Int. J. Biometeor. 1968, vol. 12, number 3, pp. 191-223

A Biometeorological Time Scale for a Cereal Crop Involving Day and Night Temperatures and Photoperiod**

by
G. W. Robertson*

INTRODUCTION

The general effects of temperature and daylength on the development of crops(progress towards maturity) has long been known but apparently only minor success has been achieved in applying this knowledge to the calculation of the progress of a crop towards maturity.Greatest success has been achieved with the use of temperature alone in the heat unit or remainder index technique for estimating the date of maturity of certain vegetable crops, chiefly peas and corn (Holmes and Robertson, 1959).

Over 200 years ago, Réaumur (1735) suggested that the sum of the mean daily shade temperature of the air between one stage of development and another was constant for a particular species of plant. Apparently this scheme advanced very slowly because a century later Boussingault (1834)calculated the total quantity of "heat" required to ripen grain by the same method. The product of mean daily temperature above 0°C for the period and the length of the period in question was known as "degree-days".

About 40 years later Tisserand (1875) modified Réaumur's and Boussingault's hypothesis that the ratio of development varied with temperature and time,by adopting the rule that work done by a plant could be represented by the product of the mean temperature and the number of hours of daylight between sunrise and sunset. Thus Tisserand disregarded the dark hours just as his predecessors disregarded temperatures below 0°C. It was not until 1920 (Garner and Allard) that the phenomenon of photoperiodism, the effect of the relative length of day and night upon plants,was fully disclosed and demonstrated.

Following this discovery the response of many plants to length of light and dark periods was investigated. Nuttonson (1948)showed that,for certain varieties of wheat, flax, eggplants and peas, the number of degree-days from emergence to maturity multiplied by the average daylength was more constant from station to station than was the number of degree-days used alone. No attempt,however, appears to have been made to set up a mathematical expression relating the progress of a crop towards maturity to the environmental conditions of temperature and daylength. Robertson (1953) reported some results which indicated that there was a lower critical limit to daylength above which cereal crops responded. This threshold value was used for calculating total hours of effective daylength by means of a summation equation similar to that for calculating total degree-days above a threshold temperature. Ferguson (1958) suggested a unique method for relating development to hourly temperatures as well as taking into account a non-linear response.The example he cites using garden peas, considered only daylight temperatures. His phenological data were from one station only and the photoperiod,which had a negligible variation from year to year, was assumed to be above the lower critical threshold at all times.

*) Agrometeorology Section, Plant Research Institute, Research Branch, Canada Department of Agriculture seconded from the Meteorological Branch, Canada Department of Transport, Ottawa, Ontario, Canada.
**) Plant Research Institute Contribution No. 665.
Received 2 April 1968

Went (1956) showed that some plants have a different response to night temperature than to day temperature. Tomatoes, in fact, were found to have a requirement for a definite nighttime temperature which was much lower than the daytime requirement. Recently Brown (1961) developed a formula for calculating "soybean development units" or SDU based on the number of hours of darkness (sunset to sunrise) as a quadratic function of the mean daily temperature.

The phenomena of photoperiodism including the interaction of light intensity, spectral quality of light and temperature has been thoroughly reviewed at a Conference on Photoperiodism sponsored by the Committee on Photobiology of the National Academy of Sciences (Withrow, 1959). Although the proceedings of this conference discuss in some detail the complexities of the light control of plant development, no attempt appears to have been made to describe this control quantitatively under natural environmental conditions. The discourses at this conference, however, reveal considerable insight into the mechanism of photoperiodism and this has been a great help in setting up the mathematical expressions developed in the present paper.

The purpose of this paper is to report on a mathematical model for calculating the daily rate of crop development and which overcomes many of the shortcomings of simple heat unit (Fig. 1) and photothermal equations.

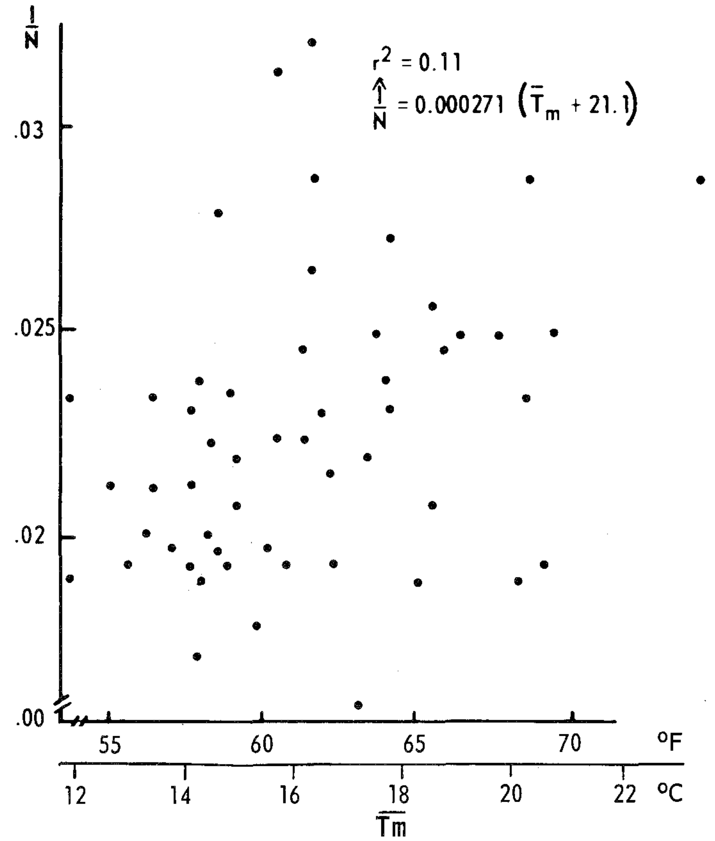

Fig. 1. Scatter diagram of the reciprocal of span (N) for period EH against mean temperature ($\bar{T}_m$) for the same period using regression data 1953-1957, showing inability of simple heat-unit equation to account for influence of temperature on development.

DEVELOPMENT OF A MATHEMATICAL EXPRESSION

Many mathematical models were developed and tested. The form of the model and the variables used were dictated by a number of factors. The availability of data, the knowledge of physical relationships between various environmental factors and of the physiological relationships between crop responses and its environment were all taken into consideration. The equation which eventually evolved for relating daily rate of development, r, and degree of maturity, M, to photoperiod, L, and temperature, T, was of the general form

$$r = \frac{dM}{dt} = F_1(L) \, . \, F_2(T) \qquad [1]$$

where F_1 and F_2 are appropriate non-linear functions of daily photoperiod and daily temperature respectively. Integration of equation [1] leads to an expression for the degree of maturity or development, M, over a phenological period from one phenological stage, S_1, to another, S_2. Thus

$$\int_{S_1}^{S_2} r dt = M = \int_{S_1}^{S_2} F_1(L) \, . \, F_2(T) dt \qquad [2]$$

Since M cannot be observed numerically it was appropriately set to the stochastic value of 1 (Ferguson, 1958) for specific physiological periods.

Equation 2 then becomes:

$$\int_{S_1}^{S_2} F_1(L) \, . \, F_2(T) dt = 1 \qquad [3]$$

The mathematical functions, F_1 and F_2, relating development to temperature and photoperiod should:

(1) Consider the response to temperature as being non-linear and allow for lower and upper critical limits as well as an optimum value (Hildreth, Magness and Mitchell, 1941).
(2) Consider the response to photoperiod also as a non-linear function allowing for the three cardinal points.
(3) Consider response to day and night temperatures separately.
(4) Integrate the influence of these three factors over fairly short phenological periods during which physiological processes are relatively uniform.
(5) Make use of temperature at least on a daily basis so that extreme conditions may be considered and not masked by any averaging procedure.

As it was necessary to use readily available meteorological data in this analysis, the choice of the factor representing photoperiod was taken as the duration of daylight in hours from sunrise to sunset and the choice for temperature was the daily maximum to represent daytime temperature and the daily minimum to represent nighttime temperature. Rather than adding together the photoperiod term and the temperature term they were multiplied together. Thus, calculated development will be zero if either one or both functions are at their critical value.

Ideally the equation might have been:

$$1 = M = \sum_{S_1}^{S_2} \Big[\left\{ a_1(L-a_o) + a_2(L-a_o)^2 \right\} \left\{ b_1(T_1-b_o) + b_2(T_1-b_o)^2 \right\}$$

$$+ \left\{ c_1(D-c_o) + c_2(D-c_o)^2 \right\} \left\{ d_1(T_2-d_o) + d_2(T_2-d_o)^2 \right\} \Big] \qquad [4]$$

where L = daily photoperiod,

D = daily dark,

T_1 = daily maximum (daytime) temperature,

T_2 = daily minimum (nighttime) temperature,

a_o, a_1, a_2, b_o, etc. are characteristic coefficients to be determined.

The integration or summation is carried out daily from one phenological stage S_1, to another S_2. A quadratic function was used for each environmental factor as the simplest expression permitting consideration of an optimum response level as well as an upper and a lower critical limit.

Unfortunately, some of the terms in this complete equation are perfectly correlated resulting in interdependent coefficients for which there is no singular evaluation. Thus it was found necessary to drop the dark period term involving D, since $D = 24-L$. Also b_o and d_o cannot be independently evaluated after dropping the dark period term. Although it was realized that the lower critical level for day temperature might differ from that for night temperature there appears to be no way of overcoming this difficulty by the mathematic treatment considered here. Therefore, it was necessary to set $d_o = b_o$. The final equation, therefore, for which coefficients could be determined was:

$$1 = M = \sum_{S_1}^{S_2}\left[\left\{ a_1'(L-a_o) + a_2'(L-a_o)^2 \right\} \left\{ b_1'(T_1-b_o) + b_2'(T_1-b_o)^2 + d_1'(T_2-b_o) + d_2'(T_2-b_o)^2 \right\}\right] \qquad [5]$$

or for simplicity

$$1 = \sum_{S_1}^{S_2} V_1(V_2 + V_3) \qquad [6]$$

If it is assumed that there is no influence of day and night temperatures and photoperiod on the rate of development, then $V_1(V_2 + V_3)$ will be a constant, say, v. Furthermore it can be shown that $v = \frac{1}{N}$ where N is the number of days from phenological stage S_1 to stage S_2. More generally, if v is evaluated from observations of several crops, $v = \frac{1}{\bar{N}}$ where $\bar{N}$ is the average length of the period from S_1 to S_2. Thus equation [6] becomes:

$$1 = \sum_{S_1}^{S_2}\left(\frac{1}{\bar{N}}\right) \qquad [7]$$

The ratio, $1/\bar{N}$, is the average daily rate of development for a given period. This simple model is equivalent to assuming that the span of time from one stage to another is a constant and is independent of the meteorological environment. This has been designated as Model 1 for further discussion.

Again, if it is assumed that photoperiod has no effect on the rate of development, V_1 can be set to some arbitrary constant, say unity. Further if it is assumed that both day temperature and night temperature have equal influence on the rate of development, i.e., set $b_1' = d_1' = 0.5k$ and that the influence is linear, i.e. $b_2' = d_2' = 0$, then equations [5] and [6] reduce to:

$$1 = \sum \left\{ .5k_1(T_1-b_o) + .5k_1(T_2-b_o) \right\} \quad [8]$$

$$= k_1 \sum (T_m-b_o) \quad [9]$$

or
$$\sum (T_m-b_o) = \frac{1}{k_1} = K_1 \quad [10]$$

where k_1 is the rate of development per day per degree F, K_1 is the summation constant and T_m the mean daily temperature. This is the simple heat unit equation of Réaumur and has been designated as Model 2.

Again, if it is assumed that the photoperiod threshold is zero, that there is equal influence of both day temperature and night temperature, and that the influences of photoperiod and both temperatures are linear, then $a_o' = 0$, $b_1' = d_1' = 0.5k_2$ and $a_2' = b_2' = d_2' = 0$ and equation [5] reduces to:

$$1 = \sum L \left\{ .5k_2(T_1-b_o) + .5k_2(T_2-b_o) \right\} \quad [11]$$

$$= k_2 \sum L(T_m-b_o) \quad [12]$$

or
$$\sum L(T_m-b_o) = \frac{1}{k_2} = K_2 \quad [13]$$

where k_2 is the rate of development per hour of photoperiod per degree F. This is equivalent to Nuttonson's photothermal concept and has been designated as Model 3 for later discussions.

Thus it can be seen that the triquadratic model, equation [5], designated as Model 4, is a more general expression, but possibly not the only one, of which the simple heat unit equation and Nuttonson's photothermal concept are special cases.

The evaluation of the coefficients in equation [5] can be undertaken by iterative regression analysis after some algebraic manipulation. Equation [6] reduces to

$$\frac{1}{\Sigma V_1} = P_o + p_1 \frac{\Sigma(V_1T_1)}{\Sigma V_1} + P_2 \frac{\Sigma(V_1T_1^2)}{\Sigma V_1} + P_3 \frac{\Sigma(V_1T_2)}{\Sigma V_1} + P_4 \frac{\Sigma(V_1T_2^2)}{\Sigma V_1} \quad [14]$$

or

$$\frac{1}{\Sigma(V_2+V_3)} = q_o + q_1 \frac{\Sigma(V_2 + V_3)L}{\Sigma(V_2 + V_3)} + q_2 \frac{\Sigma(V_2 + V_3)L^2}{\Sigma(V_2 + V_3} \quad [15]$$

where the coefficients, p's and q's, are functions of the a's and b's.

Regression analysis can be applied to equation [14] if the coefficients implied in V_1 are known or estimated. Similarly regression analysis can be applied to equation [15] if the coefficients implied in V_2 and V_3 are known or estimated. Since neither set of coefficients are known, the two equations are solved progressively by an iterative technique starting with some arbitrary value for the coefficients in V_1. This involves new calculations for each day, consequently the process is long and involved and can be done only by a digital computer.

Furthermore, since development is an irreversible process, daily values of the environmental factors below the lower critical limit or above the upper critical limit cannot reverse the progress towards maturity. Therefore a technique was used for omitting all negative daily values of the temperature and photoperiod terms, V_1, V_2 and V_3 (Bassett, Holmes and Mackay, 1961).

The coefficients, p and q, in equations [14] and [15] are related to those in equation [5]:

$$a_o = \frac{-q_1 \pm \sqrt{q_1^{\,2} - 4q_oq_2}}{2q_2} \qquad [16]$$

$$a_1' = q_1 + 2q_2a_o \qquad [17]$$

$$a_2' = q_2 \qquad [18]$$

$$b_o = \frac{-(p_1 + p_3)\sqrt{(p_1 + p_3)^2 - 4(p_2 + p_4)p_o}}{2(p_2 + p_4)} \qquad [19]$$

$$b_1' = p_1 + 2p_2b_o \qquad [20]$$

$$b_2' = p_2 \qquad [21]$$

$$d_1' = p_3 + 2p_4b_o \qquad [22]$$

$$d_2' = p_4 \qquad [23]$$

The desired form of the quadratics in equation [5] is one that is concave downward so that both arms cut the temperature or photoperiod axis, thus evaluating the lower and upper critical levels.Another acceptable form of the equation is one that is concave upward and having both arms cut the temperature or photoperiod axis. In this case, since negative values are rejected,no optimum value can be specified.One arm of this quadratic is probably meaningless. Familiarity with the distribution of the environmental data is necessary to determine which arm of the quadratic is meaningful. Should the quadratic be concave upward and not cut the axis,then the roots giving the lower and upper critical limits would be imaginary and the solution meaningless. In this case it was assumed there were insufficient data to properly define a realistic quadratic and a linear function of the particular environmental component in question was calculated instead.In some cases no solution was obtainable, i.e. functions of all daily values of a particular component were negative and were rejected. When this happened for photoperiod it was necessary to set $V_1 = 1.0$ before evaluating the coefficients implied in V_2 and V_3.

It was possible, therefore,to represent each of the three environmental components by one of the following functions:

(1) A full quadratic function, concave downwards,defining a lower and upper critical value and an optimum value. In some cases lack of sufficient range of data made the determination of one or more of these characteristic points doubtful or meaningless.
(2) One arm of the quadratic, concave upwards,defining the lower critical value only and with positive slope.
(3) One arm of the quadratic, concave upwards,defining the upper critical value only, and with a negative slope.
(4) A straight line defining the lower critical level and with a positive slope.
(5) A straight line defining the upper critical level and with negative slope.
(6) No solution.

A feature of the analysis was that the most appropriate function resulted automatically from the analysis.Examples will be illustrated in the section on results.

During the iterative solution it was necessary to check progress and determine when an appropriate solution had been obtained. After each iteration the new coefficients were used in equation [5] and a calculation made for each station for the phenological period in question. If the coefficients were exactly correct the summation would be unity for each station. However, this was not so: for some stations it was larger and for others smaller. The coefficient of variation of the summation constant was calculated for the set of stations used in the analysis (Arnold,1959). This coefficient decreased as the iterative analysis progressed. It was assumed that a stable solution was reached when the coefficient of variation changed by less than one per cent in successive iterations.

The resulting coefficients in equation [5] are not strictly independent and a unique evaluation of them is not possible. That is, if a_1' and a_2' are multiplied by any constant, then division of b_1', b_2', d_1' and d_2' by the same constant will result in an unaltered value of M. Since it will be desirable at a later stage of this study to compare coefficients and plotted response curves for various stages and for various crops, it will be necessary to make the following restrictions in order that these coefficients be unique:

(1) Set to unity the sum of the coefficients for the two daylength terms as well as the sum of the four coefficients of the temperature term. This can be achieved with no change in results by calculating new coefficient.

$$a_1'' = \frac{a_1'}{a_1' + a_2'} \qquad [24]$$

$$a_2'' = \frac{a_2'}{a_2' + a_2'} \qquad [25]$$

$$b_1'' = \frac{b_1'}{b_1' + b_2' + d_1' + d_2'} \qquad [26]$$

etc.

(2) To keep the equation balanced it will be necessary to multiply the whole expression (RHS) by

$$(a_1' + a_2')(b_2' + b_2' + d_1' + d_2')$$

To get rid of this constant it is only necessary to proportion it into equal parts, i.e. to take the square root and multiply all coefficients by this square root. This in effect distributes the unwanted coefficient equally between the photoperiod terms and the temperature terms. Thus a new set of coefficients evolve which are unique:

$$a_1 = \frac{a_1'}{a_1' + a_2'} \sqrt{(a_1' + a_2')(b_1' + b_2' + d_1' + d_2')} \qquad [27]$$

$$= a_1' \sqrt{\frac{b_1' + b_2' + d_1' + d_2'}{a_1' + a_2'}} \qquad [28]$$

$$a_2 = a_2' \sqrt{\frac{b_1' + b_2' + d_1' + d_2'}{a_1' + a_2'}} \qquad [29]$$

$$b_1 = b_1' \sqrt{\frac{a_1' + a_2'}{b_1' + b_2' + d_1' + d_2'}} \qquad [30]$$

etc.

These unique coefficients were used to determine the characteristic response curves for photoperiod, for maximum temperature and for minimum temperature for different stages of development of Marquis wheat (Fig. 2).

During regression analysis another problem arose which can best be explained by the following:

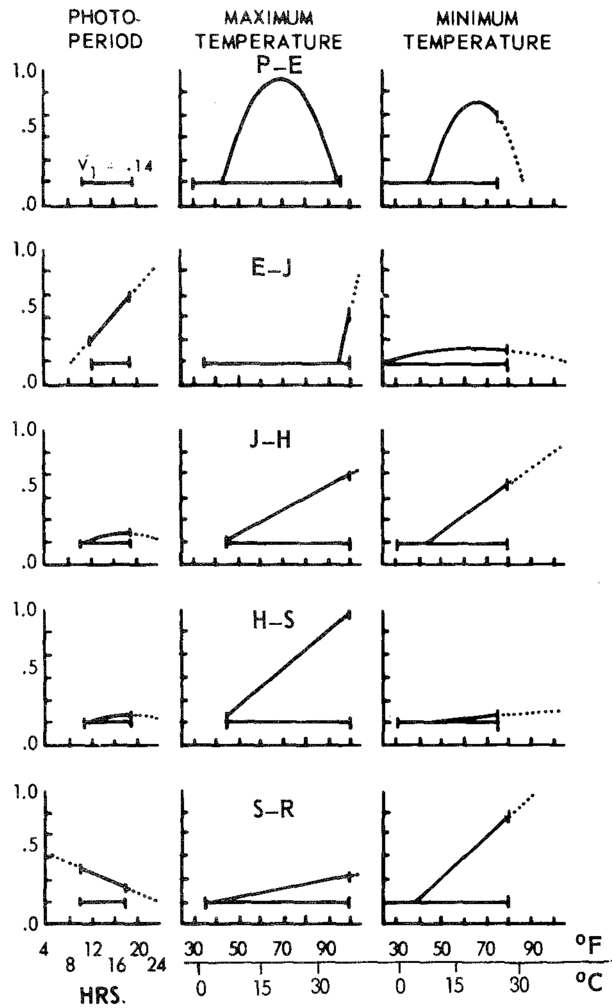

Fig. 2. Characteristic response curves for Marquis wheat based on the regression coefficients of Table 9(the dotted portions of the curves are beyond the range of observed data).The ordinates are relative values of the daily contribution of the three environmental factors to the daily rate of development.

For ease of discussion in the following, from equation [6] let

$$V_1(V_2 + V_3) = W$$

and let W_1 be for period planting (P) to crop emergence (E),W_2 for period emergence to jointing (J), W_3 for period jointing to heading (H),$W_4$for period heading to soft dough (S), and W_5 for period soft dought to ripe (R).
Then total development for the full period from planting to ripe will be:

$$\sum_{P}^{E} W_1 + \sum_{E}^{J} W_2 + \sum_{J}^{H} W_3 + \sum_{H}^{S} W_4 + \sum_{S}^{R} W_5 = 5 \qquad [31]$$

For regression analysis purposes the coefficients implied in W in:

$$\sum_{S_1}^{S_2} W = 1 \qquad [32]$$

should, at first thought,be calculated by using the set of observed dates for stage 1 and stage 2 together with the sets of observed temperature and daylength data for the period between the two stages. However, for age estimation purposes, the above 5 term equation [31] is used, starting with observed date of planting and summing until unity is reached, thus

$$\sum_{P}^{\tilde{E}} W_1 = 1 \qquad [33]$$

This marks the estimated date of emergence, $\tilde{E}$, which may or may not coincide with the observed date. After reaching this date of emergence, further summation is carried out to obtain the estimated date of jointing, J, thus

$$\sum_{\tilde{E}}^{\tilde{J}} W_2 = 1 \qquad [34]$$

If the estimated date and the observed date of emergence were the same, there would be no problem. But since there might be a difference, either due to an error in observation or in regression, it can be readily seen that summation might be carried out over a slightly different period than that for which regression analysis was done. This would result in the introduction of unwanted errors in estimation of the dates of stages beyond emergence.

To get around this, the regression analysis was carried out for the period from its estimated beginning to its observed ending; thus for period emergence to jointing the equation used was:

$$\sum_{\tilde{E}}^{J} W_2 = 1 \qquad [35]$$

In general the formulae used for regression analysis were:

$$\sum_{P}^{E} W_1 = 1 \qquad [36]$$

$$\sum_{\tilde{E}}^{J} W_2 = 1 \qquad [37]$$

$$\sum_{\tilde{J}}^{H} W_3 = 1 \qquad [38]$$

$$\sum_{\tilde{H}}^{S} W_4 = 1 \qquad [39]$$

$$\sum_{\widetilde{S}}^{R} W_5 = 1 \qquad [40]$$

and the formula used for estimation of age was

$$\sum_{P}^{\widetilde{E}} W_1 + \sum_{\widetilde{E}}^{\widetilde{J}} W_2 + \sum_{\widetilde{J}}^{\widetilde{H}} W_3 + \sum_{\widetilde{H}}^{\widetilde{S}} W_4 + \sum_{\widetilde{S}}^{\widetilde{R}} W_5 = 5 \qquad [41]$$

The total sum of 5 for the date of maturity results from the summation of the five individual development periods. The series of values which result from the integration of equation [41] from date of planting to any other development stage might be called the biometeorological time scale (BMTS). It is obvious that this time scale will not coincide with a calendar time scale but is dependent on both temperature and photoperiod (Figs. 3, 4 and 5).

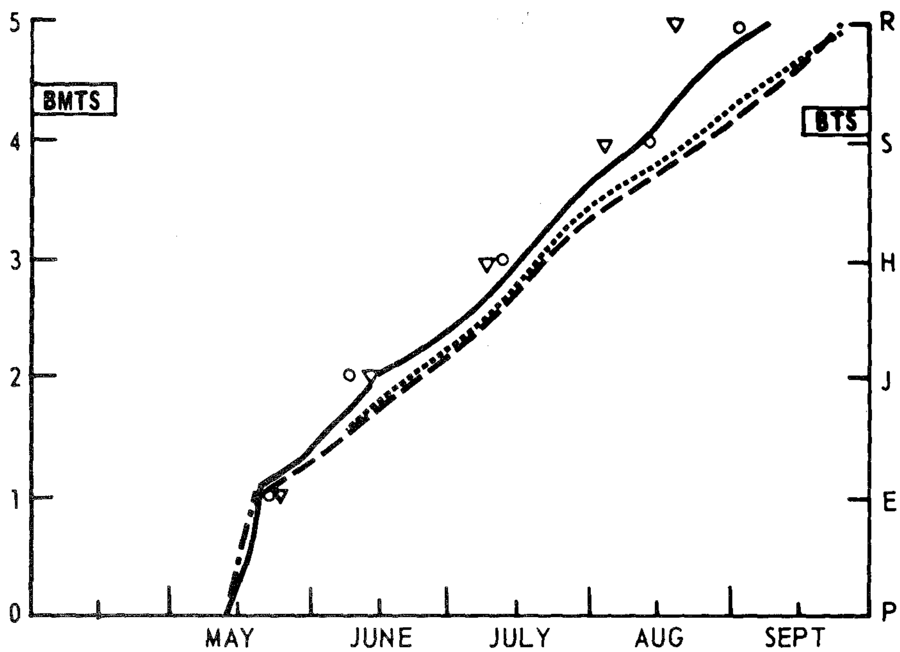

Fig. 3. The accumulated development of Marquis wheat at Beaverlodge,1959. BMTS is the biometeorological time scale to which equation [41] is referred; BTS is the biological time scale to which phenological observations are referred.

○ ○ ○ ○ observed times or stages

△ △ △ average times or stage dates for the regression data equivalent to model 1

.... model 2

- - - - - model 3

——— model 4

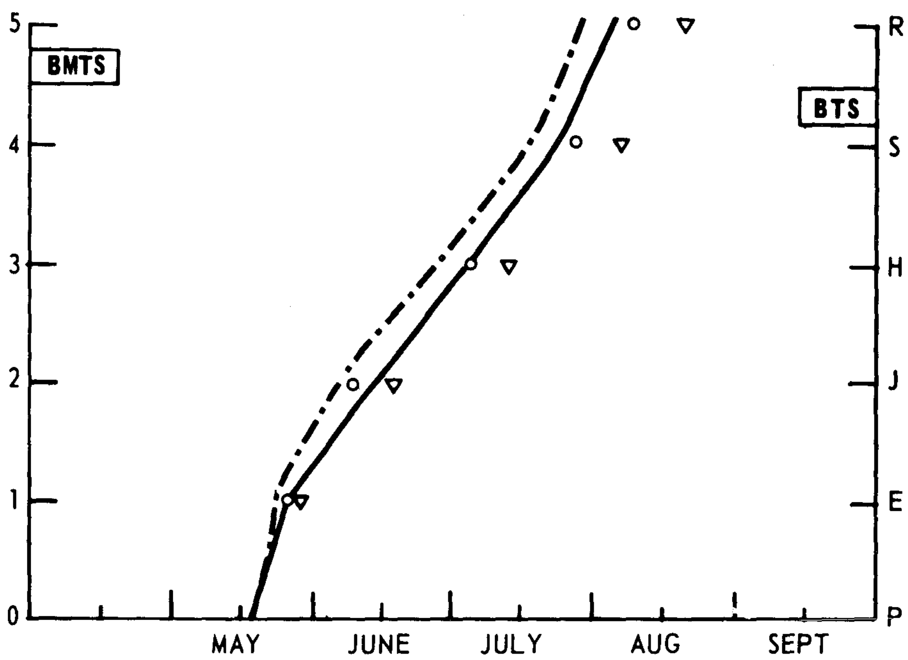

Fig. 4. The accumulated development of Marquis wheat at Swift Current 1961 (see Fig. 3 for explanation).

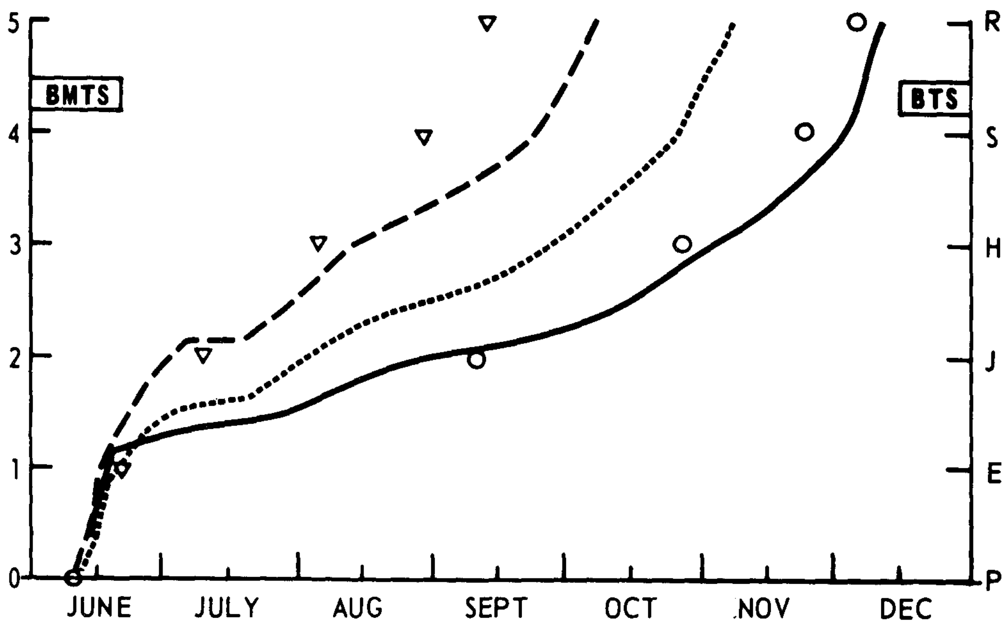

Fig. 5. The accumulated development of Marquis wheat at Buenos Aires 1965 (see Fig. 3 for explanation).

Different stages of development(biological time) correspond to numbers on this time scale as follows:

Biological time			Biometeorological time
Planting	P	=	0
Emergence	E	=	1
Jointing	J	=	2
Heading	H	=	3
Soft Dough	S	=	4
Ripe	R	=	5

Intermediate stages (or biometeorological times) are represented by decimals.

After performing the necessary iterative regression analysis using equations [14] and [15] and regression data (see below) the resulting coefficients (Table 9) were used in equation [41] to determine the estimated ages of various plantings at the five principle phenological stages (Figs. 3, 4 and 5). On comparing these estimated ages with actual ages it was found that there was a slight bias in the average of the estimated ages as compared with that of the actual ages. This was removed by iteratively altering the value of a_1', and a_2' equation [5] but preserving the constant ratio a_1'/a_2', until the bias between the averages of the estimated ages and of the actual ages at each phenological stage were less than one half day.

In the case of the simple heat unit model, equation [10] ,and the Nuttonson photothermal model, equation [13] , the value of b_0 was set to 40°F as suggested by Nuttonson (1953, 1955). The value of k and K were determined from the regression data (see below) such that the bias between the average of the estimated ages and of the actual ages was less than half a day.This was accomplished iteratively as described above.

In summary, then, four models are to be tested for their relative performance as estimators of the rate of development of wheat.For convenience in the following discussion, the four models are distinguished as follows:

Model 1: based on the average rate of development period, equation [7] (Table 6).

Model 2: based on the simple heat unit theory, equation [10] . The base temperature was set at 40°F* for all periods and the values of k_1 and K_1 for each crop period (Table 8) were calculated from the regression data.

Model 3: based on the photothermal concept of Nuttonson (1948), equation [13] . The base temperature was set at 40°F for all periods and the values of k_2 and K_2 for each crop period (Table 8) were calculated from the regression data.

Model 4: the triquadratic model, equation [5] . All coefficients for this equation for the different periods (Table 9) were calculated from the regression data.

DATA

Daily meteorological and phenological observations for several cereal crops were available from a Canada wide crop-weather study which was carried out from 1953 to 1962 in co-operation with personnel at several research establishments of the Canada Department of Agriculture (Ripley, 1958) (Table 1). Phenological datas for Marquis wheat (TRITICUM x AESTIVUM L.) at planting,emergence, jointing, heading, soft dough and hard dough or ripe were used in this study.Seeds were from foundation stock supplied by the former Cereal Division of the Experimental Farms Service,Canada Depart-

---

*) Throughout the text and in all tables Fahrenheit degrees ($^{\circ}$F) are used. Temperatures in degrees F (X) can be converted to temperatures in degrees C (Y) by the formula Y = 5/9(X-32).

TABLE 1. Location of establishments providing data for this study

	Lat.	Long.	Altitude ft
Harrow	$42^{0}02'$N	$82^{0}53'$W	626
Ottawa	$45^{0}24'$N	$75^{0}43'$W	260
Normandin	$48^{0}51'$N	$72^{0}32'$W	450
Kapuskasing	$49^{0}25'$N	$82^{0}23'$W	735
Swift Current	$50^{0}16'$N	$107^{0}44'$W	2,707
Lacombe	$52^{0}28'$N	$113^{0}45'$W	2,783
Beaverlodge	$55^{0}11'$N	$119^{0}22'$W	2,500
Fort Vermilion	$58^{0}23'$N	$116^{0}03'$W	915
Fort Simpson	$61^{0}52'$N	$121^{0}21'$W	430
Buenos Aires	$34^{0}35'$S	$28^{0}29'$W	76

ment of Agriculture. The wheat was grown in plots 21.5 by 9 ft*. Rows were spaced 6 inches* apart. Seeding rate was 380 seeds per row. Plots were fertilized for optimum production for the soil type at each site involved. Phenological events were defined as follows:

Planting (P) was simply the date the seed was put in the ground.

Emergence (E) was the date on which it was first possible to see 50 plants per plot.

Jointing (J) or earliest date of first internode elongation occurred when the growing point or primordium began to move upwards away from the crown of the young plant. This could be observed only by carefully dissecting a few plants periodically. This stage usually occurred just prior to the appearance of the 5th leaf. The jointing date was taken when the stage was found in at least two of the first 10 plants examined.This stage corresponds closely to stage 12,the first recognizable stage of floral initiation, used for scoring morphological stages by Friend, Fisher and Helson (1963).

Heading (H) was defined as the stage when the base of the rachis(or head)reached the same height as the ligule (or base of the shot blade). The date of this stage was taken when the first 50 plants in a plot reached this stage.

Soft dough (S) was determined by examining a kernel from the central portion of the head.At this stage the kernel should still be easily deformed when pressed between the fingers but no "milk" or liquid should exude under such pressure. The date was recorded when at least 5 such kernels were found in the first 10 heads examined.

Ripe (R) was taken when the crop was at the hard dough stage.This occurred when it was no longer possible to deform the kernel by pressure between the fingers but the kernel could still be cut by pressure from the fingernail.On so breaking the kernel open,the interior should display a white, floury appearance.The date for this stage was taken when such kernels were found in the central portion of 5 of the first 10 heads examined.

Weather observations (Table 2) were taken according to Canadian Meteorological Service standards which correspond closely to those of WMO (1961).Temperatures were expressed in degrees Fahrenheit.

*) One foot (ft) = 12 inches = 0.3048 meters.

TABEL 2. Averages of daily maximum and minimum temperatures by months for the normal period 1931-1960 and the photoperiod for 21st of each month

	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	Maximum temperature, °F								
Harrow	55	67	78	82	81	73	62	46	35
Ottawa	51	66	75	80	78	68	55	40	25
Normandin	42	59	69	74	72	62	49	33	16
Kapuskasing	43	58	69	74	72	61	48	29	15
Swift Current	49	63	70	79	76	65	53	34	25
Lacombe	51	64	69	76	73	65	54	36	25
Beaverlodge	47	62	67	72	70	61	49	31	21
Fort Vermilion	45	62	70	75	71	60	44	20	4
Fort Simpson	37	57	69	74	69	55	37	12	-4
Buenos Aires	72	66	60	59	62	65	71	77	82
	Minimum temperature, °F								
Harrow	37	48	59	63	62	54	44	34	23
Ottawa	32	45	55	59	57	49	38	27	10
Normandin	22	37	47	52	49	41	33	20	0
Kapuskasing	22	35	47	52	50	42	33	18	-2
Swift Current	29	40	48	55	51	43	33	18	8
Lacombe	25	37	44	49	45	37	27	13	2
Beaverlodge	27	38	44	48	46	39	31	16	5
Fort Vermilion	21	37	44	49	45	35	25	5	-13
Fort Simpson	15	35	46	50	47	37	23	0	-18
Buenos Aires	53	49	45	44	45	48	53	58	62
	Photoperiod, hr								
Harrow	13.6	14.7	15.2	14.8	13.7	12.3	10.9	9.6	9.1
Ottawa	13.8	15.1	15.7	15.2	13.9	12.3	10.7	9.3	8.7
Normandin	14.0	15.5	16.2	15.6	14.1	12.3	10.6	9.0	8.2
Kapuskasing	14.0	15.6	16.3	15.7	14.2	12.3	10.5	8.9	8.2
Swift Current	14.1	15.7	16.4	15.8	14.2	12.3	10.5	8.8	8.0
Lacombe	14.3	16.0	16.8	16.1	14.4	12.4	10.3	8.5	7.7
Beaverlodge	14.5	16.5	17.4	16.6	14.7	12.4	10.2	8.1	7.1
Fort Vermilion	14.8	17.1	18.3	17.3	15.0	12.4	9.9	7.5	6.4
Fort Simpson	15.3	18.1	19.7	18.3	15.5	12.5	9.6	6.7	5.2
Buenos Aires	11.1	10.2	9.8	10.1	11.0	12.0	13.1	14.1	14.5

Data from observations taken during the 5-year period 1953-57, called regression data, were used for calculating the coefficients and constants required for all four models (Table 3).

TABLE 3. Phenological information for regression data 1953-1957

Station	Planting date	Span in days for period				
		PE	EJ	JH	HS	SR
Normandin	25-5-53	8	*	(45)	27	26
	15-6-54	6	*	(38)		
	27-5-55	9	20	17	31	15
	29-5-56	7	22	26		
	30-5-57	12	23	20	36	15
Ottawa	8-5-53	8	23	21	21	11
	26-5-53	8	16	23	17	11
	10-6-53	6	17	23	19	7
	24-6-53	6	17	26	19	8
	9-7-53	8	19	34		
	22-7-53	8	18	47		
	6-8-53	8	16			
	20-5-54	6	19	27	28	10
	8-6-54	5	18	23	27	12
	18-6-54	4	20	20	31	8
	21-7-54	6	12			
	5-5-55	8	21	21	20	7
	27-5-55	4	20	15	16	5
	23-6-55	6	19	16	43	
	20-7-55	8	16	38		
	8-6-56	4	23	26	29	9
	4-7-56	4	19	35		
	1-8-56	5	23			
	7-5-57	6	27	18	30	7
Harrow	13-5-53	7	27	13	18	10
	21-4-54	6	*	(49)	14	21
	2-4-55	9	28	29	21	4
	9-4-56	16	33	21	28	8
	57	No report				
Kapuskasing	25-5-53	11	15	32	*	(40)
	1-6-53	11	16	28	*	(40)
	8-6-53	10	12	28	*	(42)

TABLE 3. Continued

Station	Planting date	Span in days for period				
		PE	EJ	JH	HS	SR
Swift Current	16-5-53	13	*	(53)	24	14
	19-5-54	12	*	(46)	46	8
	19-5-55	8	25	26	28	8
	17-5-56	6	19	33	23	14
	8-5-57	10	27	26	16	18
Lacombe	14-5-53	22	24	26		
	21-5-54	11	23	29	49	
	11-5-55	9	25	34	20	22
	18-5-56	9	22	29	35	17
	16-5-57	7	16	35	34	27
Beaverlodge	21-5-53	8	27	22	28	23
	17-5-54	8	25	28	26	32
	4-5-55	15	22	26	25	24
	11-5-56	11	21	29	25	25
	6-5-57	12	24	30	27	33
Fort Vermilion	23-5-53	6	24	19	23	13
	28-5-54	16	15	16	33	15
	17-5-56	9	8	28	19	14
	18-5-57	8	17	25	36	12
	16-5-57	11	25	18	45	21
Fort Simpson	15-5-53	10	27	18	20	15
	23-5-54	6	11	21	18	16
	18-5-55	10	14	21	14	5
	7-5-56	17	14	30	17	20
	8-6-57	7	14	27	22	42

* Date of one stage missing.
() sum of two periods.

The data gathered during the second 5-year period, called test data, were used as independent data to test these four models and their coefficients (Table 4).

As a further test of the four models, independent data for Marquis wheat grown in the Argentine were available. These data were obtained for several dates of planting each year over the period 1961 to 1965 at the Experimental Field of the Agronomic and Veterinary Faculty of the University of Buenos Aires (Table 5). Seeds and instructions were provided by the author so that data would be compatible with that from Canada.

TABLE 4. Phenological information for test data 1958-1962

Station	Planting date	Span in days for period				
		PE	EJ	JH	HS	SR
Normandin	3-6-58	10	25	28	28	27
	2-6-59	6	21	23	29	25
	-60	No report				
	25-5-61	14	*	(42)	26	28
	22-5-62	9	18	23	28	37
Ottawa	15-5-58	6	25	23	15	19
	4-6-58	7	20	22	12	23
	6-5-59	6	21	24	20	11
	19-6-59	5	19	11	21	29
	18-5-60	5	20	27	21	15
	27-6-60	7	28	22		
	12-5-61	6	20	27	22	19
	16-6-61	5	21	18	22	18
	16-5-62	5	22	21	27	16
Harrow	27-5-58	6	31	9	32	12
	14-4-59	10	25	23	26	14
	20-4-60	7	36	15	31	9
	6-4-61	21	40	11	32	10
	18-4-62	10	27	17	18	25
Swift Current	14-5-58	8	26	24	28	7
	1-5-59	14	24	31	32	21
	12-5-60	8	25	31	21	11
	17-5-61	8	13	26	23	13
	11-5-62	13	16	28	33	14
Lacombe	19-5-58	6	14	37	24	26
	27-5-59	6	15	35	47	9
	23-5-60	6	22	30	36	14
	26-5-61	6	13	27	29	19
	16-5-62	9	20	28	36	21
Beaverlodge	5-5-58	12	14	27	23	23
	13-5-59	8	18	33	32	20
	3-5-60	15	29	32	23	30
	10-5-61	13	12	32	30	18
	11-5-62	15	16	35	30	25
Fort Vermilion	9-5-58	11	20	21	25	27
	3-6-59	8	19	16	44	21
	13-5-60	10	25	19	27	25
	16-5-61	6	22	12	24	24
	14-5-62	11	27	17	34	20
Fort Simpson	27-5-58	10	16	18	29	14
	15-5-59	10	20	24	28	40
	20-5-60	10	16	21	31	23
	-61	No report				
	23-5-62	10	15	26	28	26

* Date of one stage missing.
() sum of two periods.

TABLE 5. Phenological information for test data from Buenos Aires, 1961-1965

Planting date	Span in days for period				
	PE	EJ	JH	HS	SR
2-8-61	12	54	33	27	6
21-7-62	13	54	36	31	11
14-6-63	16	87	45	34	17
4-7-63	9	82	40	34	17
30-7-63	17	68	31	29	11
14-9-63	8	41	27	29	6
11-6-64	21	78	40	37	7
7-7-64	14	73	33	29	15
5-8-64	12	55	30	33	8
2-9-64	11	44	22	31	7
10-6-65	8	84	47	28	12
6-7-65	17	74	29	29	7
6-8-65	8	55	33	28	7
7-9-65	11	37	28	26	8
Average	13	63	34	30	9

RESULTS AND DISCUSSION

The data-gathering part of this study provided, in most cases, ten years of information at eight or nine sites across Canada (Tables 3 and 4). Problems with hail, frost and other uncontrollable accidents reduced the number of crops at some stations. At Kapuskasing, data from three dates of planting were obtained the first year only. At Ottawa and Buenos Aires more than one date of planting were made each year. Certain phenological observations were missed or the data were very doubtful because of the difficulty of making the observation. This was particularly so with the date of jointing and the date of soft dough both of which might have passed unnoticed if daily inspection was not carried out.

Each station, each year and each date of planting provided some variability in the daily meteorological environment which contributed to variations in the durations of the phenological periods under investigation. The total range of daily maximum temperature was well over 70°F, while that for daily minimum temperature was over 50°F. Photoperiod ranged from about 12 hr to nearly 20 hr. These ranges for the various phenological periods are illustrated by the horizontal bars in Fig. 2.

At Buenos Aires, unusual results were obtained by planting at abnormal dates (Table 5). Planting dates were as early as June during their mid-winter when photoperiod was less than 10 hr and the minimum temperature was in the 30° to 40°F range. Plantings were made as late as September when photoperiod was 12 hr and minimum temperatures in the range 40° to 60°F.

For comparing the climates at the stations involved in this study the average temperatures for the normal period 1931-1960 (Meteorological Branch 1964-1965) and the photoperiod (Robertson and Russelo, 1967) for the 21st of each month are shown in Table 2.

Although there is little natural variation in the photoperiod on a given date at a given site considerable variation in the photoperiod during specific phenological periods was obtained between sites, and between years and plantings by the variations in the date of planting. For example, a difference of two weeks in the date of planting at a given station could alter the photoperiod during period EJ by 0.5 hr at Harrow and 1.3 hr at Fort Simpson.

Considerable variation was obtained in the duration of the various phenological periods for both the regression data (Table 3) and the test data (Table 4). Because of the abnormal dates of planting and the unusual temperatures and photoperiod combinations, the duration of the various phenological periods at Buenos Aires were considerably different than for Canada (Table 5) e.g. it took 149 days, on the average, to ripen wheat whereas in Canada it took only 95 days. Thus the Buenos Aires information provided a set of powerful test data for the models under consideration.

Model 1, equation [7], is based on the average rate of development, $1/\bar{N}$ of Marquis wheat as determined from the regression data (Table 3). The use of this model would be equivalent to assuming that the span of time, say from planting to ripe, is a constant dependent only on the varietal characteristic and independent of the meteorological environment. The period PE was shortest averaging 9 days while the periods JH and HS were of about equal length, averaging respectively 26 and 25 days. The average span for period SR was 15 days. The average daily rate of development for each period is the reciprocal of each of these values (Table 6).

TABLE 6. Average span, rate of development and age for various phenological periods based on data for period 1953-1957

Period	No. of cases	Average age from P to end of period (days)	Average span (days)	Average daily development rate ($days^{-1}$)
PE	56	9	9	0.1111
EJ	51	29	20	0.0500
JH	53	55	26	0.0385
HS	43	80	25	0.0400
SR	44	95	15	0.0667

The bias in the averages of the estimated ages (Table 7) provides also an indication of the average span of time for each crop period for the test data and the Buenos Aires data. The bias is small for the first 4 periods of the test data. This is to be expected since the test data were from the same sites as the regression data although the climate during the second 5-year period may have been a little different than during the first 5-year period. An unexpected anomally of over 6 days showed up in the bias of the test-data period SR. On the average the span for this period was 21 days, 6 days longer than the average for the test data. This large bias may have resulted because of a change in instructions for taking observations during the second 5-year period. During the first 5-year period observers were asked for the date of hard dough and during the second 5-year period for the date of "ready to cut for stocking" to distinguish from "ready to cut for combining". It was assumed that the former was identical to the hard dough stage which has been used as the "ripe" stage in this paper.

At Buenos Aires the use of Model 1 resulted in a large bias in the estimated ages at various stages (Table 7). The span of time for the five periods were respectively, 13, 63, 34, 30 and 9 days (Table 5), considerably different than for the Canadian regression data (Table 6).

Besides this large variation between the averages of Canadian data and that of the Buenos Aires data, there is also a large variation between spans for the same period at different stations, for different years, and for different dates of planting

TABLE 7. Bias in averages of the estimated ages at phenological stages for various models and data sources (unit is day)

Phenological stage	Data source	Model			
		1	2	3	4
	Regression	0.2	0.1	0.1	0
Emergence	Test	0.9	0.4	0.5	-0.8
	Buenos Aires	-3.6	-2.6	0.9	-3.9
	Regression	0.1	-0.1	0.1	-0.1
Jointing	Test	-1.2	1.1	1.4	-0.4
	Buenos Aires	-47	-41	-23	-12
	Regression	0.2	-0.1	0.0	-0.1
Heading	Test	1.0	3.0	2.9	1.0
	Buenos Aires	-55	-40	-17	+2
	Regression	-0.1	+0.3	-0.1	-0.1
Soft Dough	Test	-1.5	0.0	-0.9	-1.2
	Buenos Aires	-60	-43	-22	+2
	Regression	0.0	0.0	0.0	0.0
Ripe	Test	-6.2	-4.0	-4.2	-7.5
	Buenos Aires	-54	-41	-20	0.0

(Tables 3, 4 and 5). The standard deviation of the individual lengths of various phenological periods could be obtained by multiplying the standard deviations of the stochastic 1 (Table 10; model 1) by the average spans (Table 6) for the respective periods. These SD's are 3.6, 5.0, 6.8, 8.5 and 8.1 days for the respective period PE to SR for the regression data.These results suggest that a fixed calendar age at phenological stages or a constant rate of progress towards maturity, independent of environment, is not a characteristic of Marquis wheat.

Model 2, based on equation [10] is the simple heat unit concept of Réaumur which assumes that the rate of crop development is a simple linear function of one environmental factor, mean temperature. The base temperature, b_0, was set at 40°F as suggested by Nuttonson (1955) for Thatcher wheat and assumed applicable to all spring wheats. In order to avoid any possibility of bias resulting from observational techniques, separate summation constants, K_1, were calculated for each period using the regression data (Table 8).These were calculated in such a manner that the resulting averages of the error in the estimated ages for the regression data were approximately zero (Table 7; model 2). When the results were applied to the test data, the bias for the average age at various phenological stages ranged from zero to ± 4 days. When applied to the Buenos Aires data the bias ranged up to -43 days (Table 7).

The summation constant at heading for this simple model was found to be 1,083 degree days (Table 8) about 20% more than the 990 degree days determined by Nuttonson (1955) for Thatcher wheat. The constant at ripe was 1,907 degree days about 2% less than the 1,950 degree days found by Nuttonson for Thatcher. For ease of comparison the summation constants were reduced to a stochastic 1, and the standard deviation of this statistic calculated for each period (Table 10).

TABLE 8. Summation constants for the simple heat unit equation (Model 2) and Nuttonson's photothermal equation (Model 3) for various phenological periods determined from regression data 1953-1957

Period	Model 2			Model 3		
	k_1	K_1	ΣK_1 (from P to end of period	k_2	K_2	ΣK_2 (from P to end of period
PE	0.009451	106	106	0.0005940	1,684	1,684
EJ	0.002501	400	506	0.0001510	6,623	8,307
JH	0.001733	577	1,083	0.0001060	9,434	17,741
HS	0.001835	545	1,628	0.0001155	8,658	26,399
SR	0.003580	279	1,907	0.0002330	4,292	30,691

TABLE 9. Final regression coefficients in the triquadratic equation, Model 4 as determined from 1953-1957 data

	Period				
	PE	EJ	JH	HS	SR
a_o	$V_1 = 1$ equation [6]	8.413	10.93	10.94	24.38
a_1		1.005	0.9256	1.389	-1.140
a_2		0	-0.06025	-0.08191	0
b_o	44.37	23.64	42.65	42.18	37.67
b_1	0.01086	-0.003512	0.0002958	0.0002458	0.00006733
b_2	-0.0002230	0.00005026	0	0	0
b_3	0.009732	0.0003666	0.0003943	0.00003109	0.0003442
b_4	-0.0002267	-0.000004282	0	0	0

TABLE 10. Values of the standard deviation of the summation constants(stochastic 1) for various models and phenological periods for the regression data 1953-1957

Period	Model			
	1	2	3	4
PE	0.40	0.41	0.41	0.30
EJ	0.25	0.32	0.28	0.21
JH	0.26	0.27	0.21	0.19
HS	0.34	0.28	0.24	0.21
SR	0.54	0.44	0.45	0.43

It would appear, on this basis, that the simple heat unit concept, model 2, is no better than model 1 for periods PE, EJ, and JH and only a little better for periods HS and SR.

A further demonstration of the inability of the simple heat unit concept to serve as a model for relating rate of crop development to temperature is obtained by plotting reciprocal of span for a period against the mean temperatures ($\bar{T}_k$)for that period. It can be shown by simple algebraic manipulation that equation [10] reduces to

$$\frac{1}{N} = k_1(\bar{T}_m - b_o) \qquad [42]$$

providing that mean daily temperatures, T_m, lower than b_0 are set equal to b_0. Equation [42] is a simple linear regression equation and k_1 and b_0 can be evaluated by regression analysis. The results for the period EH (Fig. 1) show that no significant correlation ($r = 0.11$) exists for the composite data used and that the value of the threshold temperature ($b_o = -21.1$) is quite unrealistic.

Model 3 is based on Nuttonson's photothermal concept, equation [13]. Again the base temperature, b_0, was assumed to be 40°F as suggested by Nuttonson and the regression data was used to calculate the summation constants (Table 8)so that the bias in the estimated average age at various stages was near zero (Table 7). The resulting summation constants at heading, 17,741 degree day hours,were only slightly greater and at ripe, 30,691 degree day hours,were only slightly less than the 16,541 and 31,686 found by Nuttonson for Thatcher wheat (1955).

The standard deviations of the stochastic 1 for this model indicate that it was no better than Model 1 and Model 2 for periods PE and EJ (Table 10). This may be expected for period PE where photoperiod should have no influence on germination. It was surprising that it was no better than Model 1 and only slightly better than Model 2 for period EJ when photoperiod might have a large influence on rate of development.

When Model 3 was used as an estimator of the effect of temperature and photoperiod on the rate of development of crops in the test data the bias in the average estimated age (Table 7)ranged from half a day at emergence to about 3 days at heading and -4 days at ripe. These were about the same as for the other models.When Model 3 was used with the Buenos Aires data, the biases at all stages were much smaller than those for Models 1 and 2, even though they ranged up to -23 days. It appears therefore that the photothermal concept takes into consideration some of the influence of photoperiod on rate of development but there is also much room for improvement.

Model 4 is the triquadratic equation developed in this paper, equation [5]. The coefficients (Table 9)were determined by a technique outlined earlier using the regression data.Adjustments were made so that the bias in the average of the estimated ages would be near zero (Table 7).

It should be pointed out that all the coefficients in Model 4 (Table 9) were determined by an iterative regression technique which provided the best relationship for the rate of development as influenced by the three environmental factors and their interactions for the set of regression data used. This was not the case for Models 2 and 3 where the minimum critical temperature, b_o, was predetermined and the only adjustment was to assure that there would be little or no bias in the average of the estimated ages at different stages for the regression data. As with all regression analysis it is generally easy to obtain a set of coefficients which fit well the regression data, particularly where a small sample is involved. It is more difficult, however, to obtain a set of coefficients which can be applied with success to independent test data.Fortunately two sets of independent test data were available for assessing the reliability of the coefficients found for the regression data.

From these coefficients (Table 9) characteristic response curve for each of the environmental factors were determined (Fig. 2).Several of these characteristic curves indicate a curvilinear response. However, because of the absence of extremely high values at the stations involved in this study, values at the critical or maximum level were not reached in most cases. In such cases the responses are generally linear. The dotted portion of the response curves are beyond the limits of observed data.

For the period PE there is no response to photoperiod as would be expected. For this period it would be expected that V_1 would be unity. However, with the redistribution of constants according to equation [28] it is found that $V_1 = 0.14$. The response to both maximum and minimum temperatures was curvilinear with a threshold, b_0, of 44.4°F, close to the value of 40°F suggested by Nuttonson (1955). The upper limit for maximum temperature was 95°F which agrees with the value of 35°C reported by Friend, Helson and Fisher (1962a) for the upper limit of continued growth. The optimum for maximum temperature was found to be 70°F and for minimum 66°F.

It is difficult to find experimental work in the literature in which the optimum rate of germination of Marquis wheat is related to temperature. Friend, Helson and Fisher (1962b) report that the optimum rate of leaf primoridia development during the first week of growth was at 25°C (78°F) as determined under controlled conditions in a growth room. Considering the differences in the biological and temperature measurements used by Friend and for this paper, this inconsistency in optimum temperature might not be too unreasonable.

During the period EJ the strong response was to photoperiod. Since the range of photoperiods for the regression data for this period was small the only measurable response was a linear one. The threshold photoperiod, a_0, of 8.4 hr may not be well defined because it is beyond the range of data. Nevertheless it appears real enough and agrees with independent experimental results. Under controlled conditions, Friend (1961) found that Marquis wheat remained vegetative for more than 4 weeks at a photoperiod of 8 hr and at a constant temperature of 20°C (68°F). Even after 7 weeks under these conditions the morphological stage score exceeded 12, the first recognizable stage of floral initiation, by only a small amount.

There was only a weak, curvilinear response to minimum temperature with a lower critical value, b_0, at 23.6°F and an optimum at 65°F. The low threshold temperature may be quite real as temperatures lower than this were observed during the period with no apparent injury to the crop.

The optimum of 65°F is consistent with results of Friend, Fisher and Helson (1963) who report data from a controlled environment which indicates that the number of days to floral initiation (score 12) was a minimum at a temperature of 20°C (68°F) for light intensities from 1,000 to 2,500 ft-C.

The response to high maximum temperatures above 92°F may be fortuitous as very few temperatures were observed above this value.

During the period JH the response was weaker to photoperiod but stronger to both maximum and minimum temperature than during the previous period. The response to photoperiod was curvilinear with a threshold value, a_0, at 10.9 hr and an optimum at 19 hr. This is surprisingly close to preliminary results found by Robertson (1953). Using data from several dates of planting during one year at Ottawa, a threshold photoperiod of 10.7 hr was determined for Redman wheat for the period EH, even when temperature was ignored. This threshold may also be compared with results reported by Friend, Helson and Fisher (1967) who found that there was little increase in flowering score above 12 units (Friend, Helson and Fisher, 1962b) during an 8-week period when Marquis wheat was grown in a controlled environment with an 8-hr period at 20°C (68°F). Increasing the photoperiod beyond 8 hr hastened floral development.

The curvilinear response to photoperiod has also been observed by Greis et al. (1966) who report data indicating that certain varieties of spring wheat have a nonlinear response to daylength, i.e. the change in the average rate of daily development decreased with increasing daylength.

During the period JH, it appears that wheat, as far as rate of development is concerned, can benefit from high temperatures as there was no indication of a decreasing response as temperatures increased to as high as 90° or 100°F. This also appears to be the case for succeeding periods. Friend, Fisher and Helson (1963) show data which indicates a similar response of Marquis under controlled conditions.

During the period HS, there was a continuing decrease in the response to daylength with the threshold at 10.9 hr and indications of an optimum value at 20 hr. Carder (1957) noted that after heading the stimulus of long days at high latitudes ceased and that the phasic development was then dependent on temperature. The threshold temperature was determined to be 42.2°F. The response to maximum temperature was stronger, $b_1 = 0.00025$, than to minimum temperature, $b_3 = 0.000032$. This higher response to daytime temperature might be related to photosynthesis which is essentially a daytime process.

The surprising result during the period SR was the negative response to photoperiod. Friend (1961) suggests that chlorophyll content per unit leaf area decreases with decreasing light intensity which usually accompanies a decrease in daylength. Thus the negative response of rate of development to daylength in this period may reflect a slowing of the active growth, resulting in an increasing ripening rate. Another explanation might be the human "panic factor": as days become shorter there may be a tendency to estimate the ripe stage too early in order to harvest the crop before frost or snow. The strong response to minimum temperature may be associated with conversion of carbohydrate to protein during the dark period.

When the triquadratic model was used to estimate the ages of various stages using the test data, the resulting biases were of about the same magnitude as for the other models: a little smaller at jointing and heading and larger at emergence, soft dough and ripe. When applied to the Buenos Aires data, however, the biases showed a marked improvement; being near zero at heading, soft dough and ripe. The largest bias, 12 days, occurred at jointing but even this was half the size of the bias obtained by using model 3. This large error at jointing date may come about because of the difficulty of observing the phenomena and the added problem that development near this stage at Buenos Aires was extremely slow (Table 5). At the normal rate of development in Canada, jointing was readily recognized within 2 or 3 days after its occurrence. At Buenos Aires this 2 or 3 day period was extended over a week or more.

All four models were used in conjunction with equation [41], using the appropriate function for $W = V_1(V_2 + V_3)$ as determined by equations [5], [7], [10] or [13] for calculating the age of various phenological stages. The results of such calculations are shown for three typical cases, 1959 at Beaverlodge (Fig. 3), 1961 at Swift Current (Fig. 4) and 1965 at Buenos Aires (Fig. 5). The right hand scale shows the biological time scale (BTS) or the phenological stages. The left hand scale shows the biometeorological time scale (BMTS). The BTS has 6 discrete points, the various phenological stages, which were observed. The BMTS is more or less continuous since it can be calculated on a day to day basis from the existing weather data.

In the case of the Beaverlodge crop (Fig. 3), the season was cool and the crop developed much slower than the average. Both models 2 and 3 overemphasize the effect of this cool temperature and therefore underestimate the rate of development or overestimate the age at various stages. Model 4 gave a reasonably good estimate of all stages. The Swift Current example (Fig. 4) is one in which the season was warmer than usual and the crop developed faster than the average. Here models 2 and 3 overemphasize the warm temperatures and indicate a too-rapid rate of development. Again model 4 gave a more reasonable result. The Buenos Aires crop (Fig. 5) was grown under cool temperatures and short photoperiods until the SR period when temperatures were above average for the corresponding biological period in Canada. This resulted in a very slow rate of development for the first four periods and a rapid final ripening period. Neither models 2 nor 3 explained this response to the unusual environment. Model 4 came fairly close at all stages. These are only 3 selected cases out of some 55 to 60 in addition to the regression data. These cases were analysed by correlation and regression analysis and the results follow.

Three more or less independent comparisons were used to demonstrate the relative superiority of the four models for calculating the progress of the crop toward maturity.

The first of these comparisons concerned the reliability of the model for estimating the span of time from one stage to another. As was indicated in equations [9],

[12] and [5] each of the four models can be put into the form of a summation equation, adding to the value of stochastic unity when the end of the given phenological stage is reached. In actual practice, because of an incomplete model, errors in the phenological data, heterogeneous biological material and nonrepresentative environmental measurements, the summation does not always add up to unity for specific cases although for a large number of cases the average summation values was unit(by design). Thus the standard deviation of the individual summation values could be used as a measure of the relative performance of each model. This type of comparison was done only for the regression data (Table 10). From these data it can be seen that the simple heat unit equation (model 2) is no better than using the average rate of development (model 1) for the first three phenological periods and is only slightly better for the last two periods. The photothermal concept (model 3) is no better than the average-rate model and the simple heat until model for the periods JH and HS. It is better than the average rate for period SR but no better than the simple heat unit model. The triquadratic model shows some degree of superiority over all models for all phenological periods.

This type of comparison is, in some ways, not too satisfactory. For one thing an error in the observation of one phenological stage, say J for example, introduces an error in both periods EJ and JH. Such errors will be reflected in all models. Thus a statistical test of the significant difference between models is not practical.

The second comparison consists simply of the root mean square error(RMSE) between the actual age at different phenological stages and that estimated by the various models (Table 11).

TABLE 11. Root mean square error (RMSE) between actual age at various phenological stages and that estimated by different models (unit is day)

Phenological stage	Date source	Model			
		1	2	3	4
Emergence	Regression	3.5	3.1	3.3	2.5
	Test	5.7	3.8	3.9	4.8
	Buenos Aires	3.8	2.1	2.3	2.2
Jointing	Regression	6.6	7.3	6.1	4.5
	Test	7.5	7.4	6.5	5.3
	Buenos Aires	18.0	15.9	9.3	6.6
Heading	Regression	8.4	10.8	8.7	4.4
	Test	8.1	6.8	5.1	4.0
	Buenos Aires	23.5	16.2	8.4	4.9
Soft dough	Regression	12.5	13.0	10.4	8.1
	Test	11.1	9.8	7.2	8.1
	Buenos Aires	24.7	12.6	6.4	4.2
Ripe	Regression	15.6	11.8	9.7	8.8
	Test	12.1	14.4	14.4	6.8
	Buenos Aires	26.9	14.2	7.9	5.4

This was done separately for all three sets of data: regression, test and Buenos Aires. For the majority of data sources and phenological periods model 2 was better than model 1, 3 was better than 2, and 4 was better than 3. The greatest number of exceptions occurred during the period PE when the measured environment, in the instrument shelter 4.5 ft above ground,could have had greatest deviation from the actual soil environment where the seeds were germinating. Furthermore, this was the shortest period and the exact date of emergence was somewhat difficult to estimate. The greatest overall improvement in the RMSE with increasing complexity of model occurred at all periods, excepting PS, of the Buenos Aires data.

The third comparison consisted of a set of correlation data based on the actual dates of various stages and those estimated by the four models.Again the three sets of data were treated separately.The following correlation statistics were calculated and each throws some light on the relative superiority of the different models: the coefficient of determination ($CD = r^2$) (Table 12),the intercept (Table 13), the regression coefficient (Table 14) and the standard error of estimate (SEE)(Table 15).

The coefficient of determination was not aparticularly powerful statistic for determining the superiority of one model over another in this study. It must be remembered that the coefficients in none of the four models being considered were derived from the regression data by linear regression of actual age at various phenological stages on age estimated by the model or on the environmental factors included in the model. Thus when a correlation analysis was made of the actual age against estimated age, the CD might have ranged from zero to one, the intercent on the axis of the independent variable might not necessarily be zero,and the slope of the regression line might not necessarily be unity.

TABLE 12. The coefficient of determination ($CD = r^2$) for actual age at different stages correlated with calculated ages using various models and data sourced

Phenological stage	Date source	Model			
		1	2	3	4
Emergence	Regression	0	0.50	0.47	0.48
	Test	0	0.78	0.74	0.66
	Buenos Aires	0	0.83	0.91	0.67
Jointing	Regression	0	0.43	0.54	0.53
	Test	0	0.35	0.47	0.51
	Buenos Aires	0	0.22	0.80	0.87
Heading	Regression	0	0.25	0.38	0.73
	Test	0	0.57	0.74	0.75
	Buenos Aires	0	0.62	0.92	0.97
Soft dough	Regression	0	0.37	0.52	0.58
	Test	0	0.50	0.65	0.48
	Buenos Aires	0	0.89	0.96	0.98
Ripe	Regression	0	0.61	0.71	0.68
	Test	0	0.61	0.61	0.69
	Buenos Aires	0	0.88	0.95	0.96

TABLE 13. The intercept (A_{yx}) for the regression of actual age at different stages on calculated age using various models and data sources

Phenological stages	Data source	Model			
		1	2	3	4
Emergence	Regression	9	3.6	4.0	1.0
	Test	9	2.5	3.0	-1.2
	Buenos Aires	9	5.4	3.9	3.2
Jointing	Regression	29	16.0	13.2	1.6
	Test	29	14.2	11.2	0.4
	Buenos Aires	29	38.1	1.5	13.2
Heading	Regression	55	36.0	28.8	5.8
	Test	55	20.5	14.5	1.2
	Buenos Aires	55	-3.7	-8.6	8.9
Soft dough	Regression	80	41.7	31.3	4.2
	Test	80	34.6	20.3	7.6
	Buenos Aires	80	-20.9	-1.5	10.6
Ripe	Regression	95	33.8	25.4	-0.8
	Test	95	58.4	60.5	17.3
	Buenos Aires	95	-29.9	-10.4	1.9

TABLE 14. The slope (M_{yx}) for the regression of actual age at different stages on calculated age using various models and data sources

Phenological stage	Date source	Model			
		1	2	3	4
Emergence	Regression	0	0.58	0.54	0.89
	Test	0	0.73	0.66	1.15
	Buenos Aires	0	0.73	0.64	1.07
Jointing	Regression	0	0.45	0.54	0.95
	Test	0	0.51	0.60	1.00
	Buenos Aires	0	1.09	1.41	0.98
Heading	Regression	0	0.34	0.47	0.90
	Test	0	0.59	0.69	0.96
	Buenos Aires	0	1.63	1.28	0.90
Soft dough	Regression	0	0.48	0.61	0.95
	Test	0	0.58	0.76	0.92
	Buenos Aires	0	1.66	1.19	0.91
Ripe	Regression	0	0.64	0.73	1.01
	Test	0	0.44	0.42	0.89
	Buenos Aires	0	1.65	1.24	0.99

TABLE 15. The standard error of estimate (SEE) for the regression of actual age at different stages against calculated ages using various models and data sources (for expanation of asterisk* see text)

Phenological stage	Data source	Model			
		1	2	3	4
Emergence	Regression	3.5	2.5*	2.6*	2.5
	Test	5.7	1.6*	1.7*	2.0*
	Buenos Aires	3.8	1.6*	1.1*	2.2
Jointing	Regression	6.6	4.9*	4.5*	4.5
	Test	7.5	6.1*	5.5*	5.3
	Buenos Aires	18.0	15.9	8.0*	6.6
Heading	Regression	8.4	7.2*	6.6*	4.3*
	Test	8.1	5.3*	4.1*	4.0
	Buenos Aires	23.5	14.5*	6.8*	4.2*
Soft dough	Regression	12.5	9.9*	8.7*	8.1
	Test	11.1	7.9*	6.6*	8.1
	Buenos Aires	24.7	8.4*	4.9*	3.5*
Ripe	Regression	15.6	9.7*	8.4*	8.8
	Test	12.1	7.6*	7.6*	6.8
	Buenos Aires	26.9	9.7*	5.9*	5.4

Certainly if the CD was unity, the intercept zero and the slope unity, all at the same time a perfect relationship existed. However, these three statistics are independent and no one of them alone is a sufficient test of the superiority of a model. For example, consider model 3 for estimating emergence stage at Buenos Aires. Even though the CD was 0.91, better than any of the other 3 models (Table 12), the RMSE of age estimate was larger for model 3 than for models 2 and 4 (Table 11). The reason for this is apparent when the slopes of the regression line are considered (Table 1). Model 3 had the smallest slope of models 2, 3 and 4. The slope for model 4 was nearly unity while its intercept was closest to zero (Table 15). Obviously the larger intercepts and smaller regression coefficients for models 2 and 3 were a result of unaccounted-for environmental factors and interaction which apparently were removed to a greater degree in the more complete triquadratic equation (model 4). After correction due to regression was accounted for, model 3 gave the smallest standard error of estimate of 1.1 days (Table 15).

The above example is probably an extreme case, nevertheless, considering estimates for all stages and all data sources there were only 5 cases when the CD's for model 4 were smaller than for model 3 (Table 12). Of these, however, every case had a slope nearer unity and an intercept nearer zero for model 4 than for models 1, 2 or 3.

All statistics indicated that the triquadratic model performed almost as well for the test data as for the regression data. The one serious exception appears to be for the ripe stage where the intercept was 17.3 days, although the slope was near unity, actually 0.89. The bias in the mean estimated age at ripe for all models was large and negative even though it was near zero for the previous (soft dough) stage (Table

7). It appears that possibly some systematic error or discrepancy crept into the observational technique during the second five years of data collection. During the first 5 years, observers were asked to give the date of hard dough while for the second 5 years they were asked to give the date when the crop was ready to cut for stocking. At the time it was felt that there was no difference between these two conditions and for the purposes of this paper they were considered as the ripe stage. On the other hand the Buenos Aires data was collected using the instructions given for the second 5-year period and there the bias (at ripe) was zero, the intercept 1.9 days and the slope 0.99 for model 4.

It is noteworthy that the triquadratic model out-performs the other three quite markedly at Buenos Aires. This is in spite of the fact that the coefficients in the model were determined from Canadian data gathered under considerably different environmental conditions. This is possibly the strongest proof that the triquadratic model approaches the true nature of the response of the crop to the three environmental factors under consideration. Furthermore, since the coefficients in this model appear to work equally well on the test data and the Buenos Aires data as on the regression data, it appears that the coefficients are indicative of genetical characteristics of the crop.

Comparison of the standard errors of estimate (SEE) (Table 15) with the corresponding RMSE's (Table 11) gave an indication of the total contribution of slope and intercept, as determined by regression, to the final estimate of the age. If SEE equalled RMSE then regression contributed nothing and it was assumed that the model gave an unbiased estimate of the effect of the environment on the age of the crop. For example, for estimating the effect of temperature and photoperiod on age at ripe, the use of model 4 gave the same SEE as RMSE for all data sources. Furthermore, the values of both SEE and RMSE were smallest for model 4. Thus it can be concluded that model 4 gave the best unbiased estimate of this particular phenological stage. On the other hand SEE equalled RMSE for model 1 also. However, their magnitudes were larger than for other models. Thus it gave an unbiased (as the average value should) but not the best estimate. Likewise it can be seen that model 2 is better than model 1 but there was a large bias. This was possibly because the threshold temperature was preselected rather than determined by regression. Model 3 was better than model 2 as determined by the relative magnitudes of SEE and RMSE but resulted in a biased estimate since values of SEE were smaller than those of RMSE. This was obviously a result of the arbitrary selection of the threshold temperature and of ignoring the possibility of a threshold photoperiod.

Similar comparisons could be made for other stages. To facilitate these an asterisk(*) has been placed after each SEE (Table 15) which is smaller than the corresponding RMSE (Table 11) thus indicating a bias in the age estimate. In nearly all cases model 2 and model 3 were biased, sometimes to a considerable degree, whereas model 4 was slightly biased on only three occasions and moreso on a fourth, the emergence stage for the test data.

SUMMARY AND CONCLUSIONS

(1) A mathematical model was found which is superior to the simple heat unit equation and the photothermal concept for determining the influence of temperature and photoperiod on Marquis wheat development (morphological progress towards maturity).

(2) The model consists of three quadratic terms, one each for photoperiod, maximum temperature and minimum temperature.

(3) Coefficients in the model can be determined by a special iterative regression technique using limited data from widely separated sites in different climatic zones in Canada.

(4) The coefficients can be used for determining the three cardinal development points of the crop. These cardinal points appear to correspond to characteristics determined independently under controlled environmental conditions.

(5) The cardinal points differ from one phenological stage to another, indicating that the crop responds differently to the environment during different developmental periods.
(6) The suggested model together with coefficients based on one set of Canadian data was successfully used to explain the rate of development of an independent set of Canadian data and also of an independent set of Buenos Aires data where both the meteorological and the biological data were quite different than that for Canada.The implication is that the model closely represents the crop development response to the environment and that the coefficients in the model represent genetical characteristics of the crop and are independent of the environment.

The coefficients of the photoperiod term (Table 9 and Fig. 2) provide a reliable means of evaluating the intensity of the response to photoperiod,a practical problem facing plant breeders and recently discussed by Martinic (1966).

The model might be used along with historical weather records for calculating the probability distribution of the date of phenological stages(biometeorological times) of a crop and relating these to drought, freezes,and wet spells as to their effects on grain yield and quality and on sowing and harvesting operations.

ACKNOWLEDGEMENTS

A great many people played a role in helping to make this study possible:staff at Canada Department of Agricultural Research Stations and Experimental Farms,who were reponsible for the phenological and meteorological observations; staff of the Meteorological Branch, Canada Department of Transport,who were responsible for supplying instruments, inspecting sites and verifying and publishing data; staff, present and past, of the Agrometeorology Section who offered valuable suggestions during analysis of the data and preparation of the manuscript;and those in the Canada Department of Agriculture Data Processing Service who provided electronic data processing facilities. Specifically, the valuable assistance of the following is gratefully acknowledged: Dr. P.O.Ripley, one time Chief of the former Division of Field Husbandry,Soils and Agricultural Engineering, who suggested the project and gave much encouragement during the data gathering stages; Dr. Andrew Thomson and Dr. P.D. McTaggart-Cowan, former Directors of the Meteorological Branch, who provided encouragement and support for continuing the project; Prof. Antonio J. Pascale, Climatologia Y Fenologia Agriolas, Facultad de Agronomia Y Veterinaria, Universidad de Buenos Aires,who provided valuable data from the Argentina; and Mr. D.A.Russelo who prepared the many computer programs used in the analysis.

REFERENCES

ABBE, C. (1905) : First report on the relation between climate and crops. U.S.Department of Agriculture,Weather Bureau,Washington.

ARNOLD, C.Y. (1959) : The determination of significance of the base temperature in a linear heat unit system. Proc. Amer. Soc.Horticult. Sci., 74 : 430-445.

BASSETT, I.J., HOLMES, R.M. and MACKAY, K.H. (1961):Phenology of several plant species at Ottawa, Ontario and an examination of the influence of air temperatures. Canad.J.Plant Sci., 41:643-652.

BOUSSINGAULT, J.J.B.D. (1837): Economie rurale considérée dans ses rapports avec la chimie, la physique et la meteorologie 1st ed.,8° Paris, cited by Abbe (1905), p. 73.

BROWN, D.M. and CHAPMAN, L.J. (1961): Soybean Ecology III:Soybean development units for zones and varieties in the Great Lakes Region.Agron. J., 3 : 306-308.

CARDER, A.C. (1957) : Growth and development of some field crops,as influenced by climatic phenomena at two diverse latitudes. Canad.J. Plant Sci., 37 : 392-407.

FERGUSON, J.H.A. (1958) : Empirical estimation of thermoreaction curves for rate of development. Euphytica, 7 : 140-146.

FRIEND, D.J.C. (1961) : Control of chlorophyll content by daylength in leaves of Marquis wheat. Canad.J.Bot., 39 : 51-63.

FRIEND, D.J.C., HELSON, V.A. and FISHER, J.E. (1962a): The rate of dry weight accumulation in Marquis wheat as affected by temperature and light intensity. Canad.J.Bot., 40 : 939-955.

FRIEND, D.J.C., HELSON, V.A. and FISHER, J.E. (1962b): Leaf growth in Marquis wheat, as regulated by temperature, light intensity, and daylength. Canad.J.Bot., 40 : 1299-1311.

FRIEND, D.J.C., FISHER, J.E. and HELSON, V.A. (1963): The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. Canad.J.Bot.,41:1663-1674.

FRIEND, D.J.C., HELSON, V.A. and FISHER, J.E. (1967): Effect of daylength on the growth of wheat. Canad.J.Bot., 45 : 117-131.

GARNER, W.W. and ALLARD, H.A. (1920): Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. J.Agric.Res., 18 : 553-606.

GREIS, G.A., STEARNS, F.W. and CALDWELL, R.M. (1966): Response of spring wheat varieties to daylength at different temperatures.Agron.J., 48 : 29-32.

HILDRETH, A.C., MAGNESS, J.R. and MITCHELL, J.W. (1941): Effects of climatic factors on growing plants. In: Climate and Man, pp. 292-307.U.S. Department of Agriculture, Washington, D.C.

HOLMES, R.M. and ROBERTSON, G.W. (1959): Heat units and crop growth. Canada Department of Agriculture, Ottawa, Publ. 1042, pp. 32.

MARTINIC, Z. (1966) : Response of various genotypes of common wheat to shortened photoperiod in natural environment of spring sowing.Fifth Yugoslav Symposium on Research in Wheat,Novisad, pp.585-600.

METEOROLOGICAL BRANCH (1964-1965): Temperature and Precipitation Normals by Province, CDS series; Meteorological Branch, Canada Deaprtment of Transport, Toronto, Ontario.

NUTTONSON, M.Y. (1948) : Some preliminary observations of phenological data as a tool in the study of photoperiodic and thermal requirements of various plant material.Vernalization and photoperiodism - A Symposium. Chronica Botanica. Waltham Mass, 129-143.

NUTTONSON, M.Y. (1953) : Phenology and thermal environment as a means for a physiological classification of wheat varieties and for predicting maturity dates of wheat. Amer. Inst. Crop Ecol., Washington, D.C.

NUTTONSON, M.Y. (1955) : Wheat-climate relationships and the use of phenology in ascertaining the thermal and photo-thermal requirements of wheat. Amer.Inst.Crop Ecol., Washington, D.C.,pp.388.

REAUMUR, R.A.F. de (1735): Observations du thermomètre, faites à Paris pendant l'année 1735, comparées avec 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. Paris Memoirs,Acad.Sci.Cited in Meteorological Monographs; Recent studies in Bioclimatology, 2 : 1-3; American Meteorological Society(1954).

RIPLEY, P.O. (1959) : Crop-weather relationship studies. Field Husbandry,Soils and Agricultural Engineering Division, Canada Department of Agriculture, Ottawa. Progress Report 1954-1958,pp.13-15.

ROBERTSON, G.W. (1953) : Some agro-meteorological problems in Canada. Royal Meteorological Society, Canadian Branch, 4 : 1-21.

ROBERTSON, G.W. and RUSSELO, D.A. (1967): Astrometeorological Estimator for estimating time when sun is at any elevation,elapsed time between these elevations in the a.m. and p.m., and hourly and daily values of solar energy, Q_0. Agric.Meteor.Tech. Bul. 14. Agrometeorology Section, Plant Research Institute, Canada Department of Agriculture, Ottawa.

TISSERAND, E. (1875) : Mémoire sur la végétation dans les hautes latitudes,p.271. Mémoires de la Société Centrale d'Agriculture. Cited by Cleveland Abbe (1905), p. 73.

WENT, F.W. (1956) : The role of environment in plant growth. Amer.Scientist, 44 : 378-399.

WITHROW, R.B. (ed.) (1959):The photoperiodism phenomena in plants and animals.Amer. Ass.Advanc.Sci.Publ.55, Washington, D.C., 903 p.

WORLD METEOROLOGICAL ORGANIZATION (1961): Guide to Meteorological Instrument and Observing Practices. 2nd Ed., Wld.Meteor.Org., Geneva.

ABSTRACT.- A mathematical equation is suggested which relates rate of development of a wheat crop to photoperiod and to day and night temperatures. The model takes into consideration lower and upper critical limits and the optimum value of each of these three environmental factors. Coefficients in the model were evaluated by a special iterative regression technique using a set of crop data gathered at several stations across Canada over a 5-year period. Reproducibility of results was demonstrated by using a second of test data from the same stations for a second 5-year period as well as by using a third set of completely independent data from the Argentine.This model (called a triquadratic model)was compared with three others: model 1 based on the average rate of development, model 2 based on the simple heat unit concept and model 3 based on the photothermal concept.It was found to be superior to these three models as an estimator of the influence of the environmental factors on the rate of development of a wheat crop for all three sets of data. Integration of the equation on a day by day basis gives an indication of the daily rate of progress towards maturity as influenced by the environment thus resulting in a biometeorological time scale.

ZUSAMMENFASSUNG.- Es wird eine mathematische Gleichung vorgeschlagen, die die Entwicklung eines Weizenbestandes zur Strahlungsdauer und zu den Tag- und Nachttemperaturen in Beziehung setzt. Das Modell berücksichtigt untere und obere kritische Grenzen sowie den optimalen Wert für jeden dieser drei Faktoren der physikalischen Umgebung. Die Koeffizienten des Modells wurden durch eine spezielle iterative Regressionstechnik berechnet, die eine Reihe von phänologischen Daten von mehreren, über ganz Kanada verteilten Stationen aus einer 5-jährigen Periode benutzt. Die Reproduzierbarkeit der Ergebnisse wurde anhand einer zweiten Serie von Testdaten von den gleichen Stationen aus einer anderen 5-Jahresperiode sowie durch Einbeziehung einer dritten völlig unabhängigen Serie aus Argentinien nachgewiesen. Dieses Modell (ein sogen. triquadratisches Modell) wurde mit 3 anderen verglichen: Modell 1 basierte auf dem Durchschnittsbetrag der Ertragsentwicklung, Modell 2 auf einem einfachen Temperatursummenkonzept und Modell 3 auf der Strahlungswärme. Es ergab sich, dass unser Modell als ein Weg zur Abschätzung des Einflusses der Umgebungsfaktoren auf die Entwicklung des Weizenertrage aller drei Serien besser war als die genannten drie Modelle. Die Ergänzung der Gleichung auf der Tag- für-Tag-Basis liefert einen Hinweis auf den täglichen Zuwachs in Richtung auf die Reife,wie er durch die physikalische Umwelt beeinflusst wird, und damit eine biometeorologische Zeitskala.

RESUME.- On propose ici une équation mathématique qui met en relation le développement d'une culture de blé d'une part, la photo-périodicité et les températures diurnes et nocturnes d'autre part. Le modèle tient compte des limites critiques supérieure et inférieure ainsi que de la valeur optimum de chacun de ces trois facteurs du milieu ambiant. Les coefficients du modèle ont été évalués selon une technique spéciale de régression interative dans laquelle on a fait intervenir des observations recueillies durant 5 ans en plusieurs endroits du Canada. On a démontré ensuite que les résultats ainsi obtenus étaient reproduisibles en se servant d'autres données

provenant cette fois d'une part des mêmes stations, mais pour une autre période de 5 ans, d'autre part d'une troisième série d'observations absolument indépendantes recueillies en Argentine. Ce modèle (appelé triquadratique) a été confronté à trois autres: un modèle basé sur le degré moyen de développement des plantes, un deuxième tenant compte uniquement de l'idée des degrés-jours, un troisième enfin se référant à l'indice photo-thermique. On a trouvé que le modèle développé initialement était supérieur aux trois autres pour déterminer l'influence des facteurs du milieu ambiant sur le taux de développement d'une culture de blé déterminé et cela pour les trois séries d'observations. L'intégration au jour le jour de l'équation indique le degré journalier de maturité en partant des influences du milieu,en d'autres termes selon une échelle biométéorologique du temps.