

Chapter 11

PREDICTING MAIZE PHENOLOGY

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Models of development and grain yield of maize (*Zea mays* L.) have become numerous due to the wide distribution of the species and its vulnerability to climate stress. Models of maize production include the Runge-Benci model,¹ the Splinter model,² SIMAIZ,³ the “Bio-photothermal” model,⁴ the “Energy-Crop Growth” model,⁵ CORNF,⁶ and CERES-Maize.⁷

Most maize models are designed to predict the response of grain yield to environment, but they differ in terms of the type and complexity of biological processes included. These differences are especially evident in their techniques of predicting phenology. The Runge-Benci model makes no attempt at predicting development. Both the Splinter model and SIMAIZ both predict growth stages by accumulating degree days. When the sum reaches a specified value, the plant is assumed to be at the next stage. No attempt is made to quantify photoperiod sensitivity. The “Energy-Crop Growth” model also predicts phenology based solely on temperature. The temperature function is a series of four lines fit to growth-rate data. The “biophotothermal” model sums genetic, photoperiodic, and thermal factors in order to predict the number of days to tassel initiation. CORNF and CERES-Maize each use photoperiod and temperature to predict development. In both, photoperiods greater than 12.5 h delay tassel initiation in sensitive genotypes and increase the final number of leaves. However, CERES-Maize provides a more detailed system of predicting stages and number of leaves, and its components can be more easily tested and validated. Recently, a phenology model which includes leaf initiation, leaf collar appearance, and developmental stages similar to CERES-Maize was described in Japan.^{8,9} In this model, development rates are temperature dependent and photoperiod sensitivity is ignored.

The objective of this chapter is to describe a model for predicting maize phenology based on photoperiod and temperature. Tassel initiation and leaf primordia initiation are simulated to predict total number of leaves (TLNO). Rate of leaf tip appearance is simulated to predict when the last leaf will emerge, and soon thereafter silking is predicted to occur. Three phases between silking and physiological maturity are simulated. Two processes involved in phenology which are not included are the dependence of seed germination on soil water and the dependence of physiological maturity on assimilate supply. By omitting these, both a soil water balance section and an assimilate allocation section could be omitted.

Assumptions, experimental justification, and possible sources of errors are discussed for the simulated processes. Tests of the predictive ability of the model for silking date and final number of leaves are also included. Finally, areas for future research related to this model are described.

I. GENERAL MODEL DESCRIPTION

The model was written in FORTRAN and requires approximately 3 s of computer time for one season on a large mainframe computer. Simulations involving several years of weather data can be run with the same cultivar and planting date. Required input data are latitude (LAT), day of the year of sowing (ISOW), daily minimum and maximum air temperatures (TEMPMN and TEMPMX), and three cultivar-specific parameters, P1, P2, and P5. The three parameters can be independently derived as described in the text or can be estimated from values of similar cultivars.

There are nine phenological phases or stages including one for the fallow period after harvest and before planting. The system of numbering the stages is circular with an identifying integer (ISTAGE) for each (Table 1).

The model has a daily incrementing loop which executes until the end of the weather data is reached (Figure 1). Daily temperatures are read first. Next, pertinent variables are calculated. Finally, the decision is made concerning whether the next phenological stage has been reached.

Basic assumptions relate to the development rate response to temperature and to photoperiod. The model assumes rate of development increases linearly above a base temperature up to 34°C and then linearly decreases to 0 from 34 to 44°C. These rates include development from germination to seedling emergence, development in the juvenile phase, leaf initiation and leaf tip appearance, and development from silking to physiological maturity. Rate of photoperiodic

TABLE 1
Description of the Phenological Phases Used in the Model

7	Prior to sowing (fallow)
8	Sowing to germination (1 d)
9	Germination to seedling emergence
1	Seedling emergence to end of juvenile phase
2	End of juvenile phase to tassel initiation (photoperiod sensitive phase)
3	Tassel initiation to silking
4	Silking to beginning of effective filling period of grain (lag phase)
5	Effective filling period of grain
6	End of effective filling period to physiological maturity (black layer)

induction is assumed to decrease with increasing photoperiod for photoperiods greater than 12.5 h. The number of days of delay in tassel initiation per hour increase in photoperiod is assumed to be a constant for any given photoperiod-sensitive cultivar.

A. TEMPERATURE-DEPENDENT RATES

Rates of development from germination to seedling emergence, from seedling emergence to end of the juvenile phase, from silking to maturity, and rates of leaf initiation and leaf tip appearance are all simulated using a growing degree day (GDD) or daily thermal time (DTT) system. The base temperature is 8°C for all these processes except seedling emergence, with a base of 10°C. As noted, development rate is assumed to decrease to 0 as temperature increases from 34 to 44°C. When TEMPMN and TEMPMX encompass the base temperature, or 34°C, intermediate values are calculated with a zero-to-one factor (TMFAC) calculated with a polynomial fit to a sine wave curve. The interpolated values are then used to calculate the daily value for DTT.

Rate of coleoptile elongation linearly increases from a value near 0 at 10°C.¹⁰ Allowing 1 d for germination when adequate soil moisture is present, seedling emergence requires an average of 45 DTT₁₀ when the planting depth is 5.0 cm.¹¹

Two leaf developmental processes, primordia initiation and tip appearance, allow for prediction of TLNO and prediction of tassel emergence date. Both number of primordia initiated and number of tips visible outside the whorl are linear as a function of time in constant temperature growth chambers or as a function of cumulative DTT₈ in the field. This linearity in initiation was shown in growth chambers by Warrington and Kanemasu¹² and in the field by Kiniry and Ritchie¹³ (Figure 2). Likewise, tip appearance rate is constant after the second leaf in growth chambers (Figure 3) and as a function of cumulative DTT in the field.¹⁴ It is interesting to note that number of days from tip appearance to collar appearance as a function of leaf number is nonlinear (Figure 4). Stem elongation causes the last few leaf collars to come out more quickly than the earlier ones. This is why the DTT between leaf collars vary with leaf number¹⁴ and why modeling phenology based on number of leaf collars is more difficult than with leaf tips.

The response rate of leaf tip appearance to temperature (Figure 5)^{13,15} is the basis for the DTT system discussed previously. A similar response was demonstrated by Chirkov.¹⁶ Rate increases linearly from 8 to 34°C and then decreases to 0 at 44°C. A similar base temperature for leaf initiation rate can be derived using results of Warrington and Kanemasu¹² (Figure 6).

Likewise, rates of development to tassel initiation and to anthesis or silking have a base temperature near 8°C. Warrington and Kanemasu¹⁷ found rate of development to tassel initiation had a base temperature of 8.4°C for one hybrid and 7.8°C for another. Field results of Durand et al.¹⁸ support use of a base temperature of 7°C rather than the traditional 10°C for rate of development toward silking.

Development in the anthesis or silking to maturity interval can also be shown to have a base

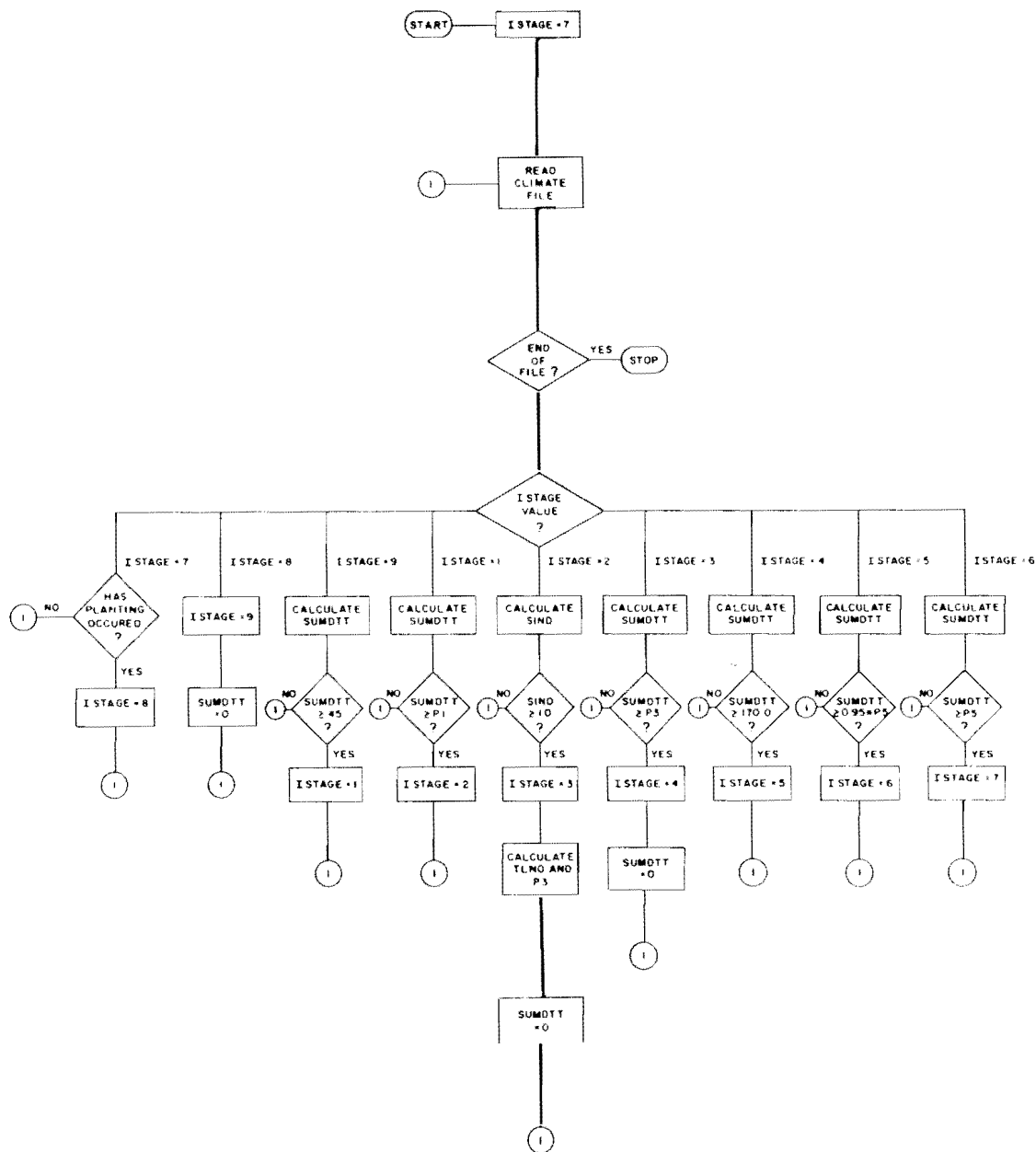


FIGURE 1. A flow diagram of the maize phenology model.

temperature near 8°C. With the admittedly scant data of Badu-Apraku et al.,¹⁹ the base temperature for development rate of maize is 8.2°C (Figure 7). With similar data for sorghum (*Sorghum bicolor* L. Moench)²⁰ with treatments of 15, 22.5, and 30°C, a fitted exponential equation forced through the x-intercept of 5°C fell very close to a response line with an 8°C base temperature (Figure 8).

B. PHOTOPERIODIC INDUCTION

Photoperiod is assumed to directly affect only date of tassel initiation.²¹ From seedling emergence until the start of the photoperiod-sensitive phase, a cultivar-specific sum (P1) (Table 2) of DTT₈ are accumulated during the photoperiod-insensitive juvenile phase. All cultivars are assumed to reach tassel initiation 4 d after the end of the juvenile period if photoperiods are 12.5 h or less. In longer photoperiods, tassel initiation is delayed according to a cultivar-specific value of sensitivity (P2) in units of days of delay per hour increase in photoperiod.^{22,23} Duration of the

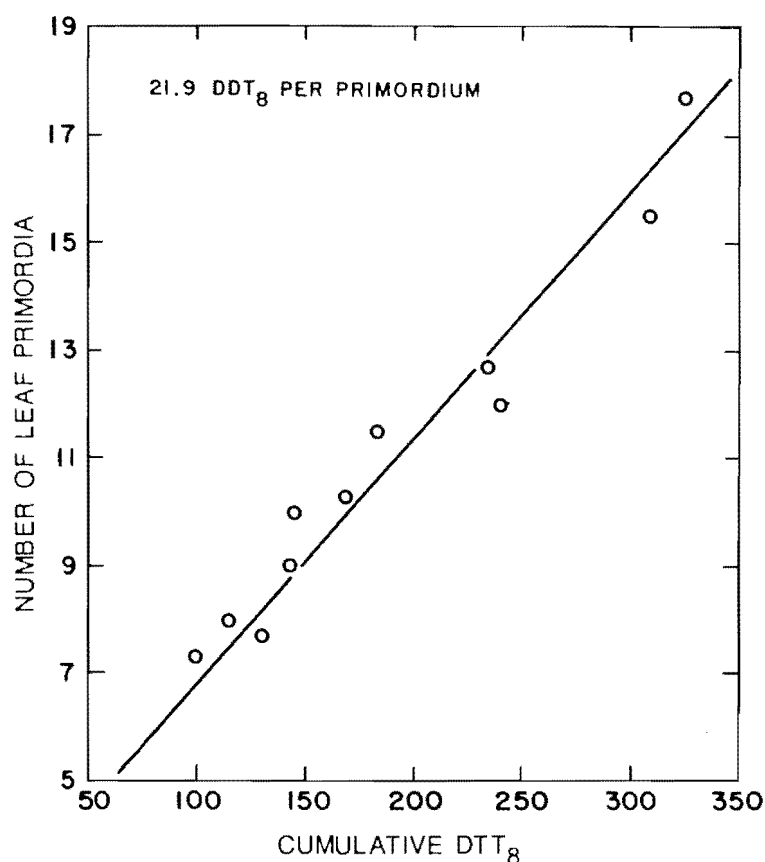


FIGURE 2. Number of leaf primordia as a function of cumulative DTT_8 for a 1981 sowing at Temple, TX of maize hybrid B73 \times Mo17.¹³

photoperiod-sensitive phase is assumed to be independent of temperature. Delay in tassel initiation due to long photoperiods causes an increased number of leaf primordia to be initiated, thus increasing the number of leaf tips which must emerge before tasseling and delaying tasseling and silking.

C. PREDICTION OF DTT-8 FOR TASSEL EMERGENCE

Since leaf initiation rate, leaf tip appearance rate, and rate of development to tassel initiation and anthesis all use the same DTT_8 system, the DTT_8 from seedling emergence to tassel initiation can be directly related to the DTT_8 from seedling emergence to tassel emergence. Likewise, the number of leaf tips visible at tassel initiation can be directly related to the TLNO produced.

The relationship between DTT_8 from seedling emergence to tassel emergence and to tassel initiation showed that for each DTT_8 unit tassel emergence is delayed, tassel initiation was delayed 0.46 units.²³ Analysis of similar data for 6 maize cultivars grown in 2 photoperiods at 24°C gave a value of 0.47 units.²⁴ Assuming the DTT_8 per leaf tip is constant after the first two leaves, a similar relationship should be true for the TLNO and the number of leaf tips visible at tassel initiation (TILNO). Three independent projects have shown this to be true. Russell,²⁵ working with a wide range of genotypes in a wide range of field environments, found:

$$TILNO = 0.44 * TLNO - 2.30$$

Similarly, Inoue²⁶ found the relationship to be

$$TILNO = 0.42 * TLNO - 2.2$$

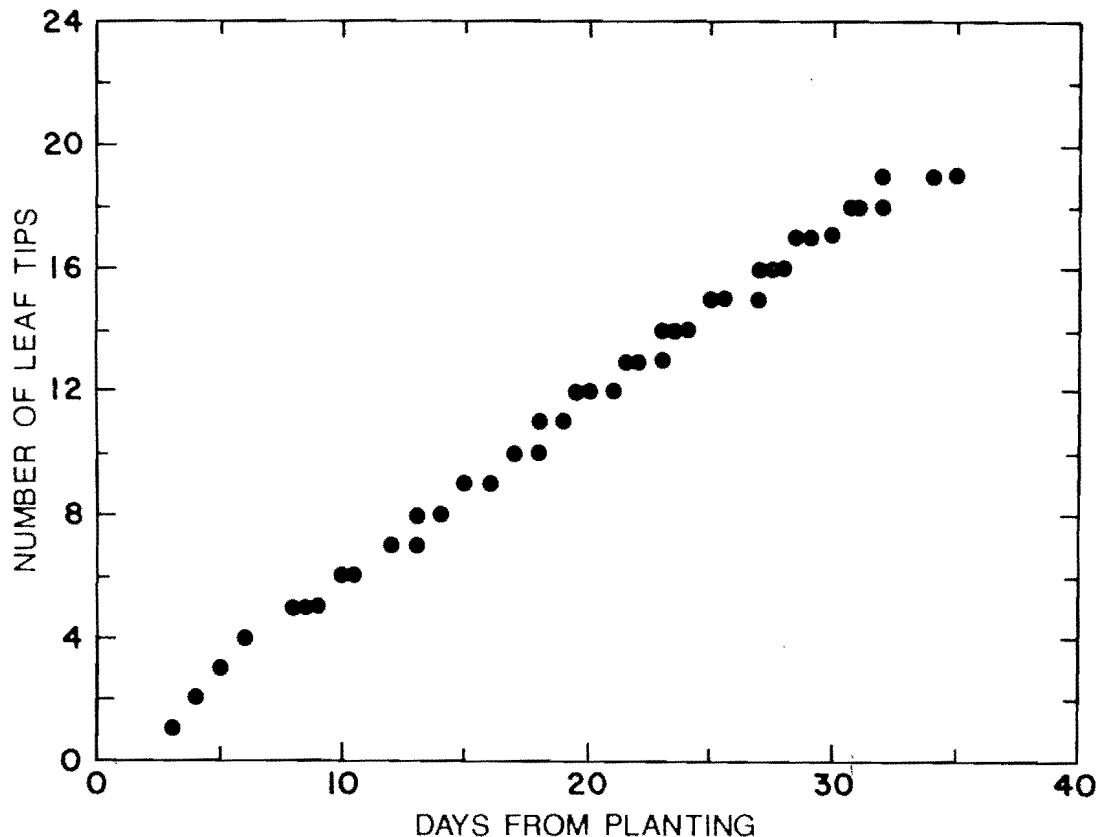


FIGURE 3. Number of leaf tips emerged as a function of days from sowing for maize hybrid Mo17 × A634 in the Duke University Phytotron at 25°C.⁴⁰

Using data with short season hybrids,²⁷ the relationship was: $TILNO = 0.44 * TLNO - 1.95$. The slope value can be thought of as representing the ratio of the DTT_8 per leaf primordium to the DTT_8 per leaf tip. For the present model, we assumed 18 DTT_8 per primordium and 39 DTT_8 per leaf tip for a ratio of 0.46. The x-intercept, 5.2 leaves for the first two equations and 4.4 for the last one, is similar to the 6 leaf primordia present at seedling emergence.^{12,13}

D. DTT_8 PER LEAF PRIMORDIA AND PER LEAF TIP

Consistency in the DTT_8 per leaf primordium or tip is vital for accuracy of the present model. Environmental alteration of the values or differences between cultivars in the values need to be identified and quantified before the model will make consistently accurate predictions.

A field experiment sown in March in Temple, TX, demonstrated that there were 21 DTT_8 per leaf primordium (Figure 2).¹³ Results in a growth chamber showed values of 19 to 21 DTT_8 per primordium.¹² The mean value for a number of cultivars grown in the field in Japan was 17 DTT_{10} per primordium.⁹ Assuming 2 d per primordia, this would be 21 DTT_8 per primordium.

However, in spite of this apparent stability in DTT_8 per primordium, there appears to be some variability between genotypes. While a fall sowing of three cultivars of drastically different maturity failed to show difference in initiation rate,¹¹ Torigoe et al.⁹ found extremes of 15.3 and 20.0 DTT_{10} per primordium. In addition, the fall sowing had 29 DTT_8 per primordium, the cause of which has not yet been determined.

Leaf tip appearance requires 36 to 40 DTT_8 per leaf in many temperate environments. Analysis of data from four sources (Figure 9) indicated that there were 36 DTT_8 per leaf tip. As noted previously, the model assumes that there are 39 DTT_8 per leaf tip after the second leaf. Variability in this value may arise due to genotypic differences or differences between the tropical and temperate environments. Tollenaar et al.²⁸ reported differences as great as 16% of

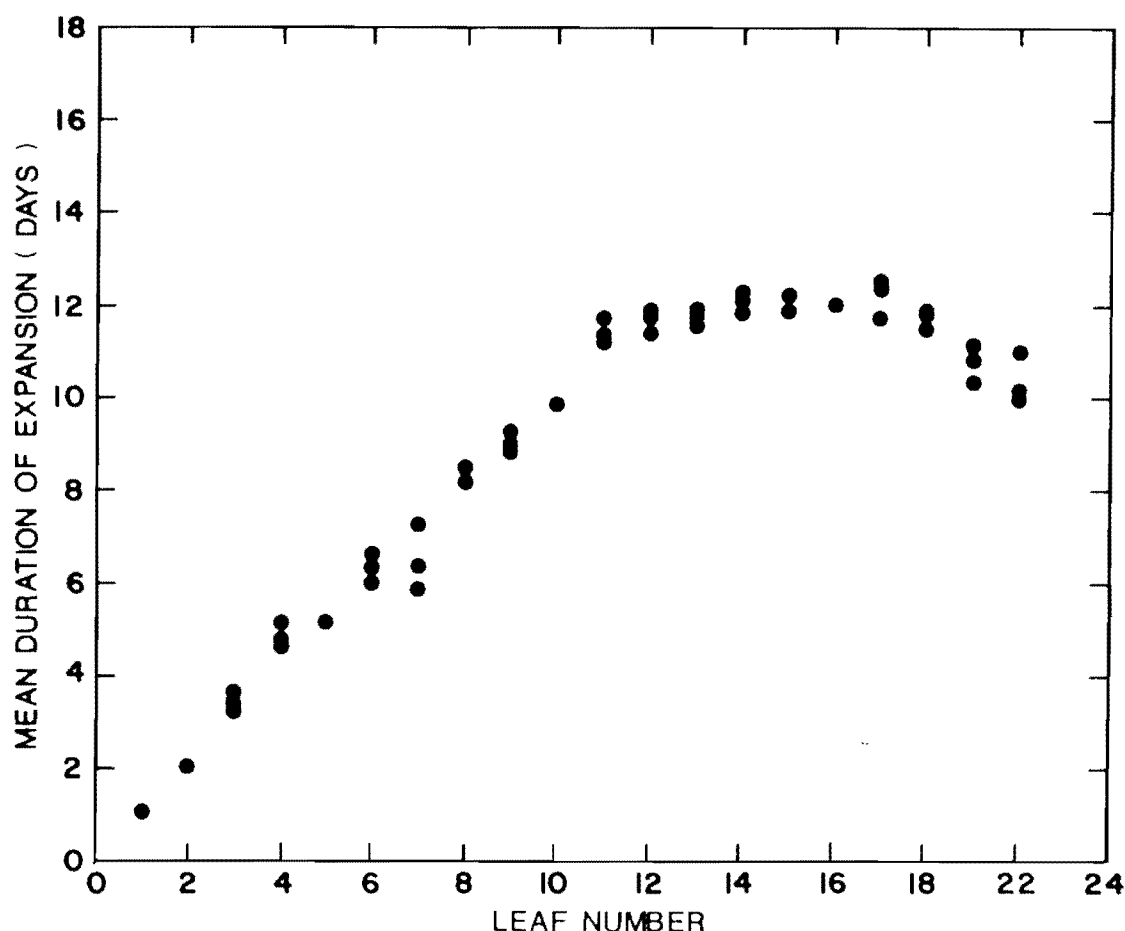


FIGURE 4. Duration of leaf expansion as a function of leaf number for maize hybrid Mo17 \times A634 in the Duke University Phytotron at 25°C.⁴⁰

the mean in the DTT required per leaf tip. Similarly, in a field planting at Temple, TX¹¹ the mean was 37.5 DTT₈ per leaf tip, while values for different hybrids ranged from 34 to 41 DTT₈ (Figure 10). Further attempts at finding maize cultivars with different temperature responses¹¹ consisted of using one inbred, Z7, which was reported as having high growth rates in cool temperatures,²⁹ and two races from Mexico, Sinaloa and Amarillo Salvadoreno, which showed promise of having unusual temperature responses.³⁰ Of the cultivars sown at Temple in 1984, only Z7 had a significantly different rate of leaf tip appearance relative to the commercial hybrid Pioneer 3780 (Figure 11). Plants of the inbred Z7 were weak and not competitive, so even its differences in development could be questioned.

Values for DTT₈ per leaf tip can be 30% greater in tropical areas than in temperate ones. Leaf appearance for 5 sowing dates of 4 cultivars in the Caribbean basin required an average of 50 DTT₈ per leaf tip.³¹ Future research into causes of such deviations will help to make the present model more general.

E. THE GRAIN FILLING PERIOD

Three intervals³² in the silking to physiological maturity (black layer) period are simulated. These phases are a lag phase, a period of nearly linear grain filling called the effective fill period, and the period from the end of the effective fill period to physiological maturity.

Summed DTT₁₀ has been shown to be less variable than days for the interval between silking and physiological maturity for different planting dates.³³ As discussed previously, the rate of development from silking to maturity in the present model uses a base temperature of 8°C. The model assumes a cultivar-specific sum of DTT₈ from silking to maturity.

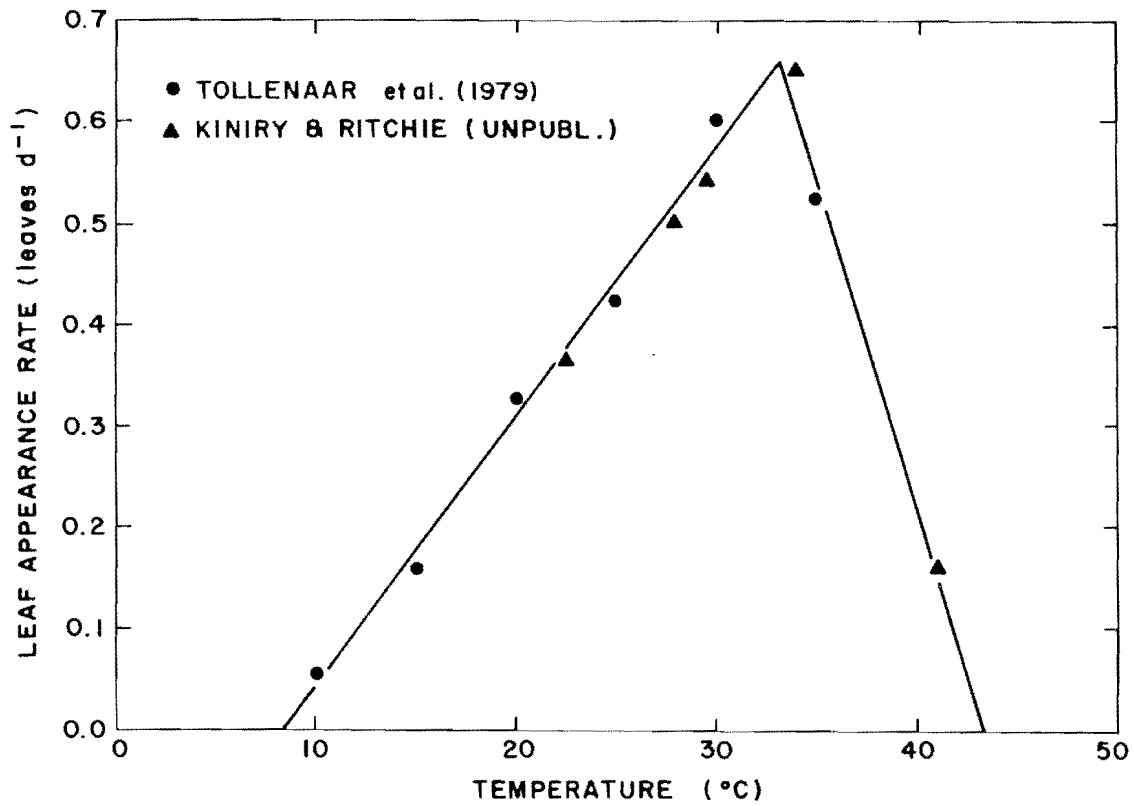


FIGURE 5. Rate of maize leaf tip appearance rate as a function of temperature.

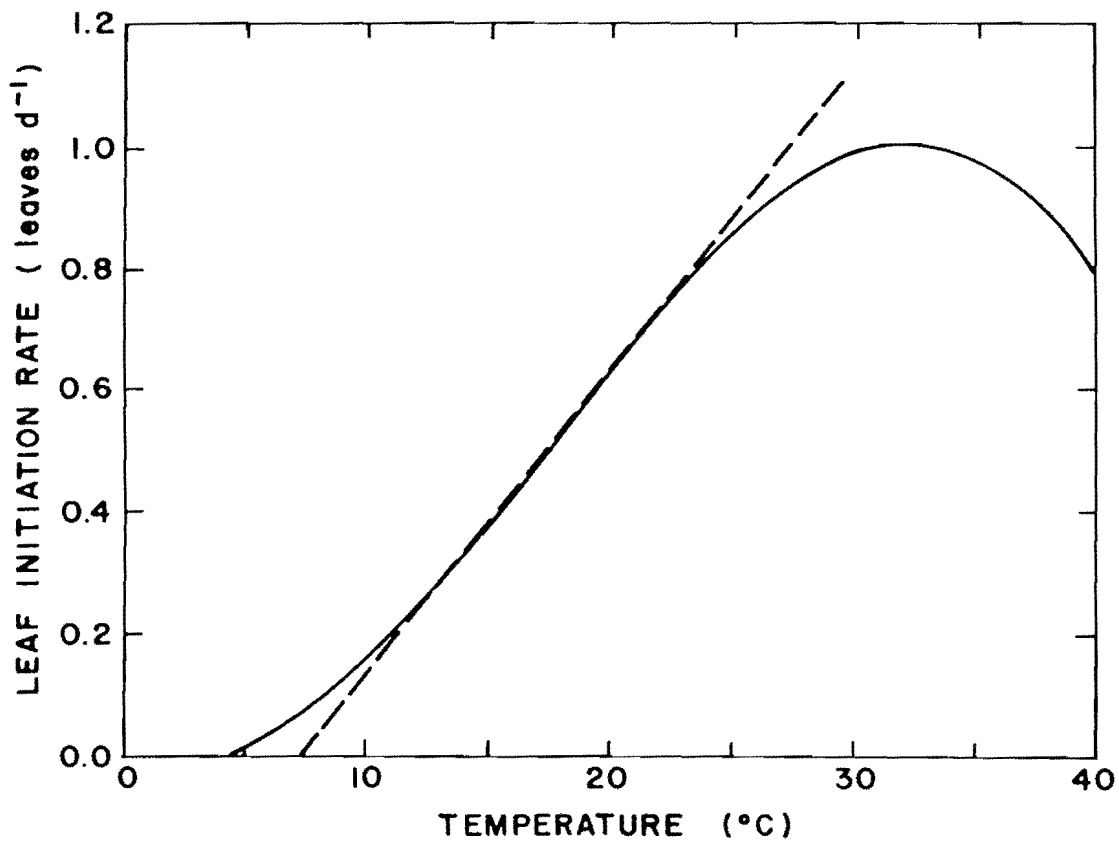


FIGURE 6. Rate of maize leaf initiation rate as a function of temperature. The solid line represents a function derived by Warrington and Kanemasu.¹²

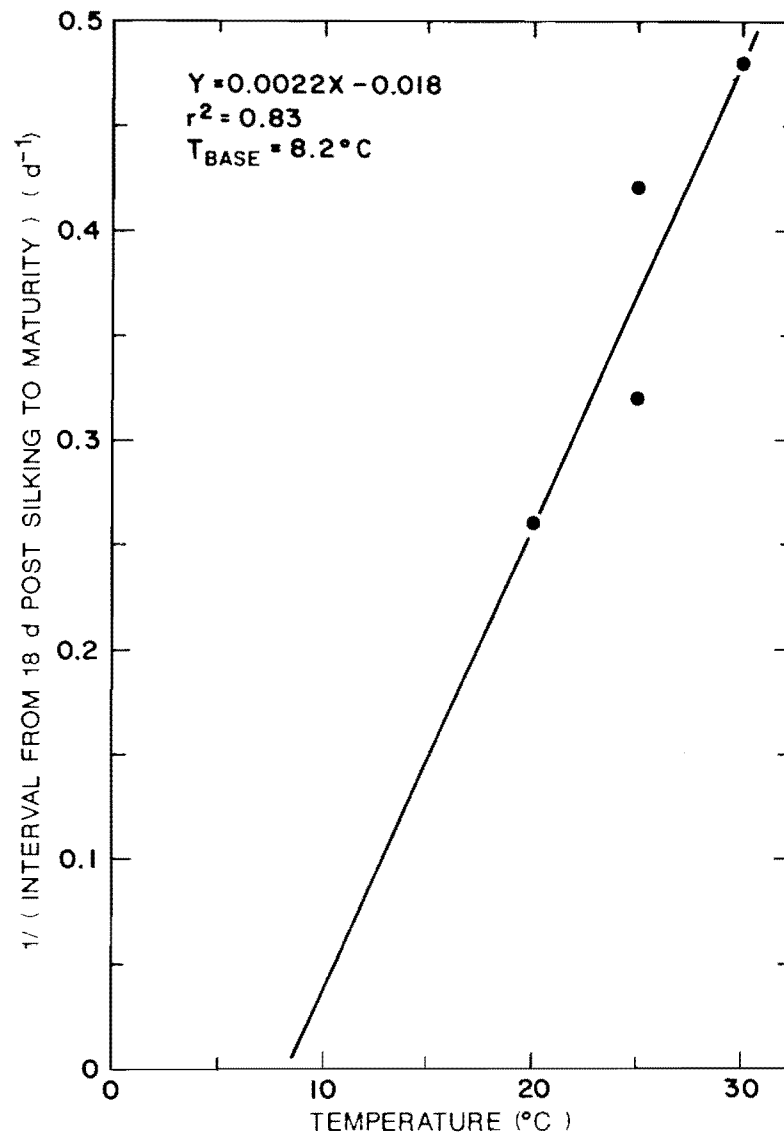


FIGURE 7. Development rate as a function of temperature during the silking to maturity interval of maize. Derived from data of Badu-Apraku et al.¹⁹

The DTT for the lag phase has been shown to not differ significantly between cultivars.³⁴ In the present model, this was determined to be 170 DTT_g.³⁵ The effective fill period begins at the end of the lag phase and ends when 95% of the total DTT_g from silking to physiological maturity have been accumulated. The last developmental phase, from the end of the effective fill period to physiological maturity, requires the last 5%. A statement was added to the model to prevent delayed maturity if cool temperatures prevent DTT accumulation during this last, short stage. If the DTT is 2.0 or less on a day during this last stage, maturity is assumed to occur.

Values for P5, the required sum of DTT_g from silking to maturity, ranged from 665 for B14 × OH43 to 940 for Pio × 304C (Table 2). These values were derived from field data with dates of silking and maturity measured.

II. TEST RESULTS

Test results will be confined to the TLNO produced and days to anthesis (measured pollen shed and simulated silking). Tests were conducted on an independent data set from Russell.²⁵ A long season, photoperiod sensitive inbred, Tx601, and an intermediate maturity hybrid, L36

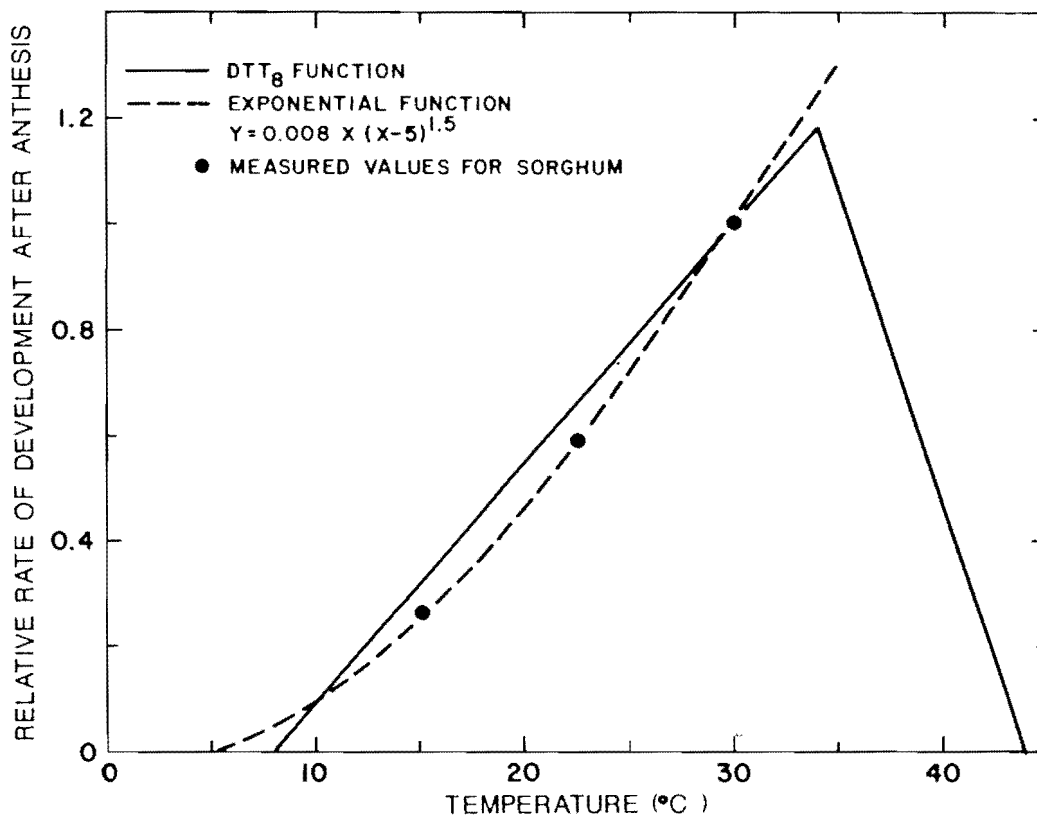


FIGURE 8. Relative rate of development as a function of temperature during the anthesis to maturity interval. The dashed line represents a function fit to data for sorghum.²⁰ The solid line is the function used in the maize phenology model.

× B14A, were evaluated. Simulated and measured TLNO were compared as were simulated days and measured days to anthesis. Values for P1 and P2 were determined using measured values for three plantings in North Carolina. Data for this location were not included in the evaluation.

Simulated TLNO was never greater than three leaves different from measured for either the hybrid or the inbred (Tables 3 and 4). The mean errors were 0 and 1, respectively, for the cultivars. In both cases the standard deviation was 2. There was no tendency for the greatest errors to be in the warmer or cooler environments. Likewise, in contrast to findings of Bonhomme et al.,³⁶ errors showed no obvious relationship to temperature near tassel initiation (Tables 3 and 4). The three largest negative errors were in California, Iowa, and South Dakota. The value from Hawaii was one of the two with the largest positive error. However errors in the similarly warm Florida location were never greater than 1.

The small range of variability in TLNO for the hybrid was not explained by the simulated values, but the model simulations accounted for much of the variability in TLNO of Tx601. The r-squares for the regression of measured TLNO as a function of simulated TLNO had values of 0.18 for the hybrid (not shown) and 0.54 for Tx601 (Figure 12). The slope for Tx601 was 0.77, fairly close to the ideal value of 1.0.

The model did a better job of accounting for differences in days to anthesis than for differences in TLNO. Regressions of measured days to pollen shed on simulated days to silking had slopes of 0.80 and 0.77 and values for r-square of 0.76 and 0.68 (Figure 13). For both cultivars the regression lines were close to the 1:1 line. There were three data sets for L36 × B14 and two with Tx601 with errors of 10 d or greater (Tables 3 and 4). The means of the errors were 2 and -1 and the values for South Dakota were 6 and 7. As was the case with predictions of TLNO, there was no apparent trend for the greatest errors to occur at the most northern or southern locations.

TABLE 2
Genotype-Specific Values for the DTT_g from Seedling Emergence to the End of the Juvenile Phase (P1): The Days Delay in Tassel Initiation for Each Hour Increase in Photoperiod (P2), and the DTT_g from Silking to Physiological Maturity (P5)

Cultivar	P1 DTT _g	P2 dh ⁻¹	P5 DTT _g
Southern Canada			
CORN281	110	0.30	—
CP170	120	0.00	680+
F7 × F2	125	0.00	732+
LG11	125	0.00	737+
PIO 3995	130	0.30	—
Northern U.S.			
INRA260	135	0.00	739+
EDO	135	0.30	—
A654 × F2	135	0.00	751+
DEKALB × L71	140	0.30	—
F478 × W705A	140	0.00	670+
PIO 3901	144	0.30	—
NE, IA, IL, NC			
PIO 3720	180	0.80	685
A632 × W117	187	0.00	730+
PIO 3382	200	0.70	—
PIO 3780	200	0.76	685
C281	202	0.30	685
Southern NE, Southern IA, Southern IL, Southern IN			
PIO 511A	220	0.30	685
PIO 3183	260	0.50	750
W64A × F546	240	0.30	741+
A632 × VA26	240	0.30	766+
W64A × W117	245	0.00	—
NEB 611	260	0.30	720
B14 × 0H43	265	0.80	665
B8 × 153R2	218	0.30	760
Central MS and KS to NC and Southward			
PIO 3147	255	0.76	685
WF9 × B37	260	0.80	710
PV82S	280	0.50	750
PV76S	260	0.50	750
B56 × C131A	318	0.50	700
B73 × Mo17	220	0.52	880
NC + 59	280	0.30	750
McCurdy 6714	265	0.30	825
Tropical Hybrids			
H610	340	0.52	840
PIO × 304C	390	0.52	940

+ Data⁴⁵ assumes maturity occurred at 30% grain moisture.

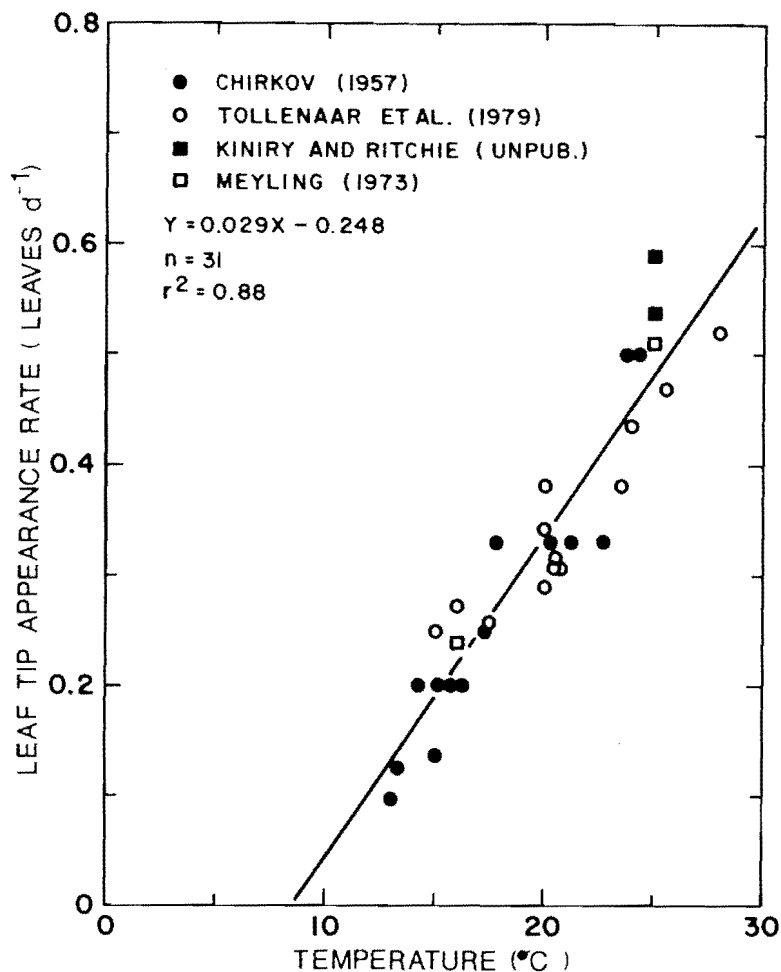


FIGURE 9. Leaf tip appearance rate of maize as a function of temperature with data from four sources.

III. DISCUSSION

A function for possible cooling effects on development rate (Figure 14), derived from unpublished results of Bonhomme and Derieux,³⁷ was tested on the data of Russell²⁵ without success. Predictions were less accurate than without the function. Likewise, rate of change of daylength at seedling emergence and error in predictions failed to show any relationship in contrast to the large effect this rate had on phenology of wheat and barley.^{38,39} Controlled environment work with maize and wheat⁴⁰ also failed to show any relationship between rate of change of daylength and leaf appearance rate.

While results of Warrington and Kanemasu¹² and Bonhomme and Derieux³⁷ indicate leaf appearance rate per day or per DTT_g was positively correlated with photoperiod, we did not incorporate this into the model. Gmelig-Meyling⁴¹ failed to find a consistent effect of photoperiod on leaf appearance rate when solar radiation exceeded $200 \text{ cal cm}^{-2} \text{ d}^{-1}$. Coligado and Brown⁴ found a slight decrease in rate of leaf initiation as photoperiod increased from 10 to 20 h. Swan et al.⁴² found that inclusion of photoperiod into a leaf emergence model failed to improve predictions.

Likewise, drought effects may show a 1.0 to 1.5 difference in leaf number visible during development, but by silking this difference in development rate will have largely disappeared.^{43,44}

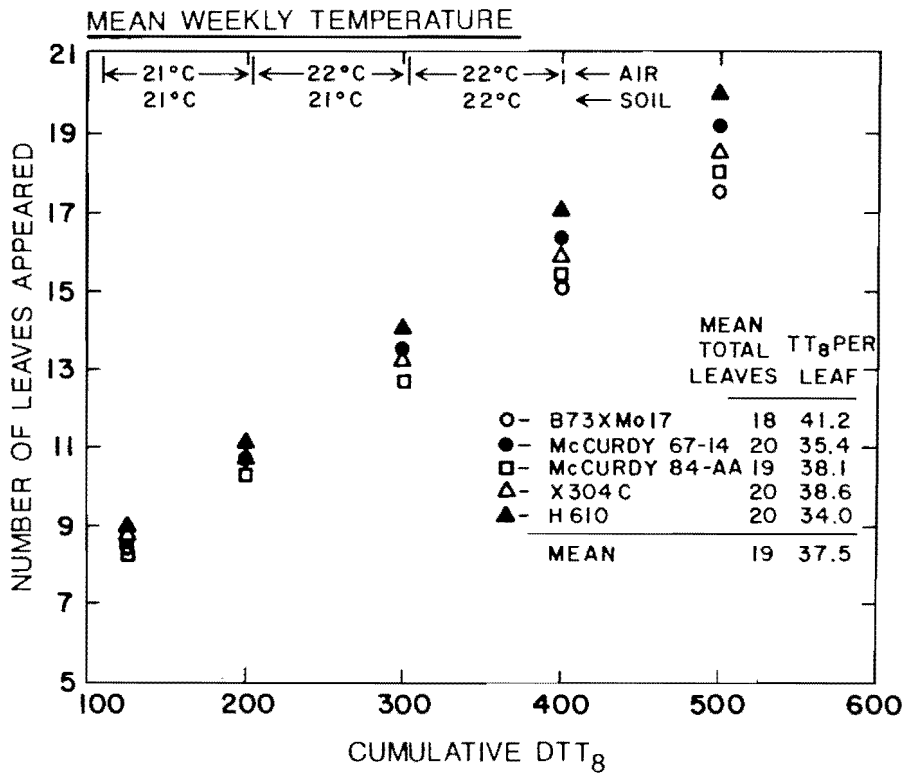


FIGURE 10. Number of leaf tips emerged as a function of cumulative DTT_8 for five maize hybrids grown in the field at Temple, TX.¹¹

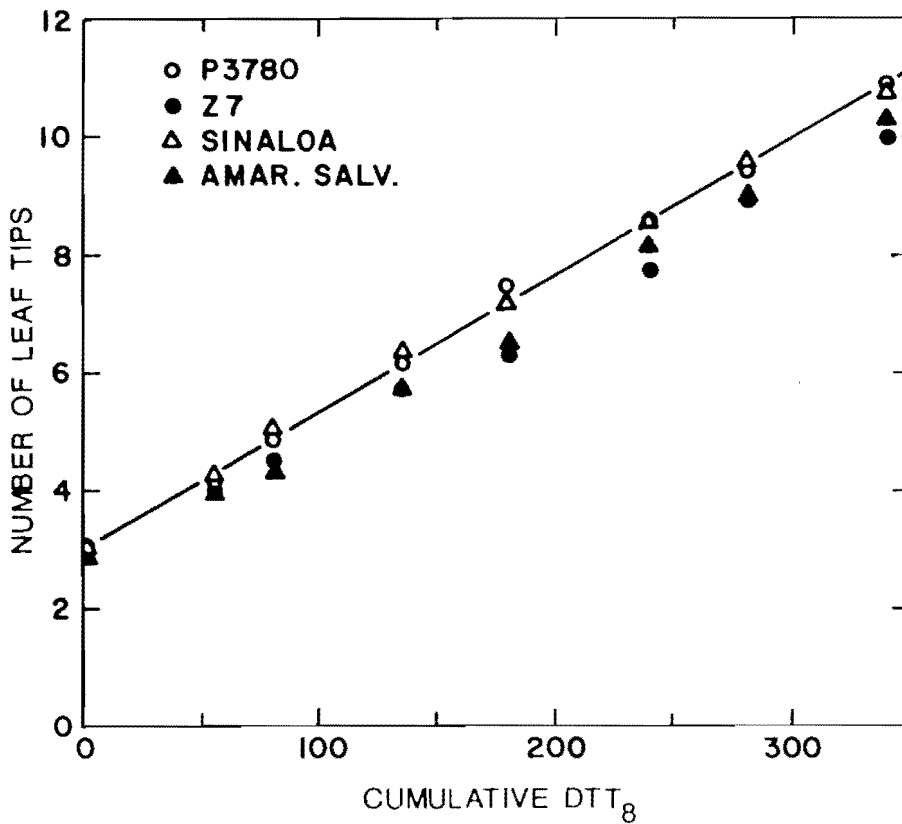


FIGURE 11. Number of leaf tips emerged as a function of cumulative DTT_8 for four maize cultivars grown in the field at Temple, TX.¹¹

TABLE 3
Measured (Ms.) and Simulated (Sim.) TLNO and Anthesis Dates (the latter was a comparison of measured days to pollen shed with simulated days to silking; there were 14 plantings of maize hybrid L36 × B14A)²⁵

Location	LAT	Planting date (day of year)	TLNO			Anthesis date			Temp+ (°C)
			Sim.	Ms.	Dif.	Sim. (d since seedling emergence)	Ms.	Dif.	
Honolulu, HI	21.18	99	23	—	—	56	47	9	24.3
Honolulu, HI	21.18	164	24	21	3	53	43	10	25.2
Homestead, FL	25.27	265	21	20	1	50	51	-1	25.3
Homestead, FL	25.27	302	20	20	0	56	69	-13	21.4
Goulds, FL	25.27	284	21	20	1	55	55	0	24.9
Knoxville, TN	35.58	122	23	22	1	61	60	1	24.8
Blacksburg, VA	37.16	161	23	20	3	69	64	5	23.2
Davis, CA	38.33	142	22	25	-3	68	66	2	20.4
Columbia, MO	38.55	123	23	—	—	64	64	0	25.1
Ames, IA	42.00	140	22	25	-3	61	64	-3	16.7
Guelph, Ontario	43.31	147	22	24	-2	84	77	7	18.5
Brookings, SD	44.18	136	22	25	-3	74	76	-2	19.4
Fargo, ND	46.53	143	24	26	-2	77	75	2	21.7
Morden, Manitoba	49.08	143	24	25	-1	86	72	14	16.6
Mean					0			2	
SD					2			6	

+ Mean temperature for the five days centered on the simulated date of tassel initiation.

TABLE 4
Measured (Ms.) and Simulated (Sim.) TLNO and Anthesis Dates (the latter was a comparison of measured days to pollen shed with simulated days to silking; there were 13 plantings of maize inbred Tx601)²⁵

Location	LAT	Planting date (day of year)	TLNO			Anthesis date			Temp+ (°C)
			Sim.	Ms.	Dif.	Sim. (d since seedling emergence)	Ms.	Dif.	
Honolulu, HI	21.18	99	27	—	—	64	60	4	25.5
Honolulu, HI	21.18	164	29	26	3	63	57	6	26.2
Homestead, FL	25.27	265	24	24	0	58	65	-7	25.1
Homestead, FL	25.27	302	24	23	1	73	84	-11	23.7
Goulds, FL	25.27	284	25	25	0	67	69	-2	24.3
Miss. St., MS	33.44	99	28	26	2	72	75	-3	22.7
Knoxville, TN	35.58	122	31	28	3	76	81	3	22.2
Blacksburg, VA	37.16	161	30	28	2	90	81	9	24.4
Davis, CA	38.33	142	29	29	0	90	83	7	19.7
Columbia, MO	38.55	123	31	—	—	81	83	-2	23.7
Ames, IA	42.00	140	28	31	-3	75	86	-11	25.3
Brookings, SD	44.18	136	29	30	-1	97	93	4	18.7
Fargo, ND	46.53	143	31	29	2	101	99	2	2.9
Mean					1			-1	
SD					2			7	

+ Mean temperature for the 5 d centered on the simulated date of tassel initiation.

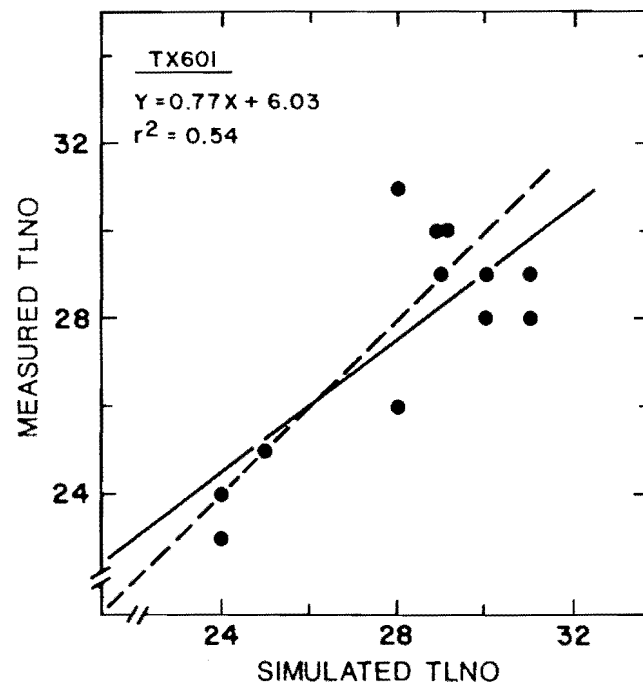


FIGURE 12. A comparison of simulated and measured TLNO for maize inbred Tx601. Data are from Russell.²⁵

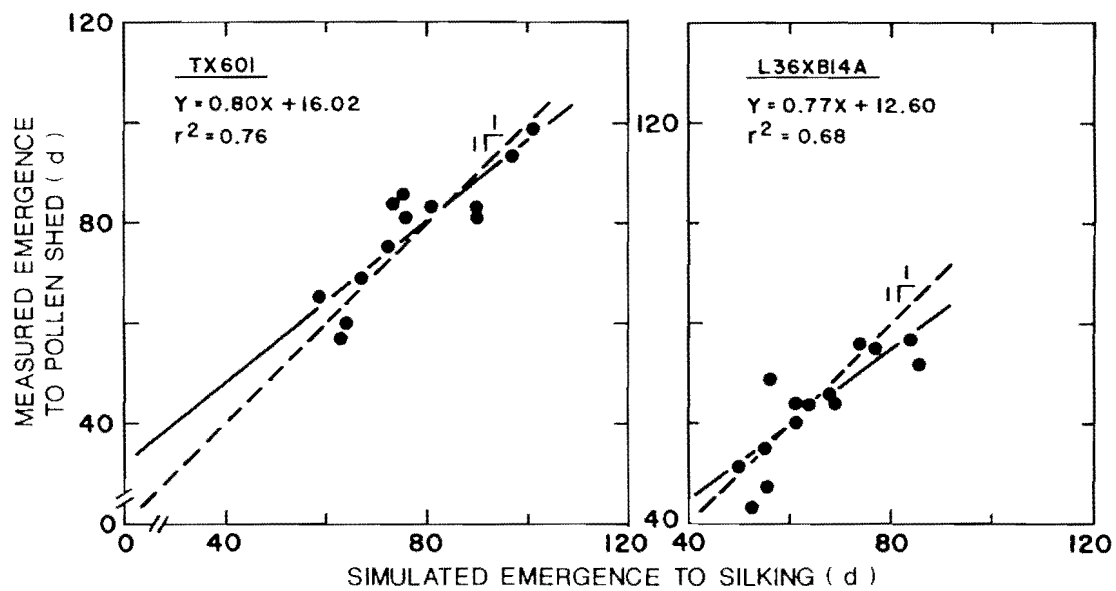


FIGURE 13. Comparisons of simulated days to silking and measured days to pollen shed for maize inbred Tx 601 and maize hybrid L36 × B14A. Data are from Russell.²⁵

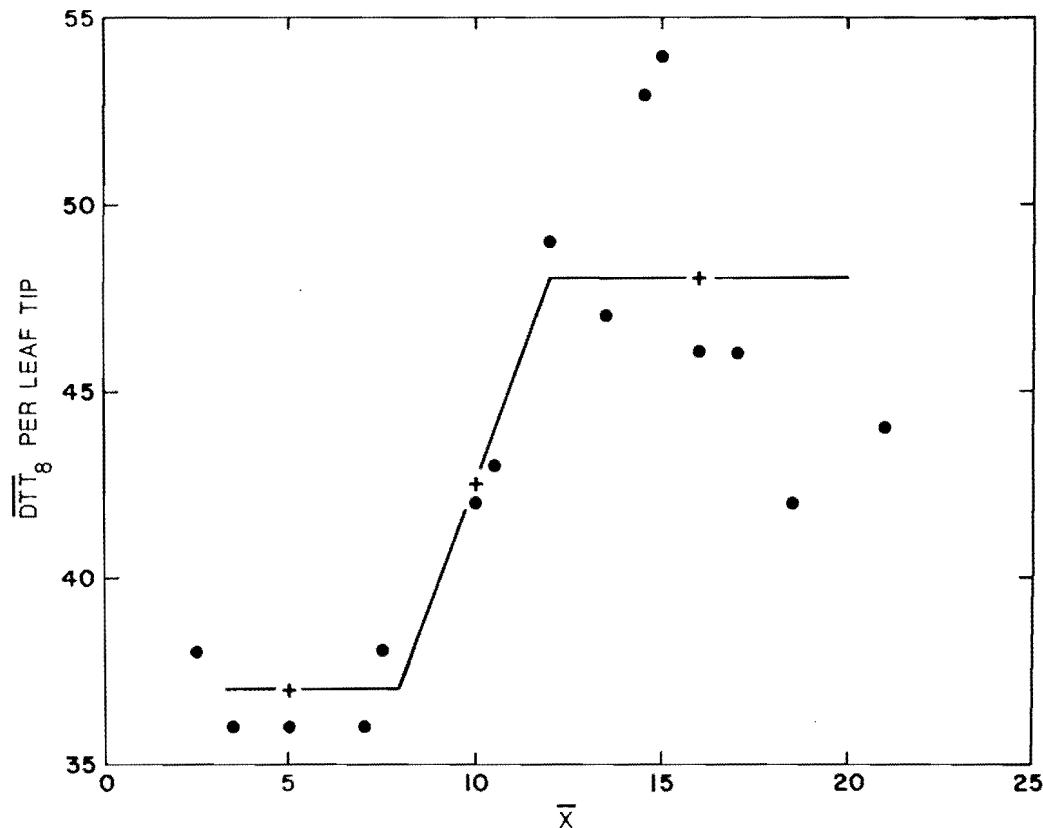


FIGURE 14. Mean DTT_8 per leaf tip for maize cultivars LG11, B73 \times Mo17, and INRA 508 as a function of mean daily minimum temperature ($\bar{X}=T_{min}$) for the 4 coolest nights in the 30 d following seedling emergence.

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