

Simulating maize development using a nonlinear temperature response model

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Abstract

Temperature is a key environmental variable that regulates growth and development of plants. The rate of change in growth and development in response to temperature is usually nonlinear with initial quasi-exponential to linear response reaching an optimum after which the rate declines steeply. This response is well mimicked by the beta distribution model whose parameters are biologically meaningful unlike polynomials. A simple simulation model of maize development was developed in which the simplified beta function was incorporated to represent temperature responses of various developmental events. The model was calibrated with data from the literature. Predictions by the simulation model compared reasonably well with independent experimental results. Implementation of nonlinear temperature response using the beta function in crop simulation model appeared to be promising, and should improve the capability of the model to simulate temperature responses mechanistically.

Media summary

This paper introduces a simulation model for maize development as a function of temperature and photoperiod using the simplified beta distribution function.

Key Words

phenology, leaf initiation, leaf appearance, crop model, beta function, *Zea mays* L.

Introduction

Development of maize plants is primarily driven by temperature. The relationships between maize developmental rates and temperature have been commonly quantified using linear functions based on a thermal-time concept, such as growing-degree-days (GDD). Metabolic responses of plants to temperatures are not necessarily linear even during the increasing phase, and have an optimum after which the rates decline steeply. Several attempts have been made to overcome the shortcomings of the linear thermal-time concept by using various types of equations including bilinear, exponential, Arrhenius, and polynomial models. Among these, the beta distribution function has received much attention as an alternative to describe temperature response of plants. The beta distribution function is flexible and requires only biologically meaningful parameters (Yin et al. 1995). Yan and Hunt (1999) evaluated a simplified version of the beta function with only three parameters. In addition to temperature, photoperiod is known to regulate the number of leaves per plant, tassel initiation, and anthesis in maize. The present paper introduces a simple simulation model for predicting vegetative development of maize using the simplified beta distribution model.

The model

Simplified beta distribution function

The simplified beta distribution function evaluated by Yan and Hunt (1999) is represented by the following equation:

$$r = R_{\max} \cdot \left(\frac{T_{\text{ceil}} - T}{T_{\text{ceil}} - T_{\text{opt}}} \right) \cdot \left(\frac{T}{T_{\text{opt}}} \right)^{\frac{T_{\text{opt}}}{T_{\text{ceil}} - T_{\text{opt}}}} \quad (1)$$

The rate of development is represented by r . T is mean air temperature as input variable. T_{opt} is the optimal temperature at which the maximal rate of development (R_{max}) occurs. T_{ceil} is the ceiling temperature at which development ceases. This equation assumes that the base (or minimal) temperature is zero. Response curve of the equation is illustrated in Figure 1.

Simulation of maize development

The simplified beta function was used to calculate the rates of emergence, primordia initiation, tip appearance, and ligule appearance of leaves as a function of daily average air temperature. Yan and Hunt (1999) showed that T_{opt} and T_{ceil} were similar among different developmental events in maize. Based on this, fixed values of T_{opt} (= 31.4C) and T_{ceil} (= 41.0C) were used, and R_{max} was the only parameter calibrated with data from the literature (e.g., Warrington and Kanemasu 1983a and 1983b). Tassel initiation, anthesis, and total number of leaves were modelled as a function of temperature and photoperiod as used in Grant (1989). The number of leaf primordia just prior to the inductive phase (i.e., minimum number of leaves without additions due to temperature or photoperiod: L_{min}) was defined as a cultivar specific coefficient (Grant 1989). Parameter values of Eqn (1) were estimated using SAS NLIN procedure (Table 1). Primordia of five leaves were assumed to be present in the embryo of a seed. The model requires day of year, daily average temperatures, and latitude as input, and runs at daily time step.

Table 1. Parameters and their values used in the model.

Description	Parameter	Value	Reference
Optimal temperature	T_{opt}	31.4 C	Yan and Hunt (1999)
Ceiling temperature	T_{ceil}	41.0 C	Yan and Hunt (1999)
Emergence	R_{max}	0.319	Warrington and Kanemasu (1983a)
Leaf initiation	R_{max}	1.05	Warrington and Kanemasu (1983b)
Leaf tip appearance	R_{max}	0.581	Yan and Hunt (1999)
Leaf ligule appearance	R_{max}	0.429	Warrington and Kanemasu (1983b)
Leaf number prior to inductive phase	L_{min}	15	Grant (1989)

Materials and Methods

Maize plants [*Zea mays* L., cv. Pioneer hybrid 3733] was grown in closed sunlit Soil-Plant-Atmosphere-Research (SPAR) growth chambers at 370 or 750 ppm CO₂ with 19/13, 25/19, 31/25, 35/29, or 38.5/32.5°C day/night temperatures at Beltsville, Maryland, USA from June to August 2002. Leaf tip appearance was monitored twice per week during the vegetative stage. Maize plants were also grown in the experimental farm of USDA-ARS in Beltsville from May to October 2002. Leaf tip and ligule appearance rates were investigated weekly or biweekly during the vegetative stage.

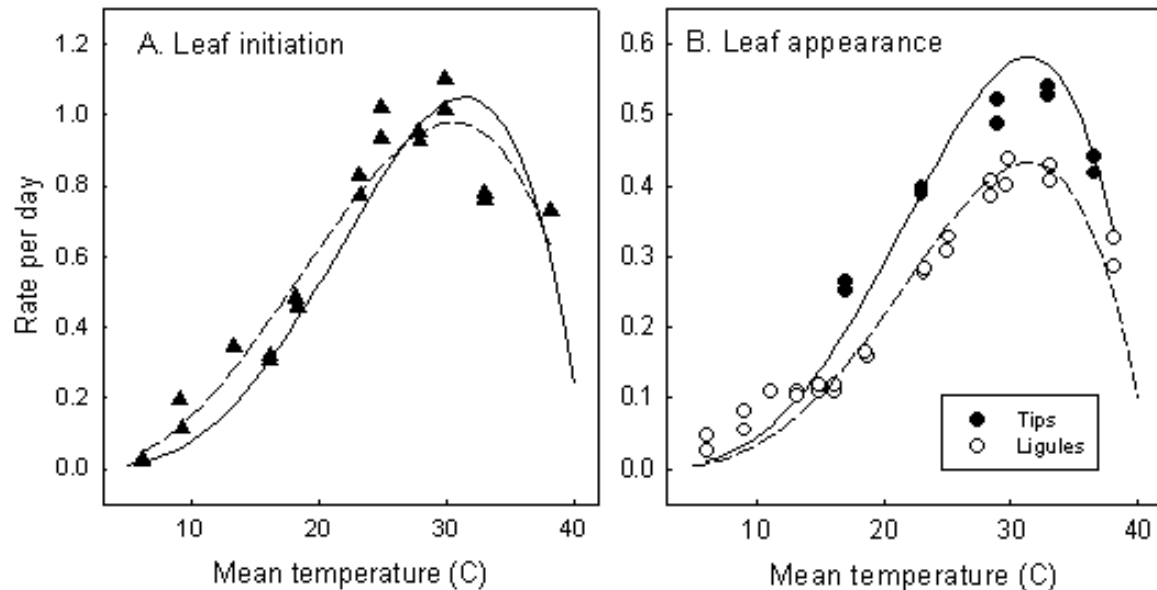


Figure 1. Leaf initiation and appearance rates as a function of daily mean air temperature. (A) Leaf initiation rate. Observations (▲) are from Warrington and Kanemasu (1983b). Solid line represents predictions of the model using parameter values in Table 1. Dashed line represents the best fit of Eqn (1) where all three parameters were fitted with observations. (B) Leaf tip and ligule appearance rates. Observations of leaf tip appearance (●) are from the SPAR chamber experiment. Observations of ligule appearance (○) are from Warrington and Kanemasu (1983b). Solid and dashed lines represent model predictions for tip and ligule, respectively, using parameter values in Table 1.

Results and Discussion

The simplified beta function described the observed patterns of temperature responses well (Figure 1). Based on the results by Yan and Hunt (1999) the estimates of T_{opt} and T_{ceil} were similar for various developmental events, fixed values of T_{opt} and T_{ceil} were used to minimize the number of parameters to be calibrated. This attempt, however, underestimated leaf initiation rate when daily mean air temperatures were lower than 25°C (Figure 1A). The best fit of Eqn (1) to the observed leaf initiation rates resulted in $T_{opt} = 30.5$ and $T_{ceil} = 42.7$ C with somewhat lower R_{max} estimated to be 0.978 (Figure 1A). Initiation of leaf primordia is a key developmental event from which other developmental events and growth rates could be derived. The best fit of Eqn (1) to leaf tip appearance rates from the SPAR chamber experiment yielded the estimates of $T_{opt} = 31.0$, $T_{ceil} = 43.3$ C, and $R_{max} = 0.524$ (data not shown). These results suggest that all three parameters of the simplified beta function may have to be estimated for different developmental events independently. The rates of leaf tip and ligule appearances from the field experiment were compared with the simulation results from the model with fixed T_{opt} and T_{ceil} estimates (Figure. 2). The model was capable of predicting the rates of leaf tip and ligule appearance of maize plants grown in the field reasonably well.

Incorporation of nonlinear temperature response function in a crop model is critical when simulating crop responses under the environment where temperature fluctuation is large near inflection point, rapidly increasing or decreasing region, or optimal region of the temperature response of the crop. Realistic representation of the nonlinear temperature response of crop development is important for predictions of the impacts of global warming on crop production. A great deal of information on developmental responses to temperature in maize is available in the literature. Many experimental reports expressed the temperature response with linear or polynomial models of GDD (Hesketh and Warrington 1989; Stewart et al. 1998). Converting the information expressed in GDD to developmental rates as used in the beta distribution model can be easily done using statistical methods without fitting actual experimental data to the model. Overall, implementation of the simplified beta distribution function into a simulation model of maize development was straightforward and feasible. Further work may include incorporating the beta function to temperature response of cell division and growth so as to mechanistically predict key developmental and growth kinetics such as leaf and internode extensions.

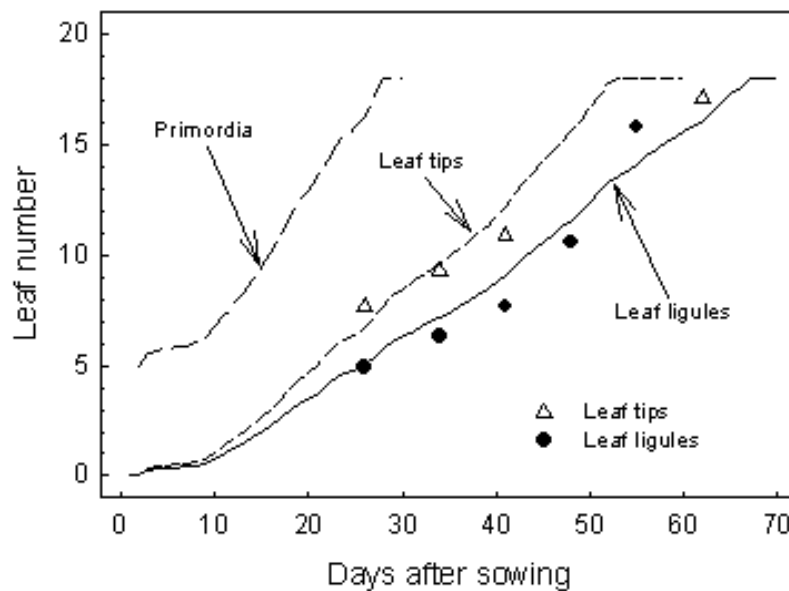


Figure 2. Simulation of leaf initiation, tip appearance, and ligule appearance. Symbols represent observations from the field experiment. Long-dashed, short-dashed, and solid lines represent predicted rates of primordia initiation, tip appearance, and ligule appearance of leaves, respectively.

Conclusions

A simple simulation model of maize development was developed using the simplified beta function. The present paper examined the feasibility of implementing the beta function into a simulation model. Strength of using the simplified beta function is that it follows the nonlinear nature of temperature responses of plants well using minimal number of parameters that are biologically meaningful. Implementation of the simplified beta function within the crop simulation model and calibration using data from the literature were fairly straightforward. Simulation results compared well with the independent field experimental data suggesting that this approach could be a promising direction for crop models.

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