OPTIMUM MEAN TEMPERATURE FOR PLANT GROWTH CALCULATED BY A NEW METHOD OF SUMMATION[1]

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Abstract. The relationship between temperature and stem elongation has been investigated for representative herbaceous plants sampled from populations of seven species which were growing under semi-natural conditions in the Botanical Garden of the University of Padua (Italy). The growth of the floral stem was measured for the following species: *Galanthus nivalis* L., *Corydalis cava* Schw. et Krt., *Anemone nemorosa* L., *Symphytum tuberosum* L., *Allium ursinum* L., *Aegopodium podagraria* L., and *Campanula rapunculoides* L.

Official records of daily maximum and minimum air temperatures have been elaborated by means of a new method of temperature summation. This method takes into consideration the concept that plants possess a range of sensitivity to temperature between maximum and minimum thresholds and that there is an optimal temperature for each stage of development. Data for stem elongation have been optimized (using the technique of best fit) as a function of a logistic curve which may represent growth under ideal conditions. Differences between the logistic curve and the real curve of growth may be related to the amount of deviation of values for environmental factors from optimal values.

The temperature ranges between 0° C and 30° C which gave the best correlations with stem elongation have been calculated for the entire period of this process of growth. The average between the two thresholds on each day has been considered as the optimum mean temperature for that day.

The optimum mean temperature increases from the start of the process to ripening, with the exception of a period just before flowering when all plants seem to require lower daily temperatures. The results of this analysis have also indicated that unknown factors other than temperature are affecting stem elongation.

INTRODUCTION

Temperature is the most important short term variable controlling plant development and growth. Fluctuations during the day-night period are of physiological importance as are the seasonal or annual changings in temperature.

It has been difficult to adequately release seasonal temperature fluctuations to those of growth. Effects of temperature occurring in plants are much more complicated when one considers the organism as a whole than appears from studies of a single biological reaction (Went 1953).

The problem appears even more complicated if one considers the interaction of other environmental factors, notably light.

In other words it is not possible to consider a linear relationship between temperature and plant growth especially in long term studies where the complete life cycle period is plotted against temperature summation. For instance the optimal growth of plants proceeds at different temperatures during the day than at night, and at different temperatures at the various stages of development (Chouard 1951).

However, a good approximation of a linear relationship between temperature and growth may be reached considering a single definite stage in the life cycle, or short periods of observation at least as long as the daily cycle.

The aim of this work was to study the temperature requirements within short terms of 3 to 4 days of observation and during the period of stem elongation. More than one developmental stage was in this way considered, since during stem elongation leaf, branch, flower, and fruit differentiation and growth may occur contemporaneously.

The plant material was growing spontaneously in the field, i.e. in conditions where light, water and other environmental factors did not act as limiting factors for growth during the period considered.

MATERIALS

Seven plant species growing under semi-natural conditions on the 0.4 ha arboretum at the University of Padua, Italy, were selected for study.

The soil of the arboretum is an alluvial, calcareous clay low in humus. Official weather data from a "Salmoiraghi" thermo-idrograph operating in a shelter sets at 0.50 m from soil of the "Ufficio Idrografico" of Padua, Italy, and at a distance of 1,500 m from the Botanical Garden, have been used as a source of temperature data. The maximum and minimum air temperature trend is presented, for the period of study, in Fig. 1.

All of the herbaceous species considered had grown and reproduced spontaneously in the arboretum for many years. They were selected because their

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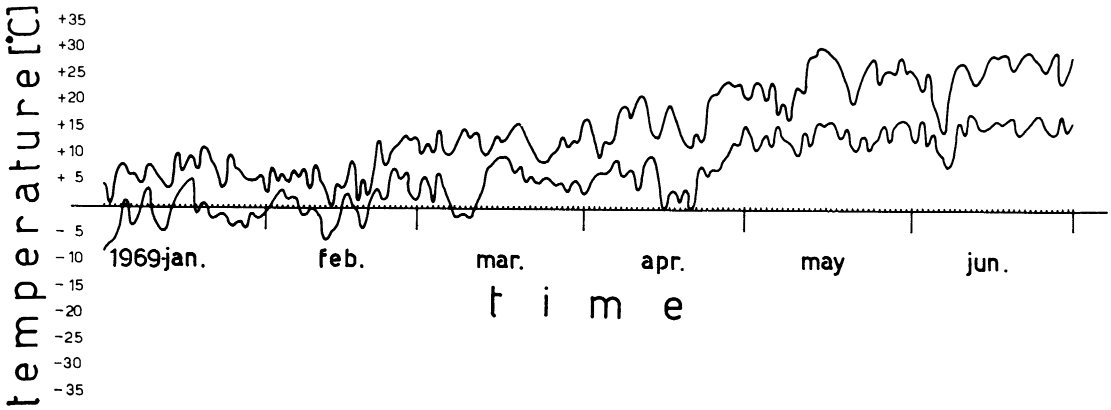

FIG. 1. Maximum and minimum temperatures in Padua, Italy during the period from January 1 until June 30, 1969.

stems elongated at different dates during the growing season (from January to the end of June).

Galanthus nivalis L. is a bulbous geophyte which has one floriferous stem with a single flower and 2 to 3 leaves at its base. *Corydalis cava* Schw. et Krt. is a tuberous geophyte with several floral stems which each have 1 to 3 leaves; the flowers grow in racemes. *Anemone nemorosa* L. is a rhizomatous geophyte with a stem that bears three leaves and a single flower. *Symphytum tuberosum* L. is a tuberous geophyte with a single stem on which the leaves and few flowers are gathered in terminal apices. *Allium ursinum* L. is a bulbous geophyte in which the stem bears 2 to 3 leaves at its base and one umbel at its apex. *Aegopodium podagraria* L. is a stoloniferous hemicryptophyte, with a sparsely ramified stalk, of which the apex and branches end in umbels. *Campanula rapunculoides* L. is a stoloniferous hemicryptophyte, with an unbranched stalk terminating in a raceme.

Three plants in each species were observed, starting at the time of peak population emergence. Data presented herein are for representative simple plants in each species.

METHODS

Temperature summation

Thermograph data for climatic conditions in Padua on the 10th, 11th and 12th of April, 1969, are shown in Fig. 2. These are typical intermediate values in terms of the entire study period from January to June.

The daily pattern of temperature fluctuations can be described graphically by utilizing the procedure of duration-summation of Lindsey and Newman (1956), which employs a base threshold temperature. The result is an area on the graph which can be expressed quantitatively by the formula:

$$A = 12 \cdot \frac{(TM - Tb)^2}{TM - Tm} \tag{1}$$

where: A = degree-hours; TM = daily maximum temperature; Tm = daily minimum temperature; Tb = base temperature.

In the present study Lindsey and Newman's method was modified by using two temperature thresholds. I found it necessary, as did Robertson (1968), to consider a possible different lower temperature threshold and an upper threshold for every growth period of 24 hours. These two points (the upper and lower thresholds) delimit the range within which growth appears to be influenced in a measurable way by temperature changes.

In Fig. 2 the areas calculated according to the method of summation-duration (triangular area) and the method here proposed (area delimitated by the trapezoid "*A,B,C,D*") are compared. In the Figure, "*Tu*" (the upper threshold) and "*Tl*" (the lower threshold) for *Symphytum tuberosum,* (18°C and 0°C respectively), are shown as an example. "*TM*" is the maximum temperature for each day and "*Tm*" the minimum.

The calculation of the temperature summation index in periods of 24 hours may be summarized as follows: an isosceles triangle is drawn which has its base equal in length to 24 hours on the chart and is located such that the base is identified as either "*Tm*" or "*Tl*," at the lowest temperature. The final area will be a triangle or a trapezoid which can be calculated by the following formula:

$$A = 12 \cdot \frac{2a - b - c}{a - d} \cdot (b - c) \tag{2}$$

where: a = larger of TM or Tu; b = lesser of TM or Tu; $c = Tl$; d = lesser of Tm or Tl.

If the daily temperature remains below the minimum threshold, the area is defined as zero, which means that on such a day, the effects of temperature on growth cannot be estimated.

Calculations have been made for the three days

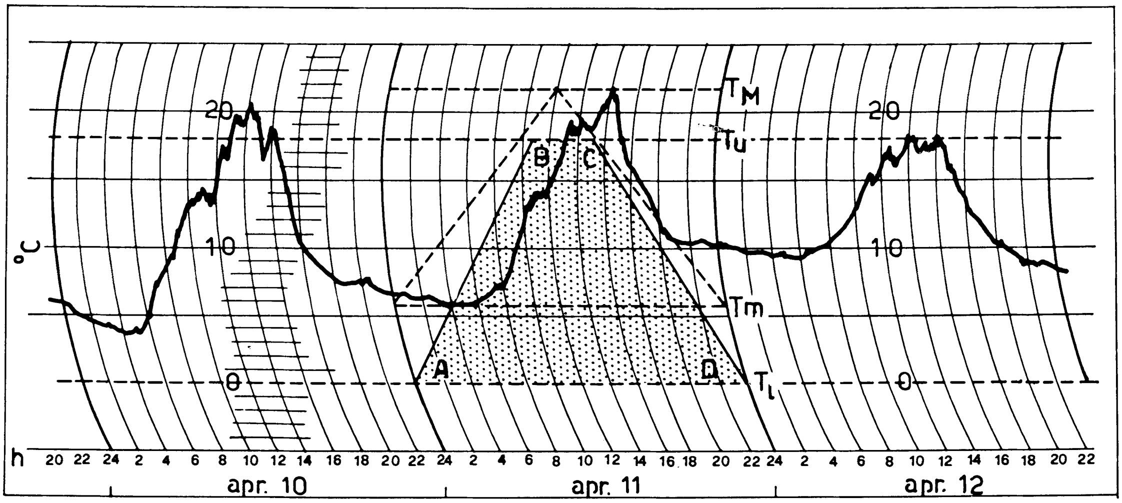

FIG. 2. Thermogram for Padua, Italy, on the 10th, 11th and 12th of April 1969, with super-imposed areas used to calculate the summation of temperature for a period of one day according to the Lindsey-Newman method (area of the hatched triangle), and according to the method proposed (dotted area of the trapezoid, A,B,C,D,).

TABLE 1. Daily values of temperature summation for the 10th, 11th and 12th of April in Padua, calculated by planimeter method (P), according to the Lindsey-Newman method, and according to the method proposed. The values in parenthesis express the "heat units," the other values are equivalents in dm^2. Lower threshold of base temperature of 0°C, and upper threshold of 18°C as given for *Symphytum tuberosum*.

	TEMPERATURE °C		METHOD OF CALCULATION				
DATES	Min.	Max.	Plainmeter (P)	Lindsey-Newman	Deviation from (P)	Proposed	Deviation from (P)
April 10	3.6	20.4	2,095	(297) 2,520	+16.8%	(242) 2,123	+1.3%
April 11	5.8	21.6	2,370	(354) 2,870	+17.4%	(252) 2,205	−7.5%
April 12	9.6	18.3	2,630	(460) 2,940	+10.5%	(219) 1,890	−39.6%

considered using the Lindsey-Newman method, the proposed method (dotted area in Fig. 2), and the planimeter method.

These data are compared and summarized in both Table 1 and Figure 2. It appears that the Lindsey-Newman method tends to give values larger than those calculated with the planimeter. The method proposed gives values very similar to those of the planimeter method only when the daily maximum and minimum temperature is not very different from the threshold values (e.g. April 10th in Fig. 2). When the maximum or minimum temperature is widely divergent from the threshold values, the method proposed and the planimeter method have very different values (e.g. April 12th and Figure 2).

The application of the method proposed is restricted to a range of temperatures in which no type of damaging effects may occur as result of stressing conditions. These conditions are never reached in the climate of Padua, Italy.

Growth representation

One of the common ways of representing growth is by means of the logistic curve (Verhulst 1838). It is used to describe the nature of increase in weight, volume, and numbers of individuals or groups as it occurs in time. Other curves such as those expressed by the equations of Gomperts or von Bertalanffy, are also used to describe growth (Ricklefs 1967).

After I compared these various methods I found that the logistic curve was the most representative of growth (stem elongation) in this study. The equation for the logistic curve is:

$$Y = \frac{K}{1 + Be^{At}} \tag{3}$$

where: A = a real negative number; B = a real number; K = a constant which by general agreement among biologists expresses quantitatively the upper limit of the process; and t = time.

We are considering then an sigmoidal curve which is divided into two portions by the point of inflection, the first portion being a phase of accelerated growth and the second one being a phase of inhibited growth (Corona 1959). Commonly it is not difficult to identify these two portions of a growth curve as well as the point at which stem elongation ceases. It is much more difficult to recognize the starting point of the same process. In practice one can overcome this problem by considering that a logistic curve tends toward 0, as $t \to -\infty$, and toward K as $t \to +\infty$. By the simple addition of a constant K_0, the curve no longer tends toward 0, but toward the value of the constant as $t \to -\infty$:

$$Y = K_0 + \frac{K_1}{1 + Be^{At}} \quad (4)$$

for when $t \to -\infty$, then $Y \to K_0$.

The use of K_0 and K_1, the two asymptoptes, which best approximate the beginning and the end of stem elongation, enables one to determine for any plant the logistic curve which best fits its actual growth. Then the formula (4) can be used. The values for the two constants, A and B, can be calculated by the method of least squares, assuming that one knows the value of K which is given by the total growth of the plant. By using the above procedures similar to the procedures elaborated by Pearl and Reed (1920), a theoretical representation of growth was determined for each species. This representation will most closely resemble actual plant growth if such growth occurs without disturbance and under optimal climatic conditions.

Rather than recording total stem elongation, the amount of extension of a stem in each given unit of time can be measured. Rate of growth can be derived from the formula for the logistic curve of growth (1):

$$Y_1 = \frac{dy}{dt} = -\frac{KABe^{At}}{(1 + Be^{At})^2} \quad (5)$$

where Y_1 = the rate of growth at a particular point in time.

The value of this derivative can be calculated graphically day by day, from the tangent $(dy)/(dt)$ at various points of the curve.

Calculation of threshold values by correlation analysis

In order to apply the method proposed for temperature summation is necessary to know the value of the upper and lower threshold for each period of time considered. On the other hand the same method can be reciprocally used for experimental determination of the thresholds.

All possible pairs of temperature thresholds, which lie between 0° and 30°C and in which there is a minimum of two degrees between the upper and lower thresholds, have been considered in the formula proposed for temperature summations. The common correlation coefficient "*r*" has been calculated in a study of correlation plotting the values of temperature summation against the values of stem growth.

Since a linear relationship between the two variables is an assumption for this analysis of correlation, the best approximation of such a relationship has been obtained considering units of growth rate and temperature summation for each 24 hour period. Furthermore in the same calculations of coefficient "*r*" it is necessary to compare several values for temperature summation with an equal number of values for rate of growth.

In order to choose the most suitable sample site of growth and temperature units the row pattern of growth and temperature for the period of study was examined. Fluctuations in temperature are not periodic, however a period of seven days was chosen as not too short and not too lengthy to describe the most common type of temperature variations in the climate of Padua (Fig. 1). In the same time it appeared that the effects of these variations were more clearly reflected in plant growth after a certain length of time such as after three days.

Therefore I have attempted to correlate the value of seven units of temperature summation with seven units in the rate of growth the latest three days postponed.

All calculations have been made with an IBM 360/44 computer (the programs are available from the author).

Results

Growth pattern

The growth patterns observed for the stem of the seven plant species in the field may be subdivided into three stages. At the beginning one finds a more or less lengthy period during which weak growth, as expressed by the measurement of stem elongation, is interrupted by long pauses in growth. During this stage, at nonoptimal temperature for growth, the plants accumulate the energy (probably through intensive photosynthetic activity) which is necessary for the succeeding rapid growth of the second stage.

Once the second stage has started, there appears to be a continuous elongation of the stem until the end of the process. At this stage ambient factors, such as temperature, may modify only the growth intensity without changing the direction of the development.

The third stage is represented generally by the small growth of the stem during the time of fruit ripening.

This process has been analyzed by using the logistic curve. The curve very closely approximates actual growth in the cases of *Galanthus nivalis* (Fig. 3, A), *Anemone nemorosa* (Fig. 3, C) and *Aegopodium podagraria* (Fig. 3, F). It would appear that 1969 was an almost optimal growing season, as regard to temperature effect on growth for these species.

For the other species the logistic curve does not

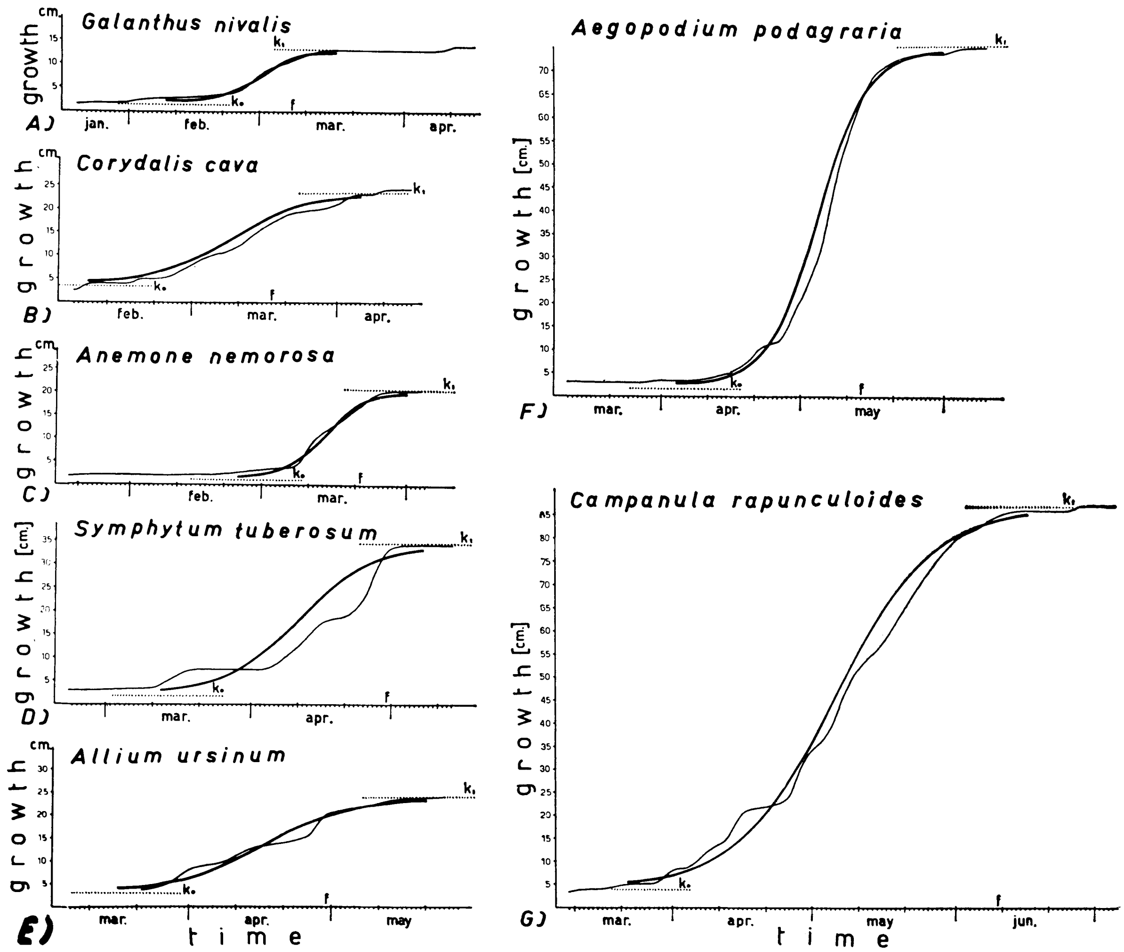

FIG. 3. Stem growth of the seven plant species considered (A to G) in 1969 (thin line) and its theoretical representation by using the logistic curve (thick line). K_0 and K_1 are the asymptotes. f = date of the beginning of anthesis.

appear to coincide so well with the measured growth curve. This suggest that strong elements of disturbance have acted during the process. Temperature may be one of these strong elements. For example with *Corydalis cava* and *Symphytum tuberosum,* the oscillations of the minimal daily temperature which take place during March, may represent a strong disturbing element. With *Allium ursinum* and *Campanula rapunculoides* growth appears much disturbed especially in April.

Optimal temperature

In Fig. 4 (A to G) are shown the pairs of temperature thresholds which gave the best correlations with stem elongation. The correlation found ranged within all the values from -1 to $+1$. Only the highest positive value for each point has been considered. In this way each curve obtained describes the tendency of stem elongation in following the changes at each level of temperature.

It is not possible to draw a line which connects all the maximum thresholds (or all the minimum thresholds) for the entire process of stem elongation since there are periods when no positive values of correlation have been found. However, it is possible to determine the mean between the two thresholds for each day and to interpolate means for days when the thresholds could not be determined. Then one can draw a line such as in Fig. 4 (A to G) which represents the probable optimal mean temperatures for stem elongation throughout the period of study.

In all species, early stem elongation is generally best correlated with low temperatures and later stem elongation with high temperatures. Temperatures increase almost continuously except during a period in which stem elongation is briefly correlated with a decrease in temperature. This decrease in temperature (the concave portion of the curves in Fig. 4) corresponds approximately with the time of anthesis for the more precocious species or with the begin-

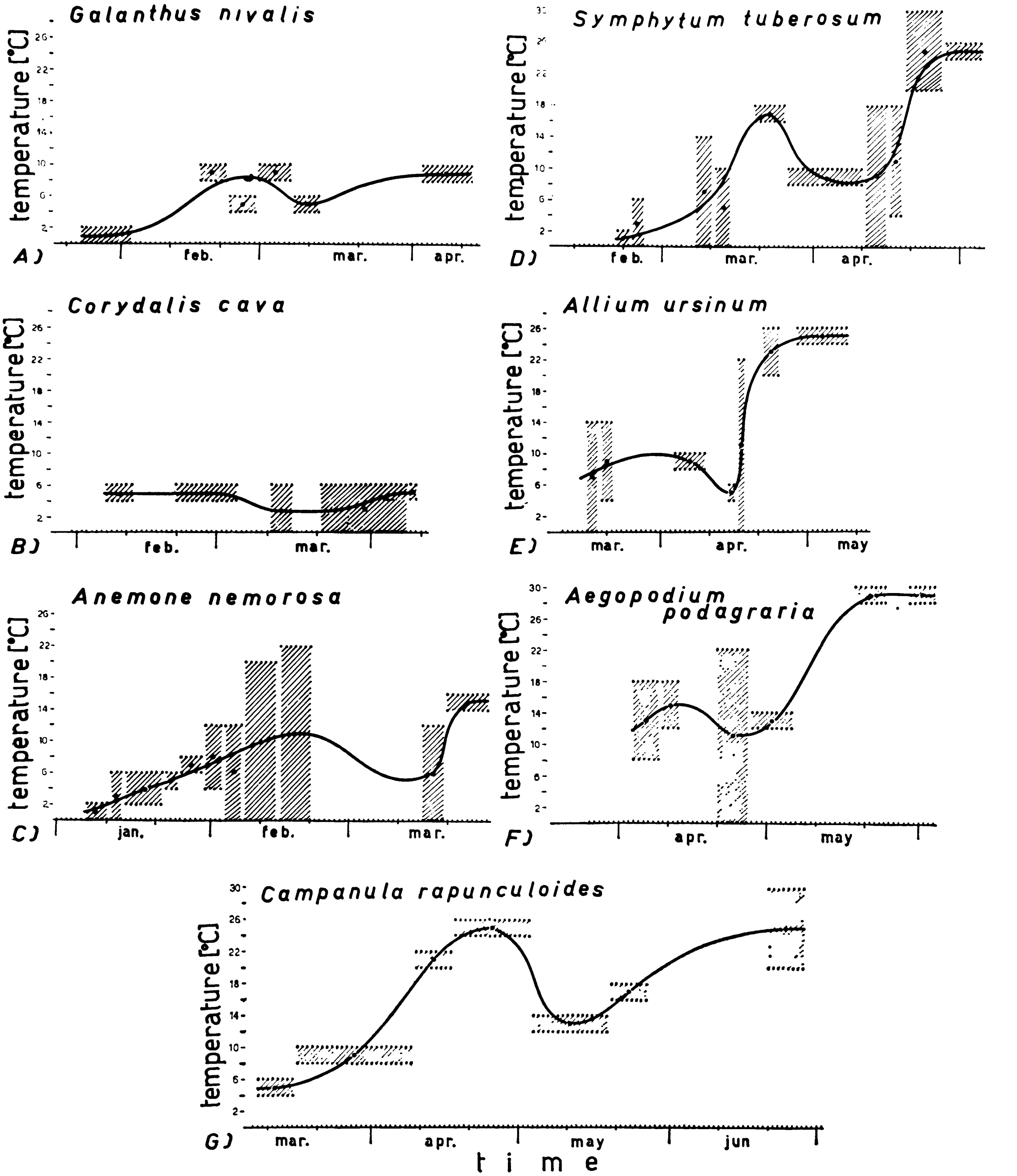

FIG. 4. Temperature thresholds for the seven plant species considered (A to G) (limits of hatched areas) which give the best positive correlation with growth rate during stem elongation in 1969. The optimum mean temperature expressed as averages between the two thresholds are shown by heavy line. The line is drawn according to values interpolated for the periods when positive correlations could not be obtained.

ning of development of the floral buds for the more tardy ones.

It also appears that the plants of the various species are sensitive to different temperatures. Thus the more precocious species such as *Calanthus nivalis, Anemone nemorosa,* and *Corydalis cava* are ones which are sensitive to lower temperatures, while *Aegopodium podagraria* and *Campanula rapunculoides* are sensitive to the highest temperatures recorded during the period of study.

Discussion

The calculation of the optimal temperature requirement for stem elongation of the seven herbaceous species has involved different problems.

The choice of plant material growing spontaneously in natural conditions has eliminated a possible strong interference of factors like light quality and intensity, photoperiod and moisture on growth. In fact, the plants were growing within the area of their natural distribution and within optimal microclimatic conditions.

Furthermore, personal observations have revealed that only *Symphytum tuberosum* and *Campanula rapunculoides* have strongly photoperiodic requirements (unpublished data).

Moisture has not been restrictive on the basis of calculations of evapotranspiration for the whole growing period considered using the methods of Thornthwaite (1948).

The temperature data have been translated into a more suitable unit as index of energy availability or "heat units" for plant growth, by means of the method of summation proposed. The values of the two biological thresholds found, as they give the best correlation with the rate of growth, express the upper and lower limits where the measurable effects of temperature on growth, under field conditions, tends toward zero.

An improvement in the correlation analysis might have obtained if more continuous date (i.e. daily) had been collected for stem elongation. One might have verified experimentally which cumulative period or which delay in growth response to temperature change have been more appropriate at any time for the calculations.

The average value between the two temperature thresholds is apparently of greater significance. It is an approximation of the mean temperature within a certain optimal daily ΔT (i.e. a certain optimal oscillation with the maximum and minimum daily temperatures) which is not known.

The concept of optimum mean temperature as here interpreted agrees with the existence of cyclic daily thermo-periodic requirements in plants as demonstrated by various authors (a review in Abrami 1969). In other words, while the upper and lower thresholds are a useful, but rather raw result of the calculation, the mean optimal temperature has a more precise empiric dimension.

Two points are evident from the results of the calculations of correlation. First, the level at which heat energy is required for stem elongation was greater at the end of the process. This trend occurred except for a period referred to previously as the concave portion of the growth curve which corresponds to an important stage in the reproductive process. In the concave portion of the curve there was a return of sensitivity to low temperatures. This period may be referred to as pseudo-vernalization since the action of temperature, which influences the development toward flowering, seems of importance at the daily minimum.

It is known that often processes of differentiation require an optimal range of alternating temperatures during the life cycle of plants (Wang 1960). Low temperatures induce flowering, especially in bulbous plants; (Blaauw et al. 1930; Went 1953, 1961; Hartsema 1961). This temporary synchronization of further development with temperatures at the lower threshold agrees with the works of Lona (1950, 1951) who stated that night temperature may act as a form of vernalization.

The second point is the lack of a positive correlation between growth and temperature during some periods of stem elongation. Morphological developments such as leaf and branch initiation which may modify the rate of stem growth cannot explain the phenomenon completely. At the same time, as already stated, we can exclude any effect of light and soil moisture.

Other causes are indicated which impinge on the temperature responses of the plants and which would have to be determined by further investigations.

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