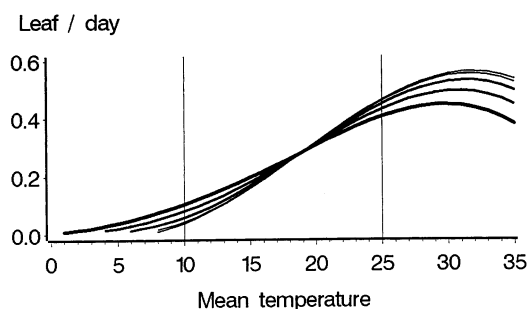


Fig. 2. Fine line: corn leaf appearance rate as a function of temperature (according to Tollenaar et al., 1979). The curves with progressively thicker lines show the deformation of this action law if the temperature under question is the average daily temperature and if it is assumed that the daily temperature variation is a sinusoidal form with an increasing amplitude (as with the thickness of the lines: 5, 10, 15 and 20°C).

Since biological phenomena take place within quite limited ranges of temperature, T_{ref} can be taken from the middle of this range; one can then limit the margin of error by replacing $T \cdot T_{\text{ref}}$ by T_{ref}^2 . Moreover, $A/(C \cdot T_{\text{ref}}^2)$ is small and one can linearize the exponential:

$$R/R_{\text{ref}} \approx 1 + \frac{A}{C T_{\text{ref}}^2} (T - T_{\text{ref}})$$

What one usually seeks to do is to extrapolate this slope so as to find the temperature threshold, T_t , for which the development rate is nil ($R/R_{\text{ref}} = 0$), in which case one has:

$$T_t = T_{\text{ref}}(1 - C T_{\text{ref}}/A)$$

The temperature threshold T_t which is estimated depends on the reference temperature around which one carries out linearization of the exponential law. Since $(C T_{\text{ref}}/A)$ is small, the higher the T_{ref} , the larger the value of T_t . It is, therefore, only possible to compare T_t between experiments, species or plants if the thermal conditions are similar. For example, results such as

those in Cao and Moss (1991), affirming that degree.day needs are higher for the final leaves than for the first leaves to appear, can only be accepted with a certain amount of precaution.

4.2. Depending on daily thermal amplitude

Throughout the day, actual temperatures vary around the daily average temperature according to an approximately sinusoidal curve. The result of this situation is that even if the daily average temperature equals the temperature threshold T_t (one should find a daily development of zero if the daily temperature remains equal to T_t), there is a certain amount of development due to the daily period during which the actual temperatures rise above T_t .

Fig. 2 shows daily growth on days of given temperatures and thermal amplitudes, assuming sinusoidal variation in daily temperatures. It was developed according to the development rate law as a function of temperature given in Tollenaar et al. (1979). The results of a linear treatment of the different curves in the 10–25°C range are shown in Table 1. It is apparent that threshold temperature drops with the increase of the daily thermal amplitude.

5. Influence of the method used in determining the action law

The value of the estimated threshold temperature also depends on the method used in determining it. Even though they have been used by certain authors, methods drawing upon relations between variables cumulated in time (for example, degree.day sum and the number of leaves which appeared) should be avoided (Malet et al., 1997).

Different types of information are sought by different authors. They can be outlined as:

Table 1

Apparent variation in the threshold temperature T_t obtained by linearization in the 10–20°C interval of the different development laws of Fig. 2 obtained for various daily thermal amplitudes

Daily thermal amplitude (°C)	0	5	10	15	20
Apparent T_t temperature threshold (°C)	9.4	9.2	8.5	7.3	5.4

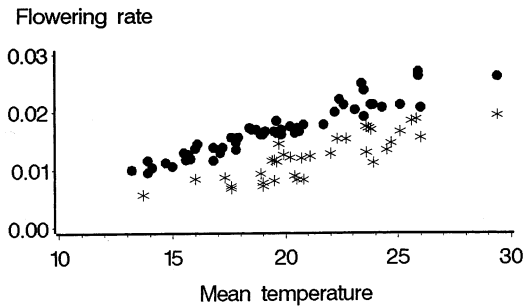


Fig. 3. Relationships between flowering rates (the inverse of sowing–flowering duration in days) and the mean temperature for the period for: an early genotype of temperate origin, LG11 (points), a late genotype of tropical origin, X304C (stars), for a set of trials in numerous countries and under conditions without stresses (Bonhomme et al., 1994).

Table 2

Estimation of the threshold temperature T_t obtained for the sowing–flowering rate of LG11 genotype (points in Fig. 3) or X304C genotype (stars in Fig. 3) using various methods (Mx, see text) for determining the development law.

Method	M1	M2	M3	M4	M5
T_t for LG11	5.66	4.62	4.55	4.53	4.52
T_t for X304C	12.03	9.09	8.77	9.35	9.38

- Either one seeks the temperature threshold which will give the best prediction of the developmental stage using the degree.day sums.
- Or one strives to display differences between species or genotypes in development rates depending on the temperature (for example, flowering or maturation, leaf appearance rate).

The temperature threshold has only statistical value, often quite distant from the ‘physiological temperature’ for which development is zero. In particular, the temperature thresholds which produce the best predictions for a given development stage are usually quite low and depend upon the statistical estimation methods used (Durand et al., 1982). The methods most often used are those seeking the T_t temperature which minimizes:

- The standard deviation in degree.day sums for a series of trials (M1).
- The standard deviation in days corresponding to these degree.day sums (M2).

- The coefficient of variation of the differences between predicted and observed dates (M3).
- The regression between the degree.day sums and the mean temperatures for the different trials (M4), finding the independence between the degree.day sums and the temperatures of the trials.

It should be noted that:

- Differences in development date estimations remain limited when the estimated temperature is only slightly lower than the real T_t value, whereas they quickly expand if too high a T_t value is used (Durand et al., 1982).
- These methods require running a large number of calculations with different possible T_t temperature thresholds. To avoid these iterative calculations Yang et al. (1995) developed mathematical formulae which make a direct calculation of T_t possible. For example, the temperature threshold T_t which minimizes the variation coefficient (M3) is:

$$T_t = \frac{\sum_{i=1}^n T_i d_i^2 \sum_{i=1}^n T_i d_i - \sum_{i=1}^n d_i \sum_{i=1}^n T_i^2 d_i^2}{\sum_{i=1}^n d_i^2 \sum_{i=1}^n T_i d_i - \sum_{i=1}^n d_i \sum_{i=1}^n T_i d_i^2}$$

where T_i is the average temperature over the total duration of the stage under study in trial i , d_i the duration of this stage in days and n the number of trials.

If one wishes to display inter- or intra-species differences in the action laws of temperature on development to select, for example, maize capable of being planted earlier and, therefore, at lower temperatures (Giauffret et al., 1995), the comparisons must be based on the abscissa at the origin and on the slope of the curve relating the relationship between development rate and temperature (M5). Whenever one makes a regression between couples (development rate, that is the inverse of the duration of the stage) \times (mean temperature during the stage) which are available over the different trials, each of the variables is flawed by error. It is therefore preferable to carry out an orthogonal regression (Dagnélie, 1973).

The sowing–flowering rates for genotype LG11 displayed in Fig. 3 (points), lead to different temperature threshold values T_t depending on the

method of estimation (Table 2). Such a result explains the large number of more or less contradictory publications relative to determining temperature thresholds. It appears quite obvious that it is just a case of temperatures with merely statistical value, since at temperatures below approximately 10°C there is no growth in maize.

6. Influence of the representational quality of the reference temperature used

It is the temperature of the developing organ which should serve to establish the action law for the phenomenon under study and, therefore, calculation of degree.day sums. Such is practically never possible, but one must still remain vigilant as to:

- The quality of measuring devices: drift, even slow, can have a large cumulative effect.
- The fact that the site at which temperatures are measured must be very near the site where the observations or the growth estimates are made, with particular attention being paid to the effects of different expositions or altitudes.
- The estimation of mean temperature on the basis of minimum and maximum daily temperatures, an approximation which is susceptible of provoking a divergence (slight over-estimate for mean photoperiods and under-estimate for short and long photoperiods; Hallaire, 1950).
- The position of the 'sensitive plant organ': for example, maize leaf emergence rate will be more closely linked to ground temperature for the first foliar stages because the apex is then at the surface of the ground, whereas subsequent leaf emergence rates will be more closely linked to air temperature (Duburcq et al., 1983; Swan et al., 1987). For spring sowings, ground temperature is always higher than air temperature, which can lead, especially for temperature around threshold level, to wide-scale divergence in the calculations of degree.day sums (Ritchie and NeSmith, 1991).

Development of relatively simple models of the energetic balance of plant organs such as the apex (Cellier et al., 1993), the zone of leaf production,

should be continued in order to replace meteorological temperatures by explicative temperatures more pertinent at the level of plant development. To witness, the work of Jamieson et al. (1995) in which it is shown that the affirmations of certain authors as to variations in wheat phyllochrone on the basis of foliar rank or photoperiod are the result of having used bad reference temperatures. These variations are greatly reduced when one first refers to ground temperature and later to plant temperature after a certain stage in growth.

7. Influence of other factors modifying development rate

The values corresponding to genotype X304C on Fig. 3 (stars) show that sowing-flowering rates are, at the same temperature, lower than for genotype LG11. This means simply that genotype X304C will flower later (that is to say, it has a higher degree.day sum).

If one seeks the temperature thresholds which would make better flowering prediction possible using degree.day sums, one finds that they are higher than for genotype LG11 (Table 2).

Since the X304C is a genotype of tropical origin, one could be led to believe that it is a question of physiological adaptation to higher temperatures than for the LG11, of French origin. In fact, one must first of all note the more marked development rate dispersion, which can be characterized by the fact that the quadratic mean error for the regression between growth rate and temperature, is 0.0014 for LG11 and 0.0020 for X304C. Fig. 3 shows a high dispersion of points at low and mean temperatures, which is due to the fact that this genotype is a 'short day' genotype (Bonhomme et al., 1994) and that, therefore, for long photoperiods development rates, at a given temperature, can be reduced by this photoperiodic sensitivity (Brisson and Delécolle, 1991).

If one assumes that:

- For a day less than 13 h in duration, there is no photoperiodic effect on development rate which, in turn, is only a function of temperature T_d : $R = a(T_d - T_l)$.

- For a day longer than 13 h, there is no interaction between temperature action and photo period, P , action (Roberts and Summerfield, 1987: $R = a'(T_d - T_t) + b'(P - 13)$).

one obtains the results shown in Table 3 for the Fig. 3 data.

It thus becomes obvious that if one takes the photoperiodic sensitivity of genotype X304C into account, its estimated threshold temperature T_t is very close to that of LG11. For this 'short day' plant, the apparent temperature threshold is increased by the long photoperiod.

It is, therefore, very important to take the possible influence of other environmental factors into account when comparing laws concerning the action of temperature on crop growth. It is thus that:

- Photoperiodic effects can be interpreted as vernalization effects on 'long day' plants, because the estimated temperature threshold can be very low for long days while photoperiodic thresholds are low (Summerfield et al., 1989).
- Water stress can accelerate or depress the development rate depending upon the importance of stress (Brisson and Delécolle, 1991). With this constraint the temperature of the plant can be considerably different from that of the air and it can be interesting to measure it so as to better estimate development stages (Casals, 1996); a 'stress degree.day' approach using canopy temperature can be used (Idso et al., 1978).
- The nutritional state of the plant can have an effect on development phenomena (the leaf emergence temperature response slightly varies with the supply of nitrogen: Gastal et al., 1992).

8. Practical conclusions

The term 'heat sums' has no physical reality and it is preferable to use the terms 'thermal time' or 'progress towards ...x stage.'

It is of no meaning in giving a degree.day sum without the temperature threshold used for calculating it.

Phyllochron is the time duration, usually given in days, which separates the appearance of two successive leaves; phyllotherm is the corresponding degree.day sum; plastochron is the time duration, in days, which separates the initiation of two successive leaves.

It is preferable not to use degree.day sums for the study of growth phenomena without previous reflection about the meaning and definition of growth ($\text{kg m}^{-2} \text{ degree.day}^{-1}$). Among others, 'Monteith type' growth analysis (Monteith, 1977; Varlet Grancher, 1982) makes it possible to clearly separate the duration of a stage (evaluated using degree.day sums) from the production of biomass during the same stage because its first approximation is linked to the duration in days, if there is not too much variation in solar radiation and foliar development.

Determining the temperature threshold is only possible if one disposes of development rates obtained for wide ranges in temperature variation and in the absence of other eventual limits to growth rate (non-optimal photoperiod, non-vernalization, water or nutritional stress, etc.).

The temperature threshold has only a slight influence on the precision in determining a stage if average temperatures are well above threshold level.

Table 3

Values of the coefficients of the relationships between sowing–flowering rates and temperature alone ($R1$; Fig. 3) or temperature and photoperiod ($R2$) for two genotypes differing in their photoperiodic sensibility.

Genotype	$R1 = a(T_d - T_t)$		$R2 = a'(T_d - T_t) + b(P - 13)$		
	a	T_t	a'	B	T_t
LG11	0.00112	4.520	0.00112	0	4.520
X304C	0.00103	9.382	0.00083	−0.00110	4.962

One must always try to measure or estimate the temperature of the developing organ even in greenhouses and growth chambers.

It is now perfectly possible to work with temperature action laws which are non-linear or with short time intervals (taking diurnal temperature variation into account), but one must first be sure whether this is really worth the effort because one loses statistical power of linear models when one uses such non-linear laws. If one uses these non-linear models, it is best to use the relatively 'flexible' mathematical laws with few parameters (for example, Beta laws: Yin et al., 1995).

References

- Bernal, J., Gonzalez, D., 1993. Experimental assessment of a degree-day model for predicting the development of parasites in the field. *J. Appl. Ent.* 116, 459–466.
- Bidabé, B., 1967. Action de la température sur l'évolution des bourgeons de pommiers et comparaison de méthodes de contrôle de l'époque de floraison. *Ann. Physiol. Vég.* 1, 65–86.
- Blacklow, W.M., 1972. Influence of temperature on germination and elongation of the radicle and shoot of corn (*Zea mays* L.). *Crop Sci.* 12, 647–650.
- Bloc, D., Gouet, J.P., 1977. Influence des sommes de températures sur la floraison et la maturité du maïs. *Ann. Amélior. Plant.* 28, 89–111.
- Bonhomme, R., Derieux, M., Edmeades, G.O., 1994. Flowering of diverse maize cultivars in relation to temperature and photoperiod in multilocation field trials. *Crop Sci.* 34, 156–164.
- Bourdu, R., 1984. Bases physiologiques de l'action des températures. In: Gallais, A. (Ed.), *Physiologie du maïs*. INRA, Paris, pp. 389–424.
- Brisson, N., Delécolle, R., 1991. Développement et modèles de simulation de culture. *Agronomie* 12, 253–263.
- Brown, D.M., 1975. Heat units for corn in Southern Ontario. Ontario Ministry of Agriculture and Food, Agdex Fact-sheet 111/31.
- Cao, W., Moss, D.N., 1991. Phyllochron change in winter wheat with planting date and environmental changes. *Agron. J.* 83, 396–401.
- Casals, M.L., 1996. Introduction des mécanismes de résistance à la sécheresse du blé dur au fonctionnement phénologique et trophique de la plante dans un modèle dynamique de croissance. PhD Thesis INA-PG, Paris, France, 130 pp.
- Cellier, P., Ruget, F., Bonhomme, R., 1993. Estimating the temperature of a maize apex during early growth stages. *Agric. For. Meteorol.* 63, 35–54.
- Dagnélie, P., 1973. Théorie et méthodes statistiques: applications agronomiques. Les Presses Agronomiques de Gembloux, Belgique, p. 378.
- Derieux, M., Bonhomme, R., 1982a. Heat unit requirements for maize hybrids in Europe: results of the European FAO sub-network. I: sowing–silking period. *Maydica* XXVII, 59–77.
- Derieux, M., Bonhomme, R., 1982b. Heat unit requirements for maize hybrids in Europe: results of the European FAO sub-network. II: period from silking to maturity. *Maydica* XXVII, 79–96.
- Duburcq, J.B., Bonhomme, R., Derieux, M., 1983. Durée des phases végétative et reproductrice chez le maïs: influence du génotype et du milieu. *Agronomie* 3, 941–946.
- Durand, R., Bonhomme, R., Derieux, M., 1982. Seuil optimal des sommes de température: application au maïs (*Zea mays* L.). *Agronomie* 7, 589–597.
- Durand, R., 1969. Signification et portée des sommes de température. *BTI* 238, 185–190.
- Edwards, G.E., 1986. Carbon fixation and partitioning in the leaf. In: Shannon, J.C., Knievel, D.P., Boyer, C.D. (Eds.), *Regulation of carbon and nitrogen reduction and utilization in maize*. Am. Soc. Plant Physiologists, Rockville, MA, pp. 51–65.
- Gastal, F., Belanger, G., Lemaire, G., 1992. A model of the leaf extension rate of tall fescue in response to nitrogen and temperature. *Ann. Bot.* 70, 437–442.
- Giauffret, C., Bonhomme, R., Derieux, M., 1995. Genotypic differences for temperature response of leaf appearance rate and leaf elongation rate in field-grown maize. *Agronomie* 15, 123–137.
- Gilmore, E.C., Rogers, J.S., 1958. Heat units as a method of measuring maturity in corn. *Agron. J.* 50, 611–615.
- Hallaire, M., 1950. Les températures moyennes nocturnes, diurnes et nyctémérales exprimées en fonction du minimum et du maximum journaliers de température. *C.R. Acad. Sci.* 231, 1533–1535.
- Idso, S.B., Jackson, R.D., Reginato, R.J., 1978. Extending the 'degree day' concept of plant phenological development to include water stress effects. *Ecology* 59, 431–433.
- Jamieson, P.D., Brooking, I.R., Porter, J.R., Wilson, D.R., 1995. Prediction of leaf appearance in wheat: a question of temperature. *Field Crops Res.* 41, 35–44.
- Johnson, I.R., Thornley, J.H.M., 1985. Temperature dependence of plant and crop processes. *Ann. Bot.* 55, 1–24.
- Katz, Y.H., 1946. The relationship between heat unit accumulation and the planting and harvesting of canning peas. *Agron. J.* 38, 74–78.
- Lehenbauer, P.A., 1914. Growth of maize seedlings in relation to temperature. *Physiol. Res.* 5, 247–288.
- Malet, P., Pécaut, F., Bruchou, C., 1997. Beware of using cumulated variables in growth and development models. *Agric. For. Meteorol.* 88, 137–143.
- Monteith, J.L., 1977. Climate and the efficiency of crop production in Britain. *Phil. Trans. R. Soc. London* 281B, 277–294.
- Niqueux, M., Arnaud, R., 1967. Recherche d'une relation entre précocité d'épiaison et températures pour quelques variétés de graminées fourragères observées en France. *Ann. Physiol. Vég.* 1, 29–64.

- Pruess, K.P., 1983. Day-degree methods for pest management. *Environmental Entomology* 12, 613–619.
- Rageau, R., 1985. Phénomène de croissance: action du climat. In: Département de Bioclimatologie (Ed.), *Les bases de la Bioclimatologie. 2-Bases biologiques*. INRA Grignon, France, pp 135–167.
- Réaumur, R.A., 1735. Observations du thermomètre faites pendant l'année MDCCXXXV comparées à celles qui ont été faites sous la ligne à l'Isle-de-France, à Alger et en quelques-unes de nos Isles de l'Amérique. *Mémoires de l'Académie Royale des Sciences*, 545–576.
- Ritchie, J.T., NeSmith, D.S., 1991. Temperature and crop development. In: Hanks, J., Ritchie, J.T. (Eds.), *Modeling plant and soil systems*. ASA, USA, pp. 5–29.
- Roberts, E.H., Summerfield, R.J., 1987. Measurement and prediction of flowering in annual crops. In: Atherton, J.G. (Ed.), *Manipulation of Flowering*. Butterworths, London, pp. 17–50.
- Sinclair, T.R., 1994. Limits to crop yield? In: Boote, K.J., Bennett, J.M., Sinclair, T.R., Paulsen, G.M. (Eds.), *Physiology and determination of crop yield*. ASA, USA, pp. 509–532.
- Summerfield, R.J., Ellis, R.H., Roberts, E.H., 1989. Vernalization in chickpea (*Cicer arietinum*): fact or artefact. *Ann. Bot.* 64, 599–603.
- Swan, J.B., Schneider, E.C., Moncrief, J.F., Paulson, W.H., Peterson, A.E., 1987. Estimating corn growth, yield and grain moisture from air growing degree days and residue cover. *Agron. J.* 79, 53–60.
- Tollenaar, M., Daynard, T.B., Hunter, R.B., 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. *Crop Sci.* 19, 363–366.
- Tyldesley, J.B., 1978. A method of evaluating the effect of temperature on an organism when the response is non-linear. *Agric. Met.* 19, 137–153.
- Varlet Grancher, C., 1982. Analyse du rendement de la conversion de l'énergie solaire par un couvert végétal. PhD Thesis, Orsay, France, 144 pp.
- Yang, S., Logan, J., Coffey, D.L., 1995. Mathematical formulae for calculating the base temperature for growing degree days. *Agric. For. Met.* 74, 61–74.
- Yin, X., Kropff, M.J., McLaren, G., Visperas, R.M., 1995. A nonlinear model for crop development as a function of temperature. *Agric. For. Met.* 77, 1–16.