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Effect of Temperature on Rate of Leaf Appearance and Flowering Date in Maize[1]

M. Tollenaar, T. B. Daynard, and R. B. Hunter[2]

ABSTRACT

Classification of development in maize (*Zea mays* L.) based on temperature is important because of the need in agriculture to determine the adaptability of genotypes to particular environments and to predict flowering dates for breeding purposes. An equation predicting the effect of temperature on rate of development of maize was obtained by measuring the rate of leaf appearance of six short-season maize hybrids. The hybrids were grown in growth cabinets at constant day/night temperatures ranging from 10 to 35 C, in 5 C increments, with a 15-hour photoperiod. Rate of leaf appearance was also measured on plants grown under 16 regimes of differential day/night temperature. The predictive value of the temperature vs. rate of leaf appearance curve was compared with calendar days from planting to silking and accumulated heat units from planting to silking, calculated by both the Degree Days and Ontario Corn Heat Unit (OCHU) methods, using date of flowering for 22 hybrids grown during 3 years at four locations.

Polynomial regression analysis of data for maize plants grown at constant day/night temperatures produced a cubic equation for rate of leaf appearance (leaves/day) vs. ambient temperature. This equation ($Y = 0.0997 - 0.0360T + 0.00362T^2 - 0.0000639T^3$) could be used to predict rate of leaf appearance in fluctuating temperature environments. For field-collected data, the equation for rate of leaf appearance vs. temperature was superior to calendar days but similar to the Degree Days and OCHU methods in predicting dates of silking. Adjustment of the predicted time to silking by accounting for the effect of mean temperature during the first 30 days after planting on maximum leaf number (increase of 0.2 leaves/C increase in temperature) enhanced the precision of the derived equation in predicting date of silking.

Additional index words: Rate of development, Temperature response curve. Heat unit methods. Thermal leaf units, *Zea mays* L.

ACCORDING to Wang (26), Reaumur was the first to report that the sum of mean daily temperatures to reach a given stage of development was nearly constant. Recent attempts to classify the rate of development in maize (*Zea mays* L.) based on accumulated temperature result from the need to determine the adaptability of genotypes to particular locations and to predict dates of flowering and harvest. Most common thermal unit systems are products of the remainder index procedure which assumes a linear relationship between rate of plant development and temperature above a specific lower base, i.e., that temperature at the lower end of the temperature range, which represents the highest temperature at which the rate of development is assumed to remain zero. The principle of the remainder index is used to predict rate of ontogeny of maize in many parts of the world. However, differences occur in estimates of the lower base temperature and in the use of an upper maximum temperature above which rate of development is assumed constant or declines (4, 6, 10, 13, 15, 17).

Although the remainder index system is attractive because of its simplicity and its higher accuracy in predicting developmental events than number of days per se, the true relationship between rate of development and temperature is not linear. Lehenbauer (19), in a classical study of the elongation of maize seedlings in relation to temperature, observed a curvilinear relationship with an optimum at about 32 C. A similar curvilinear relationship has been observed by Blacklow (5) for rate of elongation of the radicle and shoot of maize seedlings. Brown (9) developed a Corn Heat Unit Method for Ontario (OCHU) which was based, in part, on measurements of a curvilinear relationship between the rate of soybean development and temperature (8). Comparisons of the OCHU method with number of calendar days and remainder index methods have shown that over a number of locations and years, the OCHU was less variable in characterizing time to maturity in northern climates (10, 20).

The study reported herein is an attempt to quantify the curvilinear relationship between temperature and rate of development in maize from planting to silking by measuring rate of leaf appearance at a number of constant temperatures. Earlier results have shown the rate of appearance of successive leaves to be nearly constant for a given temperature (7, 18, 24); hence rate of leaf appearance should be a meaningful parameter for the study of the temperature – rate of development relationship of maize plants prior to silking.

MATERIALS AND METHODS

Experiments were conducted in growth cabinets with six maize hybrids 'Stewart 2300', 'Trojan TX68', 'United 106', 'PAG SX42', 'Pioneer 3911', and 'United 132'. All hybrids are single

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[2] Research scientist and associate professors of crop science.

crosses involving inbreds of North American origin and range in maturity from 2400 to 3200 OCHU (9), 1800 to 2400 Growing Degree Days (20), or FAO 200 to 500. With the exception of Stewart 2300 which has one flint inbred parent, all are dent hybrids.

In the first of two tests, plants were grown at constant day/night temperatures ranging from 10 to 35 C in 5 C increments, and at a 15-hour photoperiod. For each temperature regime, 30 pots (25 cm diam $\times$ 28 cm deep) were filled with a mixture of three parts medium loam soil: one part peat moss, with 40 g 5-20-20 and 24 g 34-0-0 N-P_2O_5-K_2O fertilizer blended into the soil for each pot. Two seeds were planted in each of five pots per hybrid and the 30 pots were arranged in a completely randomized design within the cabinet. Pots were thinned to one plant at the two-leaf stage, and supplied once daily with tap water (less frequently at early stages of growth). Growth cabinets had 3.6 m^2 of floor space, and were illuminated by 30 General Electric reflectorized (135° window) cool white, 215 W fluorescent lamps, plus 45 Westinghouse 40 W incandescent bulbs. Photon flux density (400 to 700 nm) at 1 m below the light bank was 50 n E cm^{-2} sec^{-1}. Height of the lights was adjusted continually so they remained at a constant distance above the uppermost leaves throughout the experiment. Temperature was monitored with shielded thermocouples suspended at soil height in the cabinets and, in some cases, by thermocouples buried 4 cm deep in the soil medium. Measurements at the two locations were generally identical except, occasionally, for a few minutes after watering.

Rate of leaf appearance was estimated by counting daily the number of visible leaves per plant. A leaf was included in the counts when its tip emerged from within the whorl. Date of appearance for the 3rd, 6th, 9th, and 12th leaf was recorded. After all plants had reached 12 leaves, pots were transferred to a larger growth room (25/20 C day/night temperature) and maintained there until tasselling when a count of total leaf number was made.

The 10 C constant day/night temperature treatment had to be redesigned because of very poor plant growth in this environment. Pots were placed in a 25/20 C temperature until the second leaf stage and then transferred to a constant day/night temperature of 10 C. Rate of leaf appearance was estimated by the time which elapsed between emergence of the third and fifth leaves. Only plants which reached the fifth leaf stage were included in the calculation; approximately half of the number of plants died before this stage due to chlorosis.

In the second growth cabinet experiment, plants were grown under day/night temperature differentials. Temperatures regimes are listed in Table 1. Treatments 1 to 12 were "square wave" temperature regimes (ie., a constant day and a constant night temperature) and treatments 13 to 16 were "sine wave" temperature regimes (i.e., temperatures during a 24-hour day followed a sine curve from the minimum to maximum to minimum temperature).

Procedures for growing the plants and recording data were identical to those described above. In the second test, soil thermocouples were used in conjunction with the exposed, shielded thermocouples in every cabinet. With square-wave regimes, a maximum of 4 hours was required for temperature at 4 cm soil depth to match the air temperature. The twice daily change in air temperature was accomplished in under 15 min. With sine-wave regimes, soil temperatures did not reach the temperature extremes of the treatment.

A comparison of four different methods for computing heat units and number of calendar days from planting to mid silking was made with data collected in a maturity test of Pioneer Hi-Bred International Inc., Des Moines, Iowa. The test consisted of 22 hybrids grown at Tipton, Ind., Mankato, Minn., and Johnston and Algona, Iowa during 1974, 1975, and 1976. Since all hybrids were not grown at all locations, total number of observations was 168. The four methods for computing heat units were as follows.

Method 1. Growing Degree Days (remainder index method)

Daily HU $=$ [(Max $+$ Min)/2] $-$ 10 C.
If Min $<$ 10 C, Min $=$ 10 C;
if Max $>$ 30 C, Max $=$ 30 C,

where Daily HU is daily heat unit accumulation and Max and Min are the maximum and minimum temperature for the 24-hour interval.

Method 2. OCHU (Ontario Corn Heat Unit method)

Daily HU $=$ (Day $+$ Night)/2.
Day $=$ 3.33 (Max $-$ 10 C) $-$ 0.084 (Max $-$ 10 C)^2.
Night $=$ 1.85 (Min $-$ 4.4 C).
If Min $<$ 4.4, Min $=$ 4.4, where Daily HU, Max, and Min are as in Method 1.

Method 3. Thermal Leaf Units (Max/Min)

Daily HU $= (R_{max} + R_{min})/2$.

$$R_{max} = 0.0997 - 0.0360\ \text{Max} + 0.00362\ \text{Max}^2 - 0.0000639\ \text{Max}^3, \quad [1]$$

where R_{max} is the rate of leaf appearance at maximum daily temperature, Max. R_{min} (rate of leaf appearance at minimum daily temperature, Min) is calculated by substituting R_{min} and Min for R_{max} and Max, respectively, in Equation I, with the condition that if Min $<$ 6, Min $=$ 6. Equation [1] was derived from results of the growth cabinet experiment (see Results and Discussion).

Method 4. Thermal Leaf Units (Sine Wave)

Daily HU $= (R_1 + R_2 + \cdots\cdots + R_{24})/24$,

where $R_1, R_2, \ldots\ldots, R_{24}$ are rate of leaf appearance calculated by Equation [1] using hourly mean temperatures ($T_1, T_2, \ldots\ldots, T_{24}$) computed over a 24-hour cycle in which ambient temperature is assumed to vary sinusoidally between Max and Min, i.e.,

$$T_1 = \text{Max},$$

$$T_2 = \frac{\text{Max} + \text{Min}}{2} + \frac{\text{Max} - \text{Min}}{2} \cos\left(\frac{\pi}{12}\right).$$

$$T_n = \frac{\text{Max} + \text{Min}}{2} + \frac{\text{Max} - \text{Min}}{2} \cos\left[\frac{(n-1)\pi}{12}\right], \text{ etc.}$$

For calculations of hourly rates of leaf appearance via Equation I, $R_1, R_2, \ldots\ldots, R_{24}$ and $T_1, T_2, \ldots\ldots, T_{24}$ were substituted sequentially for R_{max} and Max, respectively in Equation [1].

Coefficients of variability were calculated using pooled data for number of heat units (by four methods) or calendar days from planting to silking for the various hybrids in the Pioneer tests. The standard deviation of the mean date of silking was calculated for each method by dividing standard deviation for number of accumulated heat units to silking by the average number of heat units received per day during the period which bracketed silking in the various tests.

RESULTS AND DISCUSSION

Analysis of variance of results of the growth room experiments at constant day/night temperatures showed no difference in time elapsed from planting to three, six to nine, or nine to 12 leaves emerged. Rate of leaf appearance during the period from three to six leaves emerged was approximately 10% $=$ lower. A near-constant rate of leaf appearance at constant temperature is in accord with earlier reports (7, 18, 24). Polynomial regression analysis of all data revealed a highly significant ($R = 0.96$, $n = 154$) cubic relationship between rate of leaf appearance and temperature (Fig. 1). The initial polynomial equation (curve A in Fig. 1) approached but did not interest the X-axis at temperatures in the range of 0 to 10 C. To improve practical utility of the equation at low temperatures, the regression was repeated with the condition that a minimum occur at Y (rate of leaf appearance) $= 0$. The resulting polynomial (curve B. Equation [1]) caused $Y = 0$ at $X = 6$, but differed from the original by no more than 0.01 leaves/day between 11 and 36 C. Both equations predict a relationship between rate of leaf appearance and temperature in the range of 12 to 26 C that is nearly linear and maximum rate of development at 31 to 32 C. Similar relationships be-

Table 1. Mean and predicted rate of leaf appearance of six hybrids grown from planting to the 12 leaf stage in 16 temperature regimes. Treatments 1 through 12 are "square wave" temperature regimes; treatments 13 through 16 are "sine wave" temperature regimes. Predictions of rate of leaf appearance were calculated on an hourly basis (Method 4, see Materials and Methods).

Treatment no.	Temperature day/night	Mean ± $t_{0.05}S_{\bar{d}}$	Predicted
		Leaves/day	
	C		
1	35/25	0.524 ± 0.101	0.505
2	32/19	0.473 ± 0.097	0.455
3	31/25	0.521 ± 0.052	0.521
4	29/11	0.383 ± 0.073	0.358
5	28/13	0.307 ± 0.073	0.366
6	26/15	0.307 ± 0.057	0.363
7	25/15	0.344 ± 0.048	0.348
8	19/16	0.256 ± 0.048	0.236
9	16/5	0.155 ± 0.020	0.118
10	15/25	0.296 ± 0.051	0.272
11	15/5	0.158 ± 0.033	0.099
12	13/28	0.307 ± 0.046	0.261
13	32/16	0.437 ± 0.054	0.404
14	29/18	0.391 ± 0.096	0.409
15	24/8	0.272 ± 0.070	0.205
16	22/9	0.255 ± 0.045	0.186

tween rate of elongation (growth) and temperature have been reported earlier (5, 19).

Rates of leaf appearance were similar to those reported by Brouwer et al. (7), but were somewhat lower than those measured by Thiagarajah and Hunt (24). Rate of leaf appearance is affected by soil nutrient status (7, 23), soil texture (22), plant water potential (3, 25), and illuminance (21). Fairey (14) found, for example, that plants grown under nutrient culture in a synthetic medium in the field developed much faster than adjacent soil-grown plants, and differences in root temperature did not appear to be the cause. Hence, the environmental factors other than temperature influence rate of leaf appearance and this detracts from the absolute universality, if not the relative merit, of the predictive value of Equation [1].

In the first test, hybrids differed significantly for rate of leaf appearance. Although differences were generally small (i.e., less than 10% of the mean), it is probable that much greater differences exist among genotypes of more diverse origin than those used in our study.

Total number of leaves per plant increased at a rate of approximately 0.2 leaf/C in the range from 15 to 35 C. Mean leaf number was 16, 18, 17, 19, and 20 leaves at 15, 20, 25, 30, and 35 C, respectively. An increase in leaf number with increasing temperature has been reported by others (12, 16).

In general, Equation [1], developed from work at constant temperature, was satisfactory for predicting rate of leaf appearance in the fluctuating temperature regimes of the second test (Table 1). Several workers (2, 9, 11) have suggested that night temperatures exert a greater influence on rate of development than day temperatures. In many cases, much of the differential response to day and night temperatures may be attributed to the curvilinear nature of the temperature-rate of development relationship. Frequently, night temperatures are in the range where rate of development increases linearly with temperature (i.e.,

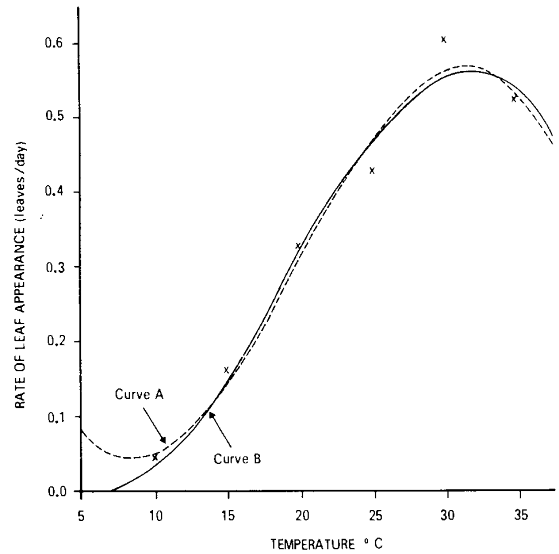

Fig. 1. Relationship between rate of leaf appearance and ambient temperature. Crosses indicate mean rate of leaf appearance at five constant temperatures (standard deviation = 0.043 leaves/day). Curve A is polynomial equation of best fit to data. Curve B is alternate polynomial in which Y = 0 when X = 6. Equation of Curve A is $Y = 0.2834 - 0.0639T + 0.00491T^2 - 0.0000823T^3$. Equation of Curve B is $Y = 0.0997 - 0.0360T + 0.00362T^2 - 0.0000639T^3$.

from 12 to 26 C), whereas, rate of development may change much less with changes in maximum day temperature (for example, in the range of 26 to 36 C). In the present study an attempt was made to examine the differential effects of day vs. night temperature by including two treatments (numbers 10 and 12, Table 1) in which the normal daily temperature differential was reversed, i.e., the higher temperature occurred at night. Although there was a tendency for measured rate of development to exceed predicted rate with high night temperatures (Table 1; compare treatments 10 and 12 with treatments 5, 6, and 7), the tendency was not statistically significant and may only reflect practical difficulties in maintaining cool daytime temperatures in growth cabinets programmed for fluctuating thermal environments. In total, we are not convinced that the use of a different temperature response for day and night (cf., the Ontario Corn Heat Unit method) is warranted.

The data provided by Pioneer Hi-Bred International were used to examine the utility of Equation [1] in predicting rate of development from planting to silking, and to permit a comparison among four different methods of calculating heat units, including two based on Equation [1] (see Material and Methods). Coefficients of variability (C.V.) of all four heat unit methods were lower than the C.V. associated with the number of calendar days to silking (Table 2). Relative precision of the four methods in predicting date of silking was estimated by calculating the standard deviation of the flowering date; the latter was computed by dividing standard deviation for number of accumulated heat units to silking by the average of heat units per day during the period which bracketed silking of all hybrids (approximately a 3-week per-

Table 2. Coefficients of variation of number of days and accumulated heat units from planting to mid-silking, and standard deviations of silking date predicted by calendar day and accumulated heat unit methods.

Method	Coefficient of variation		Standard deviation of silking date	
	Initial data	Adjusted for leaf no.†	Initial data	Adjusted for leaf no.†
	%		days	
Calendar days	8.0	–	6.0	–
Growing degree days	5.2	–	3.1	–
Ontario corn heat units	4.3	–	2.8	–
Thermal leaf units (max/min)	4.6	3.9	2.9	2.5
Thermal leaf units (sine wave)	5.2	4.0	3.1	2.5

† Adjusted for mean temperature during first 30 days after planting (0.2 additional leaves/C increase in temperature).

iod). The results (Table 2) show that, although the precision in predicting silking date could be increased by about 50% with the use of any of the four heat unit methods, differences among the heat unit methods were small.

Duration of the period from planting to silking is associated with both the rate of leaf appearance and number of leaves per plant. Temperature and photoperiod exert an influence on the duration from planting to silking through their effect on number of leaves per plant. Differences in photoperiod among the four locations and 3 years of the maturity test were negligible. However, mean temperatures during the first 30 days after planting (i.e., approximately the period from planting to tassel initiation) differed among locations and years. Adjustment of the thermal leaf unit methods for mean temperature during the first 30 days after planting (0.2 leaves/C) enhanced the accuracy of these methods (Table 2).

Arnold (1) showed that a heat unit method based on daily maximum and minimum temperatures overestimates heat unit accumulation when minimum temperature drops below the base temperature; number of heat units will be underestimated when maximum temperature excess the optimum for development. In the present study, the use of daily maximum and minimum temperatures or of a sine-wave curve for computing thermal leaf unit accumulation resulted in equal precision.

In summary, a cubic equation relating rate of leaf emergence to ambient temperature was derived from growth cabinet experiments and used as a means of predicting date of flowering in maize. The equation was equally precise as the Growing Degree Day or Ontario Corn Heat Unit methods for predicting date of silking. Precision was improved by adjusting leaf number in accordance with mean ambient temperature before flowering. Some of the variation in days from planting to silking not accounted for by heat unit methods may be attributed to environmental factors such as soil temperature, soil moisture, and soil nutrient status, which also influence rate of development.

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REFERENCES

1. Arnold, C. Y. 1960. Maximum-minimum temperatures as a basis for computing heat units. J. Am. Soc. Hort. Sci. 76: 682-692.
2. ———. 1971. Heat units used in field corn production. Ill. Res. 13(2):6-7.
3. ———. 1974. Soil moisture stress and sweet corn seedling development. Hort. Sci. 9:222-223.
4. ———. 1975. Heat unit systems in corn production. Ill. Res. 17(2):10-11.
5. Blacklow, W. M. 1972. Influence of temperature on germination and elongation of the radicle and shoot of corn (*Zea mays* L.). Crop Sci. 12:647-650.
6. Bloc, D., and J. P. Gouet. 1976. Influence des sommes de témperature sur la maturité du maïs. Association Générale des Producteurs de Maïs, Paris. p. 1-60.
7. Brouwer, R., A. Kleinendorst, and J. Th. Locker. 1973. Growth responses of maize plants to temperature. p. 169-174 *In* Plant response to climatic factors. Proc. Uppsala Symp., 1970. UNESCO, Paris.
8. Brown, D. M. 1960. Soybean ecology. I. Development-temperature relationships from controlled environment studies. Agron. J. 52:493-496.
9. ———. 1977. Response of maize to environmental temperatures: a review. Pages 15-26 *In* Agrometeorology of the maize crop. Proc. 1976 Symp., Ames, Iowa. Publ. WMO-481. World Meteorol. Organ., Geneva.
10. Bunting, E. S. 1976. Accumulated temperature and maize development in England. J. Agric. Sci. Camb. 87:577-583.
11. Coligado, M. C., and D. M. Brown. 1975. Response of corn (*Zea mays* L.) in the pre-tassel initiation period to temperature and photoperiod. Agric. Meteorol. 14:357-367.
12. Duncan, W. G., and J. D. Hesketh. 1968. Net photosynthetic rates, relative leaf growth rates, and leaf numbers of 22 races of maize grown at eight temperatures. Crop Sci. 8:670-674.
13. Dijkhuis, F. J. 1971. The use of heat units in maize production. Part II. Experimental results. Fert. Soc. S. Afr. J. 1:45-49.
14. Fairey, N. A. 1976. Assimilate distribution and utilization in maize. Ph.D. Thesis, Univ. of Guelph. Univ. Microfilms, Ann Arbor, Mich. (Diss. Abstr. 38:2981, 1978).
15. Gilmore, E. C., and J. S. Rogers. 1958. Heat units as a method of measuring maturity in corn. Agron. J. 50:611-615.
16. Hesketh, J. D., S. S. Chase, and D. K. Nanda. 1969. Environmental and genetic modification of leaf number in maize, sorghum, and Hungarian millet. Crop Sci. 9:460-463.
17. Iwata, F., and T. Okubo. 1969. Physiological and ecological studies on corn growth and yield. I. On the constancy of heat-unit accumulation in the effective degrees required for the growth of corn planted at various dates. Proc. Crop Sci. Soc. Jpn. 38:91-94. (In Japanese with English summary).
18. ———, and ———. 1970. Studies on corn growth and composition. II. On the constancy of heat-unit accumulation in the effective degrees required for leaf unfolding. Newsl. Tohoku Section Crop Sci. Soc. Jpn. 12:56-58. (In Japanese with English summary).
19. Lehenbauer, P. A. 1914. Growth of maize seedlings in relation to temperature. Physiol. Res. 1:247-288.
20. Mederski, H. J., M. E. Miller, and C. R. Weaver. 1973. Accumulated heat units for classifying corn hybrid maturity. Agron. J. 65:743-747.
21. Meyling, H. D. G. 1973. Effect of light intensity, temperature and daylength on the rate of leaf appearance of maize. Neth. J. Agric. Sci. 21:68-76.
22. Milbourn, G. M., and M. K. V. Carr. 1977. The importance of site selection for maize in Britain. p. 45-48 *In* Agrometeorology of the maize crop. 1976 Symp., Ames, Iowa, Publ. WMO-481. World Meteorol. Organ., Geneva.
23. Peaslee, D. E. 1977. Effects of nitrogen, phosphorus, and potassium nutrition on yield, rates of kernel growth and grain filling periods of two corn hybrids. Commun. Soil Sci. Plant Anal. 8:373-389.
24. Thiagarajah, M. R., and L. A. Hunt. 1979. Effects of temperature on leaf growth in corn (*Zea mays* L.). Can. J. Bot. (In press).
25. Vaclavick, J. 1969. Effect of different constant soil moisture levels on foliage development in maize. Biol. Plant. 11:68-78.
26. Wang, J. Y. 1960. A critique of the heat-unit approach to plant response studies. Ecology 41:785-790.