

## THE DYNAMICS OF A MAIZE CANOPY DEVELOPMENT : 1. LEAF ONTOGENY

Zur, B.  
Agricultural Engineering Department The Technion

Reid, J. F.  
Agricultural Engineering Department University of Illinois

Hesketh, J. D.  
ARS- USDA Department of Agronomy University of Illinois

<https://hdl.handle.net/2324/8154>

---

出版情報 : BIOTRONICS. 18, pp.55-66, 1989-12. Biotron Institute, Kyushu University  
バージョン :  
権利関係 :

# THE DYNAMICS OF A MAIZE CANOPY DEVELOPMENT

## 1. LEAF ONTOGENY\*

B. ZUR,\*\* J. F. REID,\*\*\* and J. D. HESKETH\*\*\*\*

\*\*Agricultural Engineering Department, The Technion, Haifa, Israel

\*\*\*Agricultural Engineering Department, University of Illinois, Urbana, IL 61801, U.S.A.

\*\*\*\*ARS-USDA, Department of Agronomy, University of Illinois, Urbana, IL 61801, U.S.A.

(Received October 4, 1989; accepted October 11, 1989)

ZUR B., REID J. F. and HESKETH J. D. *The dynamics of a maize canopy development. 1. Leaf ontogeny.* BIOTRONICS 18, 55-66, 1989. Crop canopy development in maize (*Zea mays* L.) was studied to observe the occurrence of individual leaf events (leaf primordia initiation, leaf tip appearance, and leaf collar appearance). The objective was to characterize factors controlling leaf development in a stand. Plants were grown in controlled environment chambers with day/night temperatures of 30/24, 26/20, and 19/14°C with 16 hours of artificial daylight per day. The rates of the observed developmental events varied with leaf node number and exhibited a nonlinear dependency with temperature. The changes in the rate of development with temperature were described using modified degree-day ( $M_{dd}$ ) thermal time scale where base temperatures ( $T_b$ ) differed for air temperatures above ( $T_b=10$ ) and below ( $T_b=7$ ) 20°C. Leaf area growth duration was defined as the difference in time, or  $M_{dd}$ , between the appearance of a leaf tip and leaf collar. The response curve for leaf area growth duration vs. leaf position was quadratic; much like that for mature area per leaf vs. position which represents its suggestive cause and effect nature. Equations are presented which provide part of the information needed to construct a corn canopy dynamics simulation model.

**Key words:** phenology; degree-days; base temperature; crop systems modeling; *Zea mays* (L.).

### INTRODUCTION

A canopy represents the surface area of a crop exposed to the aerial environment. The population of leaves in a canopy at any given time is made up of mature fully expanded leaves, of expanding leaves at various stages of growth, and of leaves yet to develop. The state of a canopy can be defined in terms of the dynamics of development and growth processes of individual leaves. This level of understanding is essential for describing the effects of environmental stresses on the plant canopy.

\* Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by the University of Illinois or the U.S. Department of Agriculture and does not imply the approval of the named product to the exclusion of other products that may be suitable.

The maximal area attained by a leaf is the product of its growth rate and growth duration. However, rate and duration of leaf area growth are essentially independent. While rate of leaf area growth is part of the overall plant growth process, duration of leaf area growth is determined by canopy developmental events. Specifically, duration of leaf area growth is the result of the difference in time between leaf maturity and leaf tip appearance. A better understanding of the development and growth of individual leaves in a maize canopy will improve our ability to model leaf area development and leaf area distribution.

The overall objective of this study was to investigate individual leaf development and leaf area growth in a maize canopy. This paper discusses dynamics of developmental events. A second paper will discuss leaf area growth. A dynamic model of leaf area development and growth will be presented in a third paper.

### THEORY

The ontogeny of an individual leaf can be defined by the four events:

*Leaf initiation*—the appearance of a leaf primordium on the shoulder of the shoot apical meristematic dome, as determined under a dissecting microscope.

*Leaf tip appearance*—the appearance of a new leaf tip from the whorl of expanding leaves at the shoot apex, as seen without disturbing the plant.

*Leaf maturity*—full expansion of leaf area as determined by the appearance of a collar at the base of the leaf.

*Leaf senescence*—determined by yellowing or loss of physiological activity.

The timing of each event in a leaf can be considered as the result of a developmental wave moving through consecutive leaves up the maize stalk. The rate of specific event waves through the canopy is expected to have a characteristic sensitivity to leaf position and temperature. When the wave of leaf initiation reaches the last primordial leaf, the tassel is ready to be initiated. When the wave of leaf tip appearance reaches the last leaf to appear, the tassel is ready to appear. And when the last leaf collar appears, anthesis takes place. The time between two consecutive developmental events defines the duration of the specific growth process. As a specific example, the time between leaf tip appearance outside of the whorl and leaf maturity defines the duration of visible expansion, or leaf area growth.

The temperature sensitivity of the rate of these events is the basis for a temperature-dependent, physiological time scale. The commonly used growing-degree day (GDD) system assumes a constant temperature sensitivity and uses a base temperature. This "thermal time" system is often used to compute the timing of phenological events in maize. The consistency of the temperature sensitivity of the rate of the developmental events was studied by Warrington and Kanemasu (7) for leaf initiation and leaf maturity by Aitken (1) and by Stapper and Arkin (4). Both Warrington and Kanemasu (7) and Tollenaar *et al.* (5) proposed nonlinear equations to describe the sensitivity of these rates to temperature. In both cases, the authors only calculated rates for a portion of the leaves on each plant and did not account for difference in the rates for leaves at different leaf positions on the plants. Also, in both cases the relationships between the rates of developmental processes and

temperature were linear within the narrow range of 18 to 26°C. Below and above this temperature range, sensitivity of the developmental processes to temperature decreased. Aitken (*I*) presented phytotron results suggesting that the sensitivity of the velocity of the leaf maturity wave to temperature is not a constant but decreases with an increase in the average daily temperature.

#### MATERIALS AND METHODS

Maize plants, Pioneer brand hybrid 3377, were grown from seed in 20 liter plastic containers filled with a mixture (2:1 by volume) of a commercial potting mix ("Jiffy Mix", shredded sphagnum peat moss and horticultural grade vermiculite) and Flannagan silt loam soil (Aquic Argiudoll) in growth chambers. The chambers were 2.5 × 1.35 × 3 m with a sliding light bank of General Electric fluorescent Deluxe Cool White lamps. The measured light flux at crop height was 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PAR. Temperature regimes used in these experiments were 26°C day–20°C night for experiment I, 30°C day–24°C night for experiment II and 19°C day–14°C night for experiment III. Air relative humidity was maintained at 70–80% during daylight hours and 95% during darkness by frequent misting at the top of the chambers. A day length of 16 hours and night length of 8 hours was used in all experiments.

Five corn seeds were planted in each container and thinned to three when plants had developed seven leaves. Twenty containers were used in experiments I and II while 30 containers were planted for experiment III because of the longer growth period associated with the cooler temperature regime. Experiments were terminated at the silking stage.

Containers were irrigated twice weekly and fertilized once a week using a solution of Rapid Grow (32-7-7) fertilizer. At frequencies decreasing from 1 to 3 days, 3 plants were destructively sampled for primordial leaf initiation by dissection under a microscope. A new leaf primordium was counted when it could be observed as a "ridge" on the shoulder of the apical dome. Leaf appearance was determined by counting total leaves on the main stem including dead leaves and new visible tips. A new leaf was counted when it was just visible above the enclosing sheath of the preceding leaf. Leaf maturation was determined by counting total numbers of leaves with visible collars at their base. Rates of the leaf events were calculated from plots of average leaf numbers vs. time. At each sampling period, the measured leaf event was the average of three plant observation.

#### RESULTS AND DISCUSSION

The stalk positions for the youngest leaf primordium, leaf tip and leaf collar from seedling emergence to silking are presented in Figs. 1–3 for the 30/24, 26/20 and 19/14°C temperature regimes. Each point in the Figs. is the average event for three sampled plants. Under all temperature regimes, the tassel was initiated when the 10th leaf tip appeared and when the 6th leaf matured. This event was observed 23, 26 and 37 days after seedling emergence for the 30/24, 26/20 and 19/14°C temperature treatments, respectively. For the same order of treatments, all leaves

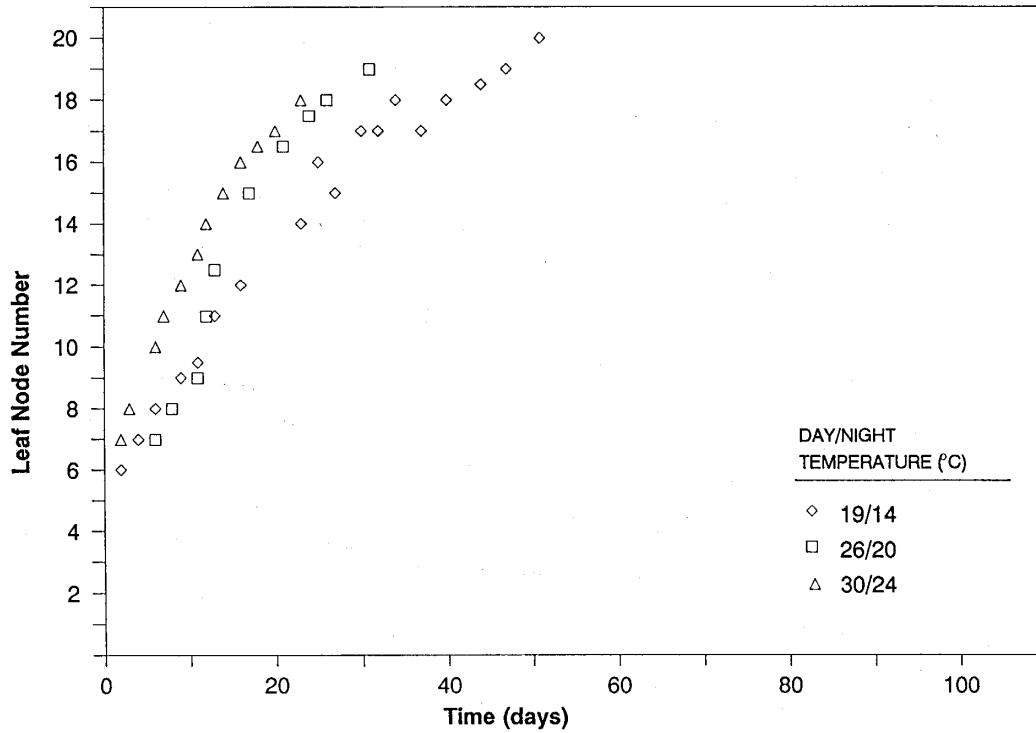


Fig. 1. Leaf primordia initiation for 3 experimental temperature regimes in maize plants.

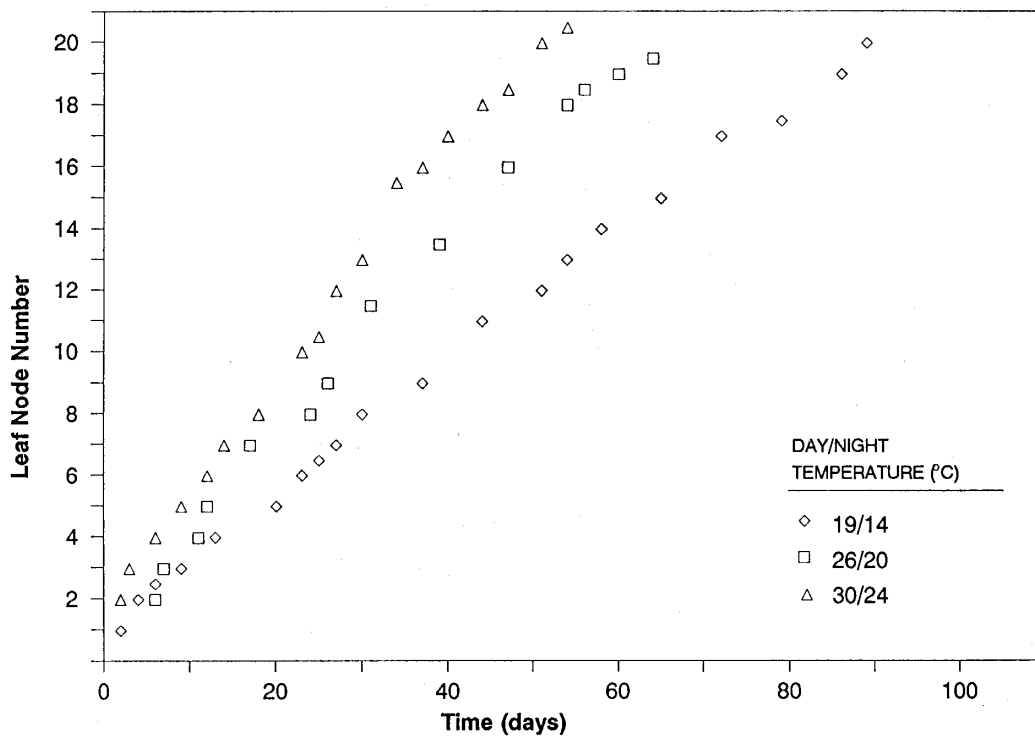


Fig. 2. Leaf tip appearance for 3 experimental temperature regimes in maize plants.

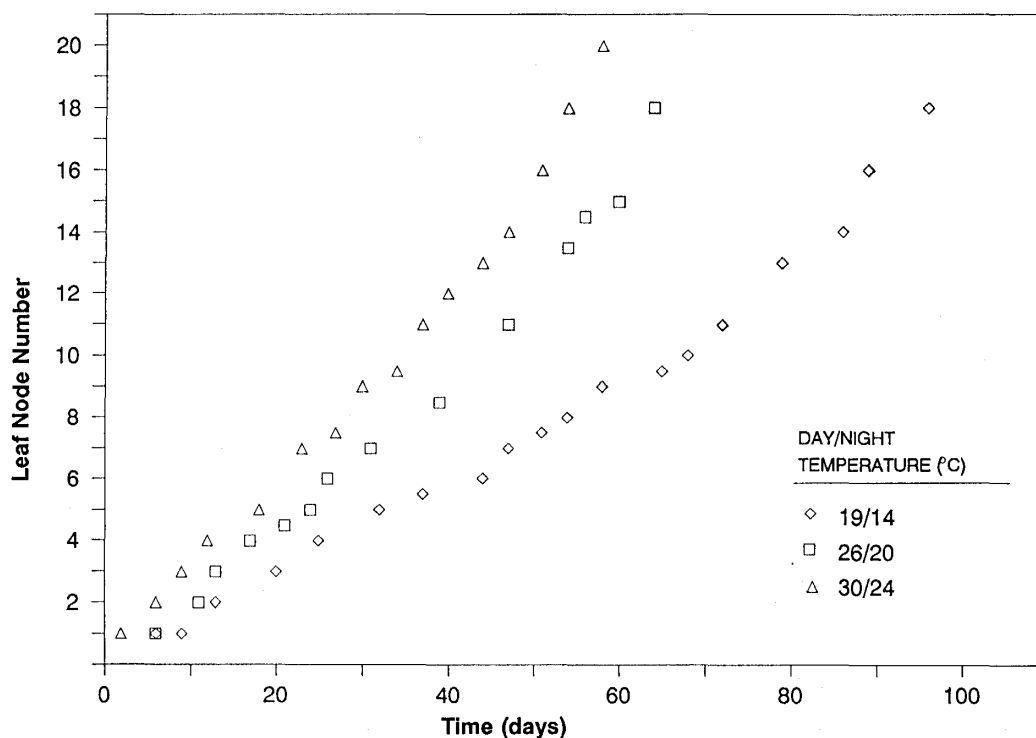


Fig. 3. Leaf collar appearance for 3 experimental temperature regimes in maize plants.

matured or were fully expanded approximately 58, 64, and 99 days after seedling emergence. Both experiments II and III were terminated before maturity of the final collar. The temperature treatments did not seem to affect the total number of leaves produced although some plants in Experiment I produced 21 leaves instead of 20.

Figures 1-3 illustrate that these leaf events are not strictly linear with leaf position. The severity of the nonlinearity varies with temperature. In Fig. 1, leaf initiation rate decreases for the upper leaf positions above 16 with the decrease becoming more pronounced as temperature decreases. The variations in the leaf primordia for leaves 6-10 of Experiment II are believed to be the result of experimental error and inexperience in making these measurements. In Fig. 2, individual leaf tip appearance rate seem to generally be constant. The 30/24 and 26/20°C results indicate that there may be a small decrease in the rate of leaf appearance for the upper leaf positions. In Fig. 3, leaf collar appearance rates increase for upper leaf positions with the effect becoming more nonlinear with decreasing temperatures.

Torigoe (6) made the observation that leaf collar appearance can be represented by two piecewise linear curves, intersecting at a turning point, with an increasing rate of leaf collar appearance for leaves after the turning point. Likewise, this describes the leaf initiation and leaf tip appearance data except that the rate slows down for leaves after the turning point. More simply, the leaf events can be described as a nonlinear function of leaf position.

Table 1. Average rates of leaf developmental events, in leaves/day, under 19/14, 26/20, and 30/24°C temperature regimes using data from this study and equations developed in previous studies. Calculated temperatures were computed using 16/8 day/night time ratios

Leaf event	Experimental results			Previous studies		
	19/14	26/20	30/24	19/14	26/20	30/24
Initiation*	0.422	0.721	0.716	0.481	0.761	0.869
Appearance**	0.222	0.345	0.368	0.200	0.402	0.494
Maturity*	0.150	0.236	0.282	0.140	0.260	0.334

\* Results for previous study calculated from equation presented by Warrington and Kanemasu (7).

\*\* Results for previous study calculated from equation presented by Tollenaar *et al.* (5).

The timing of leaf events is also a function of temperature. From Figs. 1–3 comparing 30/24 to 19/14°C, it is clear that decreasing temperature results in a decrease of the rate of individual leaf events. Warrington and Kanemasu (7) and Tollenaar *et al.* (5) have previously shown that the sensitivity of the rates of leaf events to temperature is also nonlinear. These previous works have neglected any effect of leaf position. These studies have generally only considered the earlier leaves of the canopy before any change in rate occurs. To compare our values with previous work, we computed the rates of the leaf events for the early leaves of our data, assuming a constant rate. The rate of leaf primordia initiation, leaf tip appearance, and leaf collar appearance for the first 12 leaves from Fig. 1 are presented in Table 1, along with the calculated results from equations presented by Warrington and Kanemasu (7) and Tollenaar *et al.* (5). Leaf primordia initiation was approximately 40% slower than calculated values from previous studies. Leaf tip appearance and leaf collar appearance compared more favorably with previously reported results. Leaf tips were  $\pm 15\%$  of equation calculations. Leaf collars lagged computed results by up to 18%. The results for leaf tip appearance and leaf collar maturity give our data validity with previous studies.

An attempt was made to develop a physiological time scale for the occurrence of all leaf events. It was assumed that this physiological time scale could be obtained by removing the temperature effect from the experimental data, resulting in a “blueprint” for leaf development. Previous studies have shown that the temperature effect was nonlinear, but have not accounted in changes in rates for different leaf positions and thus were not useful in developing a physiological time scale. The temperature treatments used in this study were too limited to describe the nonlinear temperature sensitivity. Therefore, the temperature effect on the development was removed by adjusting the temperature sensitivity between our experiments. One way to compute the temperature sensitivity of the developmental events,  $b$ , is the remainder index equation,

$$b = R/(T - T_b) \quad (1)$$

where  $R$  is the rate of the developmental event in leaves/day,  $T$  is the test temperature in °C and  $T_b$  is the base temperature and the intercept of a line passing through the point  $T$  and having a slope  $b$ . The units of  $b$  are leaves/degree-day.

Table 2. The sensitivity of the rates of leaf events to temperature for the 3 experimental temperature regimes (leaves/day/°C)

		Temperature regime		
		19/14	26/20	30/24
Primordia	$T_b=10$ :	0.044	0.040	0.034
	$T_b=7$ :	0.030	0.032	0.029
Leaf tips	$T_b=10$ :	0.033	0.024	0.021
	$T_b=7$ :	0.023	0.019	0.018
Leaf collars	$T_b=10$ :	0.027	0.021	0.019
	$T_b=7$ :	0.018	0.017	0.016

A constant base temperature is generally assumed and the sensitivity is constant provided that the rate of developmental events vary linearly with temperature. Table 2 contains the calculated sensitivities for developmental events using a base temperature of 10 and 7°C. For a selected base temperature, the remainder index procedure accounts for the temperature sensitivity of leaf tip and leaf collar appearance for the 26/20 and 30/24°C temperature regimes, but not for the 19/14°C temperature regime. Aitken (1) also noted that the temperature sensitivity was different for average daily temperatures above and below 20°C. The sensitivity of developmental rates to temperature can be changed by adjusting the base temperature in Eq. (1). From Table 2,  $T_b=7^\circ\text{C}$  for the 19/14°C temperature regime and  $T_b=10^\circ\text{C}$  for the 26/20 and 30/24°C temperature regimes yields approximately constant  $b$  values for the temperature range tested in the present study. A temperature of 20°C was used as the breakpoint between the 2 different sensitivities based on Aitken (1). Comparing this procedure to the more detailed temperature studies of Warrington and Kanemasu (7) and Tollenaar *et al.* (5), we have effectively formed a piecewise linear approximation of the relationship between rate of development and temperature.

Our method for accounting for the temperature sensitivity was used to convert the real time axis of Figs. 1–3 into a physiological time axis. The results of this procedure are shown in Fig. 4, where most leaf events coalesce onto a single time scale. Our procedure of modifying the base temperature to account for the nonlinear sensitivity of the rate to temperature was termed the Modified Degree Day ( $M_{dd}$ ). The particular modified degree-day we have chosen is beneficial for the nonlinear effects on leaf position observed in the present study. With more experimental data covering a broader range of temperatures, the nonlinear temperature sensitivity can be more fully described on a physiological time scale. Another approach for developing a physiological time scale would be to normalize the plant development based on the timing of a key event, like tassel initiation or anthesis. This process will result in a “blueprint” describing the physiological events in the development of the plant.

A relationship was developed between the 3 developmental processes and  $M_{dd}$  (Fig. 4). The data for leaf primordia initiation were regressed to a quadratic equation, constrained to intercept at 6 leaf primordia at seedling emergence (0  $M_{dd}$ )



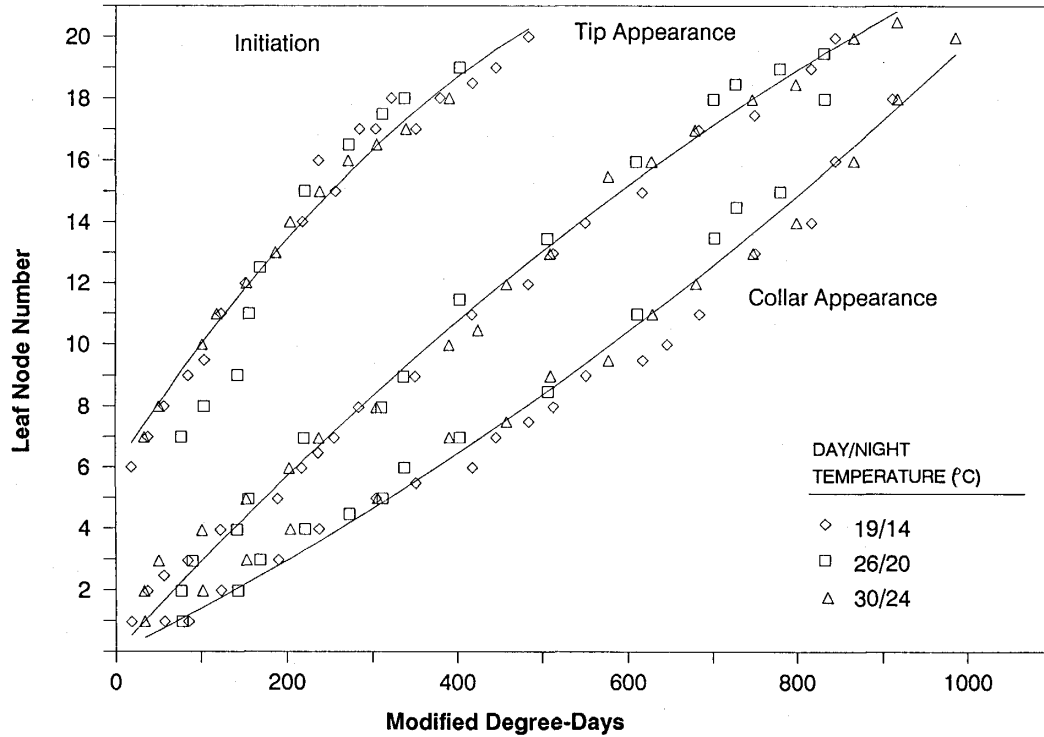


Fig. 4. Leaf primordia initiation, leaf tip appearance, and leaf collar appearance in maize plants as a function of physiological time ( $M_{dd}$ ).

( $r^2=0.93$ ):

$$N_p = 0.0425M_{dd} - 2.7 \times 10^{-5}M_{dd}^2 + 6 \quad (2)$$

where  $N_p$  is the leaf primordium node number. The relationship between leaf tip node number and  $M_{dd}$  was regressed to a quadratic equation ( $r^2=0.98$ ):

$$N_a = 0.0302M_{dd} - 8.14 \times 10^{-6}M_{dd}^2, \quad (3)$$

where  $N_a$  is the node number of the appearing leaf tip. The relationship between leaf collar node number and was regressed to a quadratic equation with ( $r^2=0.98$ ):

$$N_m = 0.0137M_{dd} + 6.12 \times 10^{-6}M_{dd}^2. \quad (4)$$

In this case  $N_m$  is the node number for the appearing leaf collar, representing a mature leaf. The regression lines are superimposed on the data points in Fig. 4. Equations (3) and (4) were constrained to pass through the origin.

Equations (3) and (4) represent the number of leaf tips and leaf collars that would appear at any given temperature compensated physiological time,  $M_{dd}$ . Subtracting Eq. (4) from Eq. (3) yields the number of leaves that are visibly expanding at any given point in physiological time,

$$N_e = N_a - N_m \quad (5)$$

From Eqs. (3) and (4) this yields:

$$N_e = 0.0165M_{dd} - 1.43 \times 10^{-5}M_{dd}^2, \tag{6}$$

which shows that the number of emerging leaves is a quadratic function of physiological time. This is indicated as a vertical distance between the leaf appearance and leaf maturity curves in Fig. 4.

Individual leaf area growth duration is the difference in time between the appearance of a leaf tip and the appearance of a leaf collar. This difference is represented by the horizontal distance between the leaf tip and leaf collar appearance curves in Fig. 4. A generalized equation relating leaf area growth duration in terms of our nonlinear time scale to leaf number was developed by taking the inverse relationship of Eqs. (3) and (4). The time of leaf tip appearance was ( $r^2=0.99$ ):

$$M_{dda}(N) = 30.978N + 0.581N^2 \tag{7}$$

where  $M_{dda}$  is the time for leaf node number  $N$  to appear. The time of leaf collar appearance was ( $r^2=0.99$ ):

$$M_{ddm}(N) = 68.559N - 0.994N^2, \tag{8}$$

where  $M_{ddm}$  is the time for leaf  $N$  to mature. The duration of leaf area growth can be expressed by subtracting Eq. (7) from Eq. (8),  $D_{dd} = (M_{ddm} - M_{dda})$ , or

$$D_{dd} = 37.6N - 1.58N^2, \tag{9}$$

where  $D_{dd}$  is the leaf area growth duration in  $M_{dd}$ . The relationship between  $D_{dd}$  and node number from Eq. (9) is demonstrated in Fig. 5. Experimental points

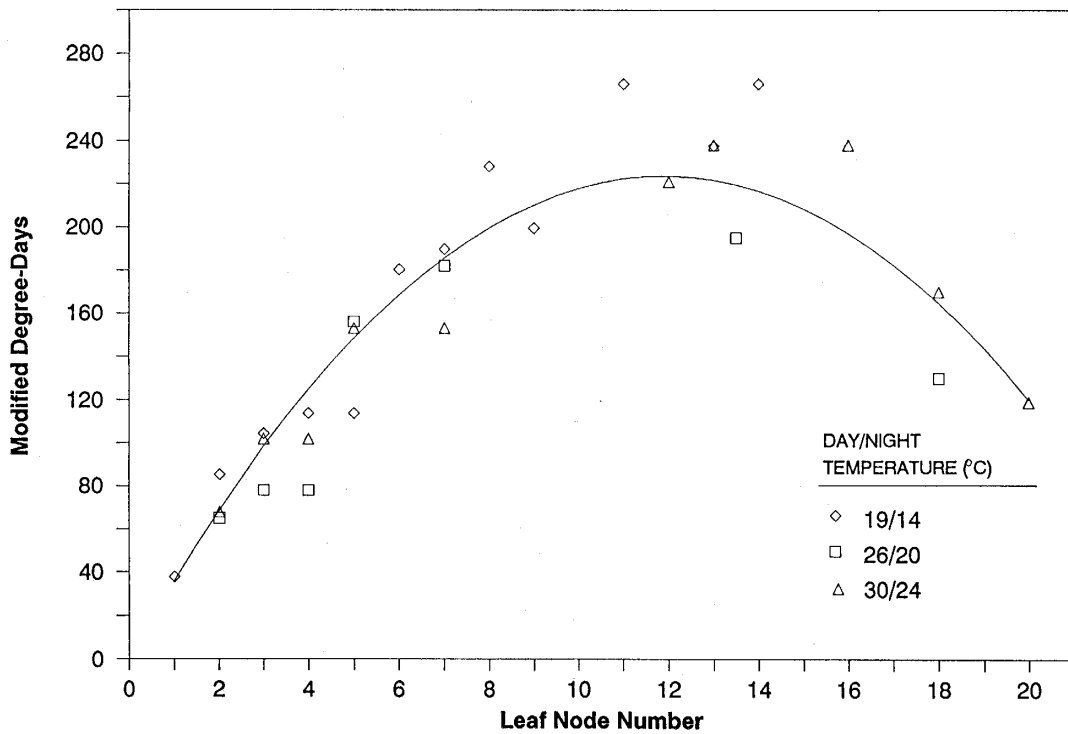


Fig. 5. Degree-day duration of leaf area growth vs. stalk node number for plants growing at the 19/14, 26/20, and 30/24°C temperature regimes.

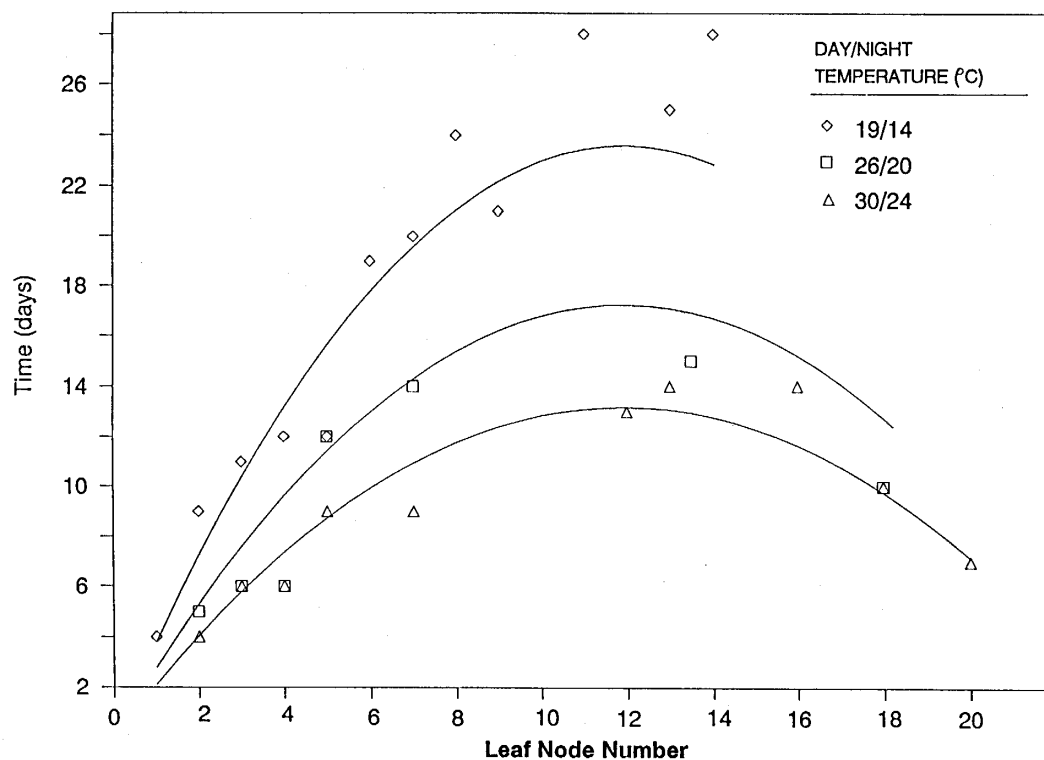


Fig. 6. Real-time duration of leaf area growth vs. stalk node number for plants growing at the 19/14, 26/20, and 30/24°C temperature regimes.

were obtained by subtracting the measured times of leaf tip and leaf collar appearance for leaves where both events were observed. The large variability around this data was attributed to experimental error in measuring leaf tip and collar appearance.

Leaf area growth duration is a quadratic function of node number with a peak duration of expansion for leaves 10 to 14. Dwyer and Stewart (3) reported that maximal area of individual maize leaves is a skewed bell-shaped function of leaf number. Maximal leaf area can be expressed as the product of the leaf area growth duration and the leaf area growth rate. Thus, the findings of Dwyer and Stewart (3) concerning the distribution of maximal leaf area can be partially explained by the quadratic nature of the duration vs. leaf number function. Note also that the quadratic nature of the duration is a result in changes in the rates of leaf tip appearance and leaf collar appearance.

The influence of temperature on the duration of individual leaf area growth maize leaves can be demonstrated by converting the time scale in Eq. (9) to real time. Computed and experimental values of duration of visible growth from the three temperature regimes as a function of leaf number are presented in Fig. 6. Temperature regime had a negative nonlinear effect on the duration of individual leaf expansion. This was also observed by Dennett *et al.* (2) for *Vicia faba*. The coldest temperature regime, 19/14°C, resulted in the longest duration of growth for all leaves. Decreasing the average daily temperature from 23 to 16.5°C increased the duration of visible expansion of leaves 10 to 13 from 16 days to 26 days. Dura-

tion of expansion of these leaves increased from 14 days to 16 days as a result of a change from an average daily temperature of 27 to 23°C.

#### SUMMARY AND CONCLUSION

Temperature sensitivity of the rate of individual developmental events in a maize canopy are often used to predict initiation and appearance of tassel and timing of anthesis. It was postulated here that a set of equations describing the temperature compensated velocity of leaf primordia initiation, leaf tip appearance and leaf collar appearance (signalling leaf maturity) totally describe individual leaf area development in a maize canopy. Results obtained in the present study and previously published in the literature show that the rates of these developmental events at tested temperature regimes are not constant. They follow a decreasing quadratic function with leaf position, and therefore with time, for leaf primordia initiation and leaf tip appearance and follow an increasing quadratic function with leaf position for leaf collar appearance. Furthermore, the temperature sensitivity of these rates is not constant, but generally decreases with temperature in the range studied.

The range and number of temperature treatments tested in the present study was not sufficient for rigorously developing a physiological time scale. The best that could be done presently was to divide the results into two temperature groups, and assign to each group a characteristic base temperature,  $T_b$ . This is the logic behind our  $M_{dd}$  time scale. Figure 4 is a testimony to the success of choosing the best  $T_b$  values which coalesced all observed leaf events onto a single time scale.

Five empirical equations which define individual leaf development in the canopy of the test maize plants were developed. The first three equations, (2), (3) and (4) describe the initiation of a leaf primordia or the appearance of a leaf tip or a leaf collar as a function of  $M_{dd}$ . The fourth equation (6), relates the number of leaves between their appearance and maturity development stages present in the canopy at any given  $M_{dd}$  time. The solution of Eq. (6) is a quadratic equation verifying our observations that the number of expanding leaves in a canopy is small at first, reaches a maximum when the middle leaves appear and then decreases as the number of leaves further increases. Equation (6) is of importance since it yields the number of leaves in the canopy at any given time the final area which is sensitive to the development of external stresses.

The fifth equation, (9), describes the duration of individual leaf area growth as a function of leaf number. The solution of this equation also results in a quadratic shape relating duration of leaf area growth to leaf number. Since the duration is expressed in terms of our temperature compensated time scale, duration expressed in real time is negatively related to temperature. Leaf area growth duration increases with a decrease in daily average temperature. Equation (9) is the direct link between developmental and growth processes, it defines the time available for expansive growth of individual leaves.

## REFERENCES

1. Aitken Y. (1974) *Flowering Time, Climate, and Genotype*. Melbourne University Press, Melbourne.
2. Dennett M. D., Elston J. and Milford J. R. (1979) The effect of temperature on the growth of individual leaves of *Vicia fabia* L. in the field. *Ann. Bot.* **43**, 197-208.
3. Dwyer L. and Stewart D. (1986) Leaf area development in field-grown maize. *Agron. J.* **78**, 334-343.
4. Stapper M. and Arkin G. (1980) CORNF: A Dynamic Growth and Development Model for Maize (*Zea mays* L.). Blackland Research Center. Program and Model Documentation. No. 80-2. Texas A & M University Experiment Station, Temple.
5. Tollenaar M., Daynard T. and Hunter R. (1979) Effect of temperature on rate of leaf appearance and flowering date in maize. *Crop Sci.* **19**, 363-366.
6. Torigoe Y. (1986) A conceptual model of developmental phases of maize on the basis of the relationship between differentiation and growth of vegetative and reproductive organs. *Japan. J. Crop Sci.* **55**, 465-473.
7. Warrington I. and Kanemasu E. (1983) Corn growth response to temperature and photoperiod. II. Leaf initiation and leaf appearance rates. *Agron. J.* **75**, 261-266.