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An Enzyme Kinetic Equation to Estimate Maize Development Rates[1]

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ABSTRACT

While use of thermal units to predict development rate is very old, nearly all thermal unit equations are empirical and have no theoretical basis. The poikilotherm equation is unique in that it has a theoretical basis and accounts for both high and low temperature nonlinear development rate responses; however, this equation had never been applied to field grown plants. In this study, the equation, along with more traditional thermal unit equations, was applied to field grown maize (*Zea mays* L.).

Three hybrids of maize were grown in two plantings at two locations in each of 2 years. The coefficient of variation across mean unit sums for each planting was used as the criterion for comparing six other equations with the poikilotherm equation. Other equations used were the growing-degree-day (GDD) 40, the GDD 50, the 50 to 86 cut-off, the heat-stress, the Ontario corn heat unit equations, and day count.

The GDD 40 equation best described the planting to tassel initiation interval. Silking appeared to be delayed by high temperatures, thus the tassel initiation to silking interval was best described by the heat-stress equation. There appeared to be no difference between different thermal unit equations for the silking to black layer formation and planting to black layer formation intervals. Even though the poikilotherm equation was based on physiology of the plant, it was no better than the other methods of accumulating heat units.

Additional index words: Growing-degree-day, Models, Thermal units, Temperature effects, *Zea mays* L.

RESEARCHERS have been quantifying plant development rates in response to temperature for more than 200 years. Reamur (18) in 1735 introduced a thermal unit concept for predicting plant development time. Since then, there have been numerous attempts at improving thermal unit or growing degree day (GDD) equations.

The simplest GDD equations (1, 16, 22) subtract the mean daily temperature (T_m) from a base temperature (T_a) to get the heat units (HU):

$$HU = T_m - T_a. \quad [1]$$

where all temperatures are reported as centigrade unless otherwise specified. The two most common of these are the GDD 40 and GDD 50 equations with 4.4 and 10 base temperatures, respectively. The simple GDD equations assume development ceases below a base temperature. Also, they assume development rate is a linear function of temperature above the base temperature. This may create two problems. If development rate response is actually non-linear for temperatures close to the base, as has been found for maize (*Zea mays* L.) coleoptile growth rate by Lehenbauer (17), then to fit the mid-range response, the base temperature will be higher than the actual threshold temperature for development. This causes an underprediction of development at the lower temperatures. Also, as temperatures increase beyond 30, maize growth rate has been found to decrease (17). If this is the case with development, the simple GDD equations will overpredict development at high temperature.

The 50 to 86 (50–86) cutoff equation (13) is the same as the 10 base GDD equation except all temperatures greater than 30 are set equal to 30. Thus, the rate of development at temperatures greater than 30 is assumed to be equal that at 30. This prevents extremely high predictions of development rate at high temperatures.

The detrimental effects of high temperature on development are estimated by the heat stress (HTSTR) equation (13). It is identical to the 10 C base GDD day equation except it assumes development rate decreases linearly with temperatures above 30. This more closely estimates the growth rate curve of Lehenbauer (17) than the other GDD methods.

The Ontario corn heat unit equation (OCHU) (6) gives another estimate of the effects of high temperature on development. The daily OCHU units are the average of two components, a Y_{max} value and a Y_{min} value. The Y_{max} value is from a second degree polynomial function of daily maximum temperature (T_{max}):

$$Y_{max} = 3.33(T_{max} - 10.0) - 0.084(T_{max} - 10.0)^2. \quad [2]$$

The Y_{min} value is a linear function of the daily minimum temperature (T_{min}):

$$Y_{min} = 1.8(T_{min} - 4.44). \quad [3]$$

This equation assumes two different responses of development rate to temperature, one for day and one for night. While it has a smoother response curve for development rate decrease above 30, it fails to describe any non-linear response near the base temperature.

The use of thermal units to predict development has not been restricted to plants. Stinner et al. (20) found that the cabbage looper, *Trichoplusia ni* (Hubner), has a non-linear development rate response to tempera-

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Table 1. Planting dates for the 2 years.

	Location and planting			
	Rollins bottom		South farm	
Year	First	Second	First	Second
1978	17 May	26 May	13 June	21 June
1979	10 May	1 June	9 May	12 June

MATERIALS AND METHODS

The experiment was conducted on a coarse-silty, mixed, acid, mesic, Typic Udifluvent of the Sharon series at Rollins' Bottom and a fine, montmorillonitic, mesic Udollic Ochraqualf of Mexico series at the South Farm, both near Columbia, Mo., in 1978 and 1979. Two planting dates were used both years at each location. Three single-cross hybrids of maize were grown. Listed in order of maturity from earliest to latest, these were 'Great Lakes 3102,' 'MFA 5802,' and 'McCurdy MSX 67-14.' Using the GDD50 equation, these reached maturity about 1,450, 1,600, and 1,700 thermal units from planting, respectively. These three hybrids will hereafter be referred to as A, B, and C, respectively.

Experimental Design and Planting Dates. In all plantings, hills were double planted and thinned with 30 cm between hills and 76 cm between rows for a plant density of approximately 44,000 plants/ha. Each plot was eight rows wide and 18 hills long. Half the rows were set aside to sample destructively for tassel initiation. All other sampling was done on the other rows.

Planting dates (Table 1) were timed to obtain the maximum differences in temperature with minimum differences in photoperiod. High soil moisture in the spring of 1978 delayed the early plantings.

The occurrence of six phenological events were observed. These consisted of tassel initiation (TI), ear emergence (EE), tassel emergence (TE), pollen shed (PS), silk emergence (SE), and black layer formation (BL). Of these, only tassel initiation and black layer formation were observable by destructive sampling techniques.

Destructive Measurements. Tassel initiation samples consisted of at least five competitive plants randomly chosen from each planting of each hybrid every other day. Plants were taken from areas of the plots separated from the non-destructively sampled plants. Each plant was taken back to the lab and dissected under a binocular microscope. A plant was considered as having initiated its tassel when the apex had visible branches as shown in Fig. 2 C of Bonnett (5). The date of tassel initiation was taken as the 1st day that at least 50% of the sample had initiated tassel.

Sequential sampling of the same ear was used to determine black layer formation. The fourth, fifth, and sixth kernels from each end of a kernel row were sampled. In 1978, ears from six plants per replication were observed Monday, Wednesday, and Friday. In 1979, five were observed every other day. The plants were chosen randomly from the non-destructively sampled plants. Each husk was peeled back to expose a kernel row. The individual kernels were removed and split in the germinal-abgerminal plane. Black layer was determined by the method of Daynard (11). We assumed removal of kernels had no effect on the development of the remaining kernels. Care was taken not to sample two adjacent kernel rows in an effort to minimize damage to kernels prior to sampling. After sampling an ear, the husk was replaced and secured by a rubber band to prevent exposure of the kernels. A plant was taken to be physiologically mature when three or more of the six kernels had reached black layer.

Non-destructive Measurements. For each hybrid and planting date, 60 plants were chosen randomly in lots of six and tagged. For each plant, days until tassel emergence, pollen shed, ear emergence, and silk emergence were recorded. This was done every other day in 1978 and Monday, Wednesday, and Friday in 1979. The criteria for the four intermediate stages were as follows:

a. tassel emergence when the tassel first became visible
b. ear emergence when the ear shoot could be seen in the leaf axil.
c. pollen shed when at least one anther was extruding from a floret
d. silking when at least one silk was visible.

Daily maximum and minimum temperatures were taken at standard weather stations at each of the locations.

Application of the Poikilotherm Model to Maize Development. Sharpe and DeMichele (19) supplied constants for maize shoot elongation based on constant temperature data from Lehenbauer (17). Although these data are not for development rates, Coelho and Dale (7) and Gilmore and Rogers (13) used them successfully to describe development rates. By using these constants, we were testing how well this non-linear function described development rate. The PK equation with these constants was used to find hourly values for development rate. The hourly temperature values from the field were calculated from a sine curve assuming daily minimum and maximum temperatures occur at 0500 and 1500 hours, respectively. These times came from observation of temperature curves during the growing season. The hourly values for development rate varied from zero to 1/24. The daily sums were then a relative rate varying from zero to one. These daily units, which we designated "optimum days," are similar to the FT units used recently by Coelho and Dale (7).

Because of a limited tassel initiation sample size, the timing from planting to tassel initiation was considered to be deterministic, thus, each planting of a hybrid had one date for tassel initiation. Development times for the later stages were stochastic, on a per plant basis.

Other Thermal Unit Equations. The 2 GDD equations used were the GDD 40 and GDD 50. With these, the daily minimum temperature was taken to be equal to the base if it was less than the base. The units accumulated were simply the mean of the maximum temperature and the adjusted minimum temperature, minus the base temperature. The 50–86 equation used a base of 10 and a cut-off maximum of 30. The HTSTR equation differed from the 50–86 equation only in that all temperatures above 30 decreased the maximum value used in the mean by the amount they exceeded 30. In all the equations, the number of heat units for 1 day was always positive or zero. Instead of reporting accumulated units for the various methods in their actual units, we standardized all the summed units. The units accumulated by an equation were divided by the number accumulated by the equation in a 30 constant temperature day. Thus all unit sums are reported in "optimum days."

The Ontario corn heat unit (OCHU) equation was the only truly nonlinear equation compared to the poikilotherm equation. The OCHU equation was implemented as described by Brown (6).

We used the coefficient of variation (C.V.) as the criterion for comparing precision of development rate equations. Several authors (2, 4, 10, 13, 21) have used C.V. to standardize the comparisons of the different thermal unit equations.

RESULTS AND DISCUSSION

Ten intervals were examined. These intervals were:
Planting to Tassel Initiation (PL-TI)
Planting to Ear Emergence (PL-EE)
Planting to Tassel Emergence (PL-TE)
Planting to Pollen Shed (PL-PS)

so new constants for the PK equation may be calculated. Even if with new constants the PK equation is a better predictor of development rates, the complexity of the equation may prevent its general use. It does, however, set a precedent for future work with theoretical models of development rate.

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