MODELLING LEAF PRODUCTION AND CROP DEVELOPMENT
IN MAIZE (Zea mays L.) AFTER TASSEL INITIATION UNDER
DIVERSE CONDITIONS OF TEMPERATURE AND
PHOTOPERIOD

C.J. BIRCH¹, K. G. RICKERT¹ and G.L. HAMMER²

¹ The University of Queensland, Gatton College, 4345, Queensland, Australia.

² QDPI/CSIRO, Agricultural Production Systems Research Unit, Toowoomba, 4350, Queensland, Australia.

Short Title: Leaf production and crop development

Telephone of Corresponding Author; +61 7 54601302
FAX of Corresponding Author +61 7 54601112
Email of Corresponding Author  C.Birch@uq.edu.au

FOR PUBLICATION IN: Field Crops Research

January 1998
MODELLING LEAF PRODUCTION AND CROP DEVELOPMENT
IN MAIZE (Zea mays L.) AFTER TASSEL INITIATION UNDER
DIVERSE CONDITIONS OF TEMPERATURE AND
PHOTOPERIOD

Abstract

Prediction of the initiation, appearance and emergence of leaves is critically important to the success of simulation models of crop canopy development and some aspects of crop ontogeny. Data on leaf number and crop ontogeny were collected on five cultivars of maize differing widely in maturity and genetic background grown under natural and extended photoperiods, and planted on seven sowing dates from October 1993 to March 1994 at Gatton, South-east Queensland. The same temperature coefficients were established for crop ontogeny before silking, and the rates of leaf initiation, leaf tip appearance and full leaf expansion, the base, optimum and maximum temperatures for each being 8, 34 and 40 °C. After silking, the base temperature for ontogeny was 0 °C, but the optimum and maximum temperatures remained unchanged. The rates of leaf initiation, appearance of leaf tips and full leaf expansion varied in a relatively narrow range across sowing times and photoperiod treatments, with average values of 0.040 leaves (°Cd)^{-1}, 0.021 leaves (°Cd)^{-1}, and 0.019 leaves (°Cd)^{-1}, respectively. The relationships developed in this study provided satisfactory predictions of leaf number and crop ontogeny (tassel initiation to silking, emergence to silking and silking to physiological maturity) when assessed using independent data from Gatton (South eastern Queensland), Katherine and Douglas Daly (Northern Territory), Walkamin (North Queensland) and Kununurra (Western Australia).
Introduction

The performances of two simulation models of maize (AUSIM-Maize, Carberry et al. 1989, Carberry and Abrecht 1991) and a model proposed by Muchow, Sinclair and Bennett (1990) (which will be referred to as the Muchow-Sinclair model) were inadequate when tested over a wide range of cultivars and environmental conditions (Birch, 1995, Birch 1996a, b). AUSIM-Maize was derived from CERES-Maize (Jones and Kiniry 1986) and contains many similar procedures for predicting crop ontogeny and leaf number. Because the number of leaves responds to photoperiod (Warrington and Kanemasu 1983, Bonhomme et al., 1991), CERES-Maize and AUSIM-Maize also include a photoperiod-sensitivity term. The Muchow-Sinclair model does not. AUSIM-Maize predicts the number of leaves per plant, from the thermal time from emergence to tassel initiation. Thermal time is calculated using base, optimum and maximum temperatures ($T_b$, $T_{opt}$ and $T_{mx}$) for plant development of 8, 34, and 44 °C and a photoperiod-sensitivity constant ($P_2$, ($^\circ$Cd$h^{-1}$)). This increases thermal time from emergence to tassel initiation by a constant number of degree days per hour when photoperiod exceeds 12.5 h.

In AUSIM-Maize, the number of leaves initiated by a plant prior to tassel initiation is estimated from thermal time for germination (assumed by the model to occur 1 day after sowing) to tassel initiation and a constant thermal interval for initiation of successive leaves ($^\circ$Cd leaf$^{-1}$). The six leaves present in the embryo are added to estimate final leaf number. This procedure predicted final leaf number poorly when applied to data of Birch (1989), Muchow (1988a,b), R. C. Muchow (pers. comm. 1992) and Karanja (1993), which include several cultivars and sowing times at Gatton, South eastern Queensland, and Katherine, Northern Territory, Australia. However, since the accuracy of prediction of final leaf number depends on prediction of tassel initiation, the coefficients used to predict tassel initiation may have been the source of the errors in prediction of final leaf number.
Final leaf number is used elsewhere in the model to calculate various aspects of crop ontogeny and growth, including individual leaf area, total plant leaf area, leaf area index, duration of the interval from tassel initiation to silking, dry matter accumulation and leaf senescence. For instance, prediction of time of tassel initiation to silking relies on final leaf number, rate of leaf tip appearance and thermal time from emergence to tassel initiation. In both CERES-Maize and AUSIM-Maize is an implicit relationship between time from emergence to silking and final leaf number, because the time from emergence to silking is simply the product of final leaf number and rate of full leaf expansion.

The Muchow-Sinclair model uses a different approach. Final leaf number is an input which determines crop ontogeny. This simple approach is useful because of the limited range of observations in many experiments. For example, total leaf number and time of tasselling are commonly measured, but the time of tassel initiation is not.

A field trial was conducted to provide data to improve the accuracy and generality of prediction of crop ontogeny and leaf number in maize models. The experiment involved five cultivars planted on seven dates in 1993-94 under natural and extended (16.5 h) photoperiod.

The objectives of the study were to:

(i) quantify rates of leaf initiation, appearance of leaf tips and full leaf expansion in thermal time,
(ii) develop a robust means of predicting the thermal and chronological duration of the intervals from emergence to silking and tassel initiation to silking, and
(iii) quantify the thermal and chronological duration of silking to physiological maturity, under a wide range of temperature and photoperiod conditions; and
(iv) validate predictions of final leaf number, duration of intervals tassel initiation to silking and silking to physiological maturity using independent data.
MATERIALS AND METHODS

Field experiment

A field experiment was conducted at The University of Queensland, Gatton College (latitude 27° 33' S, longitude 152° 20' E) on a moderately fertile black earth, Lawes series (Schafer et al., 1986). Soil analyses showed that nitrogen was deficient, and zinc marginal when assessed against accepted standards (Anon., 1991).

Five cultivars of maize (Pacific Hycorn 42, De Kalb DK529, De Kalb XL82, Pacific Hycorn 83 and QDPI Barker) were sown on each of seven sowing dates (1 October 1993, 29 October 1993, 26 November 1993, 30 December 1993, 27 January 1994, 24 February 1994 and 29 March 1994 (sowings 1 to 7 respectively). The genetic backgrounds of the cultivars are described elsewhere (Birch et al., 1998).

Two photoperiods (natural and extended to 16.5 h) were used. The natural photoperiods, including civil twilight, two weeks after seedling emergence were 13.7, 14.4, 14.8, 14.5, 13.9, 13.1 and 12.2 h for each sowing date, respectively (calculated using the method outlined in Jones and Kinyi (1986)). These changed by, at most, 10 minutes during the inductive phase of plants grown under natural photoperiod conditions.

Full details of the experimental design are presented in Birch et al. (1998). Briefly, a split-split plot design with three replications was used. Photoperiod treatment, maintained for the full crop life cycle, was the main plot, sowing date the sub-plot, and cultivar the sub-sub-plot, each randomised within the next higher level. Two rows, 0.60 m apart and 6 m long, in each sub-sub plot were sown to each cultivar on each sowing date, using designs similar to those used by Chase and Nanda (1967) and Stevens et al. (1986). Twenty seeds m⁻¹ of row were sown to ensure an established population of 9 plants m⁻¹ of row (15 plants m⁻²), which declined to 7.5 m⁻² after plants in one row
were removed for determination of tassel initiation. A 3 m guard between the sub-plots prevented the natural photoperiod treatment being affected by light from the extended photoperiod treatments. This guard area was also sown with maize. Irrigation and nutrients were applied at rates to maintain non-limiting conditions, and insect pests and weeds were controlled as required.

**Data collection**

**Temperature**

Daily maximum and minimum temperatures were recorded by an automatic weather station located adjacent to the field experiment. There was a period of high maximum temperatures in January 1994, and low minimum temperatures in May, June and early July (Figure 1). The first frost occurred in late May 1994, but there was no visible frost damage until early June 1994, and then only to sowing 7.

**Time of emergence**

The time of emergence (50% emergence (9 plants m⁻¹) of viable seed sown) was assessed from plant counts in two 1 m linear quadrats.

**Tassel Initiation**

Assessment of tassel initiation is given in detail in Birch et al. (1998). Briefly, three randomly located plants were removed every 2 to 3 d, starting 12 d after emergence. The apex was exposed under a stereoscopic microscope, and its development compared with standard micrographs (Moncur 1981). Sampling continued until the apex reached a rating of at least four (4) on a one to six scale (one being the vegetative apex and six being the apex clearly having the branched form of a tassel). Tassel initiation was recorded when the graph of apex rating against time (d) from emergence reached 2, i.e the apex had elongated and ridges had formed at its base.
Number of leaves

The fifth leaf was tagged on each of five randomly located plants in the row used for non-destructive sampling in each sub-sub-plot. Later, the tenth leaf was tagged if the fifth leaf had senesced before all leaves had expanded fully. Total leaf number present and number of fully expanded leaves on each tagged plant were counted at approximately weekly intervals from shortly after emergence until tasselling in sowings 2 to 6, but only until frost damaged the plants in sowing 7.

Tasselling and silking

The five tagged plants were also used for the determination of time of tasselling and silking. Tasselling was recorded when anther sacks were extruded on 25 to 50% of the tassel on 50% of the tagged plants. Similarly, silking was recorded when silks were extruded, and remained green (red-green on Barker), on 50% of plants.

Physiological maturity

Physiological maturity (PM) was determined by regularly sampling two cobs per sub-sub-plot to assess the presence of black layers at the base of the grain, indicating that no further accumulation of grain mass was possible (Daynard and Duncan 1969). Grains were removed from the base, middle and distal end of each of the cobs. PM was recorded when at least 75% of the grains in each sub-sub-plot had black layers.

Derived data

Calculation of the rates of leaf initiation, leaf tip appearance and full leaf expansion

The rate of leaf initiation (leaves (°Cd)^{-1}) was calculated from thermal time from germination to tassel initiation, using \( T_b \), \( T_{opt} \) and \( T_{mx} \) of 8, 34 and 40 °C (\( T_{gt} \)), as established for emergence to tassel initiation in Birch et al. (1998). These temperatures were also applied to the germination (assumed to occur 1 d after sowing, since non-
limiting conditions of water supply were maintained) to emergence interval. An allowance of 6 leaves was made for leaves in the embryo. The equation used was:

\[
\text{Rate of leaf initiation (leaves (°Cd)^{-1})} = \frac{\text{Total leaf number -6}}{\text{TT}_{gti}}
\]

(1)

To determine the rate of leaf tip appearance, the number of tips that had appeared from the whorl was regressed linearly on thermal time (°Cd) from emergence (TT_{ae}). The equation used was:

\[
\text{Number of leaf tips} = a + b \times \text{TT}_{ae}
\]

(2)

The constant \( a \) represents those leaf tips that are present at emergence, and those that appear more rapidly just before tasselling, and \( b \) is the rate of leaf tip appearance (leaf tips (°Cd)^{-1}).

The rate of full leaf expansion was calculated by regressing the number of fully expanded leaves on the thermal time since emergence (TT_{ae}), for all leaves to the fifth last leaf. The regression used was:

\[
\text{Number of fully expanded leaves} = a \times \text{TT}_{ae}
\]

(3),

where \( a \) = the rate of full leaf expansion (leaves (°Cd)^{-1}).

For the last four leaves, which reached full leaf expansion more rapidly than other leaves, a comparable equation was applied, using thermal time from full expansion of the fifth last leaf until all leaves were fully expanded.

Equation to predict time of silking from final leaf number and rate of appearance of successive leaf tips

Linear, non-linear and discontinuous functions (combinations of linear only or linear and non-linear), were explored to relate duration of tassel initiation to silking to final leaf number, the rate of leaf tip appearance, and rate of full leaf expansion, or a
combination of these variables. The equation with the highest coefficient of determination was retained.

**Data analysis**

*Experimental data*

Analysis of variance for leaf number tested the independent and interactive effects of photoperiod extension, sowing time and cultivar, using the MGLH (Multiple General Linear Hypothesis) procedure in SYSTAT (Wilkinson, 1990).

*Regression*

Linear regressions were calculated either by MGLH in SYSTAT (Wilkinson 1990) or SIGMAPLOT (Kuo and Fox, 1993). Optimised intercepts and coefficients for curvilinear relationships were calculated with the iterative procedure NONLIN (nonlinear estimation) in SYSTAT (Wilkinson 1990).

The coincidence of the regressions for various cultivars and sowing dates was tested by analysis of variance of the intercepts and slopes. For sowing dates an additional test (F), proposed by Zar (1974), was used to test the significance of the separate model for each sowing against one overall combined model:

\[
F = \frac{[(SS_t - SS_p)/2(s-1)]/(SS_p/df_p)}{SS_t}
\]  

(4)

where

- \( SS_t \) = residual sum of squares for regression fitted to all data
- \( SS_p \) = pooled residual sum of squares for the individual regressions
- \( s \) = number of sowing dates
- \( df_p \) = residual degrees of freedom of pooled data
Optimisation by DEVEL

An optimisation program, DEVEL (Holzworth and Hammer 1992) was used to determine the temperature and photoperiod responses of each cultivar for tassel initiation to silking and silking to physiological maturity. The concept and use of DEVEL is described extensively in Birch et al. (1998). Briefly, though, DEVEL is based on the concept that:

\[ \text{Rate of development (d}^{-1}) = R_{\text{opt}} \times f(T) \times f(PP) \]

where

- \( R_{\text{opt}} \) = Optimum rate of development;
- \( f(T) \) and \( f(PP) \) are functions of temperature and photoperiod.

DEVEL contains a library of temperature and photoperiod functions that can be used separately or in combination to examine the effects of temperature and photoperiod. DEVEL takes initial starting conditions together with the temperature and photoperiod conditions for the period under consideration to calculate \( f(T) \) and \( f(PP) \). To minimise the risk that optimised values of the parameters reported here are inaccurate, numerous runs of DEVEL were used for each cultivar for tassel initiation to silking and silking to physiological maturity. Substantially different starting conditions were used to guard against the identification of local optima, and to assess whether they converged, giving the same optimised values. Thus, the potential for the optimised values being artefacts of the starting conditions, or an erroneous selection from possible multiple solutions is minimised, but cannot be eliminated (Mayer et al., 1995).

Data for Hycorn 83 (March sowing) and Barker (February and March sowings) were excluded from the optimisations for silking to physiological maturity, due to uncertainty of timing of physiological maturity, because of slow and variable development of black layers in both cultivars. Also, Barker had very prolonged silking in these two sowings, making determination of silking and silking to physiological maturity difficult.
Comparison of predicted values and observed data

Both linear regression of predicted on observed values and root mean square deviation (RMSD) were used to compare predictions arising from this study and independent observed data.

Leaf number

Final leaf number, estimated from thermal time from germination to tassel initiation and the rate of leaf initiation determined in the present study, was compared with the observed final number of leaves in independent data sets. Since the date of germination was not measured in all experiments, it was assumed to be 1 d after sowing in those experiments which were planted into moist soil, or one day after irrigation, when irrigation was applied after sowing. Since accurate data on time of tassel initiation was available for only 32 of the data sets listed in Table 1, tassel initiation and final leaf number for an additional 27 data sets in Table 1 were estimated using genetic coefficients for the basic vegetative period and photoperiod sensitivity (Birch et al. 1998).

Time of silking

Two approaches to prediction of silking were taken. The first predicts thermal time from emergence to silking, calculated as the product of final leaf number and rate of full leaf appearance, assuming that end of leaf growth and silking are simultaneous (Jones and Kiniry 1986). Where time of emergence was not available in the data sets listed in Table 1, it was assumed to occur at the same thermal time after germination as in similar trials planted on comparable dates in the same location. This expands the number of data sets for independent evaluation of predictions using final leaf number and rate of full leaf expansion to predict time of silking.
The second approach, used in CERES-Maize and AUSIM-Maize, predicts duration of tassel initiation to silking. It relies on final leaf number and rate of leaf tip appearance. For this approach, an equation was developed from the present study. The comparisons of predicted with observed time (d) from tassel initiation to silking uses only the data in Table 1 for which both final leaf number and time of tassel initiation are available.

*Duration of silking to physiological maturity*

The data sets listed in Table 1 were used for comparison of predicted and observed duration of silking to physiological maturity. Predictions were made using optimised thermal durations of silking to physiological maturity derived in this paper for Hycorn 42, De Kalb DK529, De Kalb XL82, Hycorn 83 and Barker. For other cultivars, the thermal durations were recalculated (using the revised temperature coefficients derived in this paper) from those provided by Carberry and Abrecht (1991), or, for Hycorn 40, Hycorn 50, GH5019 and GH5019wx, the September data set of Karanja (1993).

**Results**

*Leaf production and final leaf number*

*Sowing time, cultivar and photoperiod effects on leaf number*

Data on final leaf number were presented in an earlier paper (Birch et al., 1998), and are not repeated in detail here. In summary, photoperiod extension increased the number of fully expanded leaves at tassel initiation, total leaf number at tassel initiation and final leaf number in all cultivars in sowings 1 to 5, but not in sowings 6 or 7. There were differences among sowing times in the natural photoperiod treatment - as photoperiod increased, number of fully expanded leaves present at tassel initiation, and total leaf number at tassel initiation increased. Differences also occurred between cultivars, whether under natural or extended photoperiod, the slower maturing cultivars e.g. Barker, having more leaves than the quicker maturing cultivars e.g. Hycorn 42.
Temperature and photoperiod effects on rates of initiation of leaves, appearance of leaf tips and full expansion of leaves

Rate of initiation of leaves

There was no significant difference in rate of leaf initiation between photoperiod treatments (0.040 ± 0.001 leaves °Cd⁻¹) or among cultivars (0.039 ± 0.001 to 0.041 ± 0.001 leaves °Cd⁻¹). However, there were differences among sowings. Rate of leaf initiation was similar in sowings 2, 4 and 5 (average 0.037 ± 0.001 leaves °Cd⁻¹, r² = 0.99), but higher and similar in sowings 3 and 6 (0.041 ± 0.001 leaves °Cd⁻¹, r² = 0.99). (Final leaf number, needed to calculate the rate of leaf initiation, was not available for sowings 1 and 7). The mean rate of leaf initiation was 0.040 leaves °Cd⁻¹, equivalent to a thermal interval between initiation of successive leaf primordia of 25 °Cd leaf⁻¹, was used in subsequent analyses, as the range in rates of leaf initiation was small.

Rate of appearance of leaf tips

There was no effect of photoperiod extension on either the constant a or the rate of appearance of leaf tips (Equation 2). Also, there were no differences in rate of appearance of leaf tips among cultivars, and no sowing date by cultivar interaction. There were, however, differences among sowing times (Table 2). When tested for coincidence, the regressions for sowings 3 and 6 are similar, but different from those for the other sowings, which were also coincident. Also, regressions for the combined data for sowings that had similar rate of appearance of leaf tips, and for all data are shown in Table 2. It is clear from the standard errors in Table 2 that, although significant differences occurred, they were small, and an average of 0.021 leaves °Cd⁻¹ (equivalent to a thermal interval of 47.6 °Cd leaf⁻¹) is appropriate to all cultivars.
Rate of full leaf expansion

Extension of photoperiod did not affect the number of fully expanded leaves until the final number of leaves on individual cultivars grown under natural photoperiod treatments was approached. At this time, additional leaves remained to be expanded in the extended photoperiod treatments, and hence, leaf numbers differed in subsequent samplings.

There were significant differences in rate of full leaf expansion of leaves up to the fifth last leaf among sowing dates (Table 3) and cultivars (Table 3), but these were small, and a single equation was adopted.

Number of fully expanded leaves = 0.019*TT_{se} (r^2 = 0.99, P < 0.01, n = 644) (5).

Thus, the rate of full leaf expansion of successive leaves is 0.019 leaves °Cd^{-1}, and the thermal interval between the full expansion of leaves is 52.6 °Cd leaf^{-1}. Similarly, there were few significant differences in the rates of full leaf expansion for the last four leaves, and a common rate of full leaf expansion for these leaves of 0.025 leaves °Cd^{-1} (thermal interval of 40 °Cd leaf^{-1}) is appropriate.

Crop ontogeny

Tassel initiation to silking and silking to physiological maturity

Temperature and photoperiod responses

Photoperiod extension did not affect the duration of tassel initiation to silking or silking to physiological maturity when assessed by DEVEL, though significant responses were found by Analysis of Variance. These significant responses are confounded by different environmental conditions affecting durations of tassel initiation to silking and silking to physiological maturity. The extension of photoperiod...
significantly increased the time from emergence to tassel initiation and the final number of leaves (Birch et al., 1998), and thus the time from emergence to silking. Since results of the DEVEL analysis were unaffected by this confounding factor, they were used in further analyses.

A three-hour broken linear function best described the temperature response, similar to emergence to tassel initiation stage (Birch et al., 1998). The base ($T_b$), optimum ($T_{opt}$), and maximum ($T_{mx}$) temperatures for emergence to tassel initiation (8, 34 and 40 °C) were also found for tassel initiation to silking. However, for silking to physiological maturity a lower $T_b$ (0 °C) was selected. There were no differences in temperature parameters among cultivars.

*Rate of development during silking to physiological maturity*

The optimised rate of development (d$^{-1}$) determined by DEVEL, with $T_b$, $T_{opt}$ and $T_{mx}$ of 0, 34 and 40 °C, is shown for each cultivar in Table 4. There were significant differences among the cultivars, the slower maturing cultivars having longer duration of silking to physiological maturity than the cultivars that mature more quickly.

*Tassel initiation to silking*

Despite a rigorous investigation of alternative equations for the prediction of thermal duration of tassel initiation to silking, a linear relationship, similar to that in AUSIM-Maize, had the highest coefficient of determination, viz:

\[ TT_{tis} = \frac{(\text{Final leaf number} - 3)}{\text{rate of leaf tip appearance}} + 159.0 - TT_{eti}. \quad (r^2 = 0.82)(6) \]

where $TT_{eti}$ is the thermal time from emergence to tassel initiation calculated from the revised $T_b$, $T_{opt}$ and $T_{mx}$, and $TT_{tis}$ is the thermal time from tassel initiation to silking.
Comparison of predictions with independent data

Leaf number

Figure 2 compares predicted and observed final leaf number using thermal time from germination to tassel initiation and the rate of leaf initiation determined earlier in this paper. Figure 2 (a) compares 32 data sets in which observed time of tassel initiation was available, and Figure 2 (b), expands the comparison by including the additional data sets in which time of tassel initiation was estimated using the genetic coefficients for thermal duration of the basic vegetative stage and photoperiod sensitivity (Birch et al. 1998). Overall, both comparisons are satisfactory. Predicted final leaf number was, with two exceptions, within 10% of observed final leaf number in both comparisons. The comparatively small coefficient of determination reflects a few relatively poorly predicted points. However, the RMSD (0.90), is small, indicating satisfactory accuracy of predicted values.

Prediction of silking

(a) From rates of full leaf expansion

Comparisons of predicted and observed time from emergence to silking are presented in Figure 3 for all data sets for which emergence date is either known or estimated. Prediction of silking was generally satisfactory, although there was a tendency to overprediction. The overprediction was more pronounced when leaf expansion was occurring under declining temperature and radiation conditions, and silking occurred in mid to late autumn.
(b) From time of tassel initiation and rate of appearance of leaf tips

Comparisons of predicted (using Equation 6) and observed duration of tassel initiation to silking are confined to the data sets with observations on tassel initiation. Most predictions are close to the observed data, with few points more than 10% above or below the observed data (Figure 4). The RMSD is low, and the intercept and slope of the regression do not differ from zero and unity respectively.

Duration of silking to physiological maturity

Figure 5 shows the comparison of predicted with observed duration of silking to physiological maturity. Most points are close to the 1:1 line, with the exception of a group of underpredicted points for long observed durations of silking to physiological maturity. These points are for the January, February and March 1991 sowings of Hycorn 50, GH5009 and GH 50129wx made by Karanja (1993), which matured under cool to cold conditions. If these nine points are excluded, the predicted durations of silking to physiological maturity are generally accurate (Regression (b), Figure 5, RMSD = 3.8 d). When all points are used, there is a greater tendency for underprediction of long durations of silking to physiological maturity (Regression (a), Figure 5), and a higher RMSD of 7.5 d.

Discussion

Leaf number

The effects of photoperiod extension, sowing date and cultivar on total and fully expanded leaf number at tassel initiation were similar to those for final leaf number, discussed in an earlier paper (Birch et al., 1998). In this paper, data on leaf number are used for calculation of rates of leaf initiation, leaf tip appearance and full leaf. Consequently, the effects of photoperiod extension are considered through these variables.
Rates of initiation of leaf primordia, appearance of leaf tips and full leaf expansion of leaves

The lack of differences in the rates of initiation of leaf primordia (in sowings 2, 4 and 5), appearance of leaf tips (sowings 1, 2, 4, 5 and 7), and full expansion of leaves (sowings 2, 4 and 5), and across cultivars, supports the use of constant values for these leaf production parameters. However, the variations for sowings 3 and 6 suggest that under certain conditions, different values may be needed. These may be caused by effects of temperature just prior to tassel initiation on leaf number as high temperature caused increased leaf number as in cultivar Guelph GX122 used (Tollenaar and Hunter 1981). However, data from the present experiment do not allow further examination of these exceptions, to quantify curvilinearity in the effect of temperature on the rates of one or more of these leaf production processes. Nevertheless, in all cases in our study, the differences were small. Thus the values of 0.040, 0.021 and 0.019 leaves (°Cd)^{-1}, can be used for rates of initiation of leaves, appearance of leaf tips and full expansion of leaves, except for expansion of the last four leaves, when 0.025 leaves (°Cd)^{-1} should be used. However, they may not apply if extremes of temperature or other environmental variables occur. Our results also differ somewhat from those of Muldoon et al. (1984), as they found greater variation among genotypes, and some curvilinearity in the relationship between the rate of leaf expansion and rate of leaf appearance, especially after the thirteenth or fourteenth leaf had appeared. Nevertheless, our results and those of Muldoon et al. (1984) show that the relationship between the number of leaf tips that have appeared and the number of leaves that are fully expanded changes close to the end of leaf growth. Additional research is needed to determine the extent of cultivar differences in leaf appearance and expansion among modern hybrids, and provide further detail on the change in the rate of leaf expansion near the end of leaf production.

Crop ontogeny

Temperature effects

The response of maize to temperature was investigated by the method of Holzworth and Hammer (1992) that has been used successfully by Olsen et al. (1993) for sweet
corn and Birch et al. (1998) for emergence to tassel initiation in maize. The $T_b$, $T_{opt}$ and $T_{mx}$ for crop development from tassel initiation to silking were 8, 34 and 40 °C, the same as for emergence to tassel initiation (Birch et al., 1998). For silking to physiological maturity, they were 0, 34 and 40 °C.

The $T_b$, $T_{opt}$ and $T_{mx}$ until silking are generally consistent with most literature sources, although different values have been reported. For example, Olsen et al. (1993) reported $T_b$ of 5.4 to 6.4 °C for sweet corn, and Warrington and Kanemasu (1983) and Major et al. (1983) found $T_b$ of 7 °C for tasselling. Duburcq et al. (1983), who examined $T_b$ for the various intervals of maize development under field conditions, found $T_b$ of 9 to 13 °C for tassel initiation to cob initiation, followed by 10 °C until silking. There was also some evidence of variation between cultivars in their study. No support was found in the present study for the lower $T_b$ reported by several authors or the higher $T_b$ of Duburcq et al. (1983). Thus, $T_b$ of 8 °C can be applied until silking for cultivars with a wide range in genetic background and crop duration.

For silking to physiological maturity, $T_b$ of 0 °C has been reported from field studies (Lenga and Keating 1990), and that value is used in the Muchow-Sinclair model. However, CERES-Maize and AUSIM-Maize use $T_b$ of 8 °C for the entire crop duration after emergence, and another maize model, CORNF (Stapper and Arkin 1980) uses a base temperature of 10 °C. In this study, $T_b$ of 0 °C was applicable to all cultivars. Apparently the $T_b$ in CERES-Maize, AUSIM-Maize and CORNF is too high for post-silking development, and $T_b = 0$ °C is more appropriate.

Our value of $T_{opt}$ of 34 °C for tassel initiation to silking, and silking to maturity was derived over a wide range of temperature, and is higher than reports from literature: 26 to 28 °C (Cutforth and Shaykewich 1989); 30 °C (Coligado and Brown 1975, Tollenaar et al. 1979, Struij et al. 1985); 28 °C (Warrington and Kanemasu 1983, Derieux and Bonhomme 1982); 26 to 28 °C (Lenga and Keating 1990) and 30 °C used in CORNF (Stapper and Arkin 1980). However, the lower temperatures have usually been derived with a limited range of cultivars in temperate or controlled environments. The notable exception is the study of Lenga and Keating (1990), which used field data from Kenya. Despite the above reports, the present study (which involved temperatures from close to 0 °C to in excess of 44 °C), provides substantial support for $T_{opt} = 34$ °C.
The maximum temperature for crop development ($T_{mx}$) has received much less attention than the base and optimum temperatures, presumably because most studies have been carried out in temperate environments. $T_{mx}$ in the present study of 40 °C, was lower than that used in AUSIM-Maize and CERES-Maize, higher than that found by Cutforth and Shaykewich (1990) (35.5 °C, for two cultivars), but similar to that of Blacklow (1972), Struik (1983) and Shaw (1988). Because of the range in temperature in the present study and the experiments at Katherine, the $T_{mx}$ of 40 °C is deemed most appropriate.

Our results establish that the temperature coefficients for crop development after silking differ from those before silking. We have found a lower $T_{mx}$ after silking than before, and thus confirm the value used by Muchow et al. (1990).

*Photoperiod effects*

No response to photoperiod during tassel initiation to silking was detected by the analysis performed with DEVEL. Longer durations of emergence to tassel initiation under long photoperiods were reported by Birch et al. (1998). The consequential extension of tassel initiation to silking was related to the initiation of additional leaves during emergence to tassel initiation, and was not an effect, *per se*, of extended photoperiod during tassel initiation to silking. The lack of significant effects of photoperiod on the duration from tassel initiation to silking and anthesis contrasts with delays in anthesis, leading to desynchronisation of anthesis and silking, under long photoperiods reported by Struik et al. (1986). The photoperiods under which desynchronisation occurred exceeded those used in the present study. The desynchronisation represents an influence on crop development from tassel initiation to anthesis and silking, specifically a delay in anthesis, under very long photoperiods (24 h). In our study, some reduction in the anthesis to silking interval i.e. delayed anthesis was observed in the tropically adapted cultivar Barker, but was not statistically significant. Thus, it seems that, provided photoperiod does not exceed the maximum used here (16.5 h), crop development after tassel initiation will not be significantly affected by photoperiod, except perhaps in cultivars bred specifically for the tropical areas.
Assessment of predictions against independent data sets

Leaf number

With few exceptions, satisfactory predictions of leaf number occurred for data sets where tassel initiation was available, and also where tassel initiation was estimated from genetic constants for thermal duration of the juvenile stage and photoperiod sensitivity (Birch et al., 1998) (Figure 2a and b). Final leaf number was predicted from Equation 1. A wide range of temperature and photoperiod conditions was covered by the independent data sets, and the generally sound predictions of final leaf number, imply that the constant rate of leaf initiation determined in the present study is applicable. Nevertheless, adjustments may be necessary for some conditions, such as consistently low temperatures, where some curvilinearity in the rate of initiation of leaf primordia can be expected (Warrington and Kanemasu, 1983).

Prediction of the time of silking from the rate of full expansion of leaves

Overprediction of the duration from emergence to silking by using final leaf number and rate of full leaf expansion (Equation 5) is probably a reflection that the simple model ignores variation in rate of full leaf expansion (Table 3). Bos et al. (1997) found that leaf expansion is related to light intensity and supply of assimilates. Our experiment shows that the simple model is a good first approximation for estimating emergence to silking, and that more work is needed to better explain variation in rate of full leaf expansion.

The accuracy of predictions from Equation 5 also depend on the accuracy of prediction of leaf number (unless an observed or nominated value is used). Where a predicted value is used, it’s accuracy depends on the accuracy of prediction of tassel initiation, using the approach described in Birch et al. (1998), and the value for leaf initiation rate reported here.
Prediction of the duration of tassel initiation to silking from final leaf number and rate of appearance of successive leaf tips

Few predictions of the duration of tassel initiation to silking in independent data differed by more than 10% from the observed data, thereby supporting the use of Equation 6. Nevertheless, the tendency was for overprediction of most independent data. The accuracy of predictions from Equation 6 relies on the accuracy of predictions of final leaf number and the value of the rate of appearance of successive leaf tips. In turn, prediction of final leaf number relies on accurate prediction of tassel initiation, as described in Birch et al., (1998), and the value for leaf initiation rate in this paper. There is evidence that the rate of appearance of successive leaves varies with both temperature and light intensity (Gmelig-Meyling, 1973, Bos et al. 1997), factors that may cause the unexplained variation in the rate of appearance of leaf tips in this study (Table 2).

Duration of silking to physiological maturity

The satisfactory prediction of the duration of silking to physiological maturity (Figure 5) in most independent data indicates that the coefficients for the thermal duration of silking to physiological maturity are appropriate. However, there were exceptions: the underprediction of silking to physiological maturity for Hycorn 50, GH5009 and GH5019wx in the January, February and March 1991 sowings contrasts sharply to the accuracy of predictions for GH5009 and GH5019wx (Hycorn 50 was not included) sown in August to December 1991. Apparently, the thermal coefficients for these two cultivars are acceptable, and the poor predictions for the January, February and March sowings of Karanja (1993) are caused by some other factor. A possible explanation is that with cool conditions and slow grain filling, the black layer, used to determine physiological maturity by Karanja (1993) does not form quickly or consistently. The result is an apparent later physiological maturity. In some cultivars, black layer formation can be prolonged (Tollenaar and Daynard, 1978). This phenomenon was
observed in the present study, especially in Hycorn 83 and Barker when grain filling occurred under cool to cold conditions. Thus, the underprediction reported here may be due to inaccuracy in the observed time of physiological maturity in the January to March 1991 sowings of Karanja (1993) rather than a limitation in the method used to predict silking to physiological maturity.

**Conclusions**

The base, optimum and maximum temperatures for crop ontogeny from tassel initiation to silking (8, 34 and 40 °C) are the same as for emergence to tassel initiation. However, after silking, the base temperature is 0 °C, the optimum and maximum temperatures remain 34 and 40 °C. Also, the base, optimum and maximum temperatures for rates of leaf initiation, appearance of leaf tips and full leaf expansion are the same as for crop ontogeny from emergence to silking. Further, there are no differences among cultivars in temperature response before or after silking, or in leaf initiation, leaf appearance and leaf expansion rates. The time from emergence to silking can be calculated from final leaf number and the rate of full leaf expansion. Alternatively, the time from tassel initiation to silking can be calculated from the final number of leaves and the rate of appearance of leaf tips. The differences among cultivars in the duration of silking to physiological maturity can be expressed in thermal time that is specific to individual cultivars and leaf number.

For generality, models must account for genotype characteristics, the number of leaves produced, and the time from emergence to silking. This study has developed and validated a series of equations that predict leaf development and ontogeny from tassel initiation to physiological maturity in diverse maize cultivars in a wide range of environments.
REFERENCES


Stapper, N. and Arkin, G.F., 1980. CORNF: A Dynamic Growth and Development Model for Maize (*Zea mays* L.). Program and Model Documentation No. 80-2. Texas Agricultural Experiment Station, Texas A&M University, College Station, Texas, USA.


Figure 1 Daily maximum and minimum temperatures 1 October 1993 to 9 July 1994 at Gatton, South eastern Queensland. The months are shown at first day of each (Note: S = sowing).
Figure 2. Comparison of predicted and observed final leaf number in (a) data sets where tassel initiation was observed (b) data sets as in (a) for all data sets including those where tassel initiation was estimated as described in Birch et al. (1998). Sources of data are listed in Table 1.
Figure 3. Comparison of predicted and observed duration (d) from emergence to silking in 56 experiments listed in Table 1. Predicted duration to silking was calculated from final leaf number and rate of full leaf expansion. Where time of emergence was not known, it was estimated from similar experiments.
Figure 4. Comparison of predicted and observed duration (d) of tassel initiation to silking for 26 experiments where tassel initiation was recorded.
Figure 5. Comparison of predicted and observed duration (d) of silking to physiological maturity. Regressions for (a) all comparisons on the graph, and (b) for comparisons with data for the January, February and March sowings of Hycorn 50, GH5009 and GH5019wx of Karanja (1993) (circles) excluded.

(a) $y = 24.9 + 0.54x$, $r^2 = 0.75$, RMSD = 7.5 d
(b) $y = 13.7 + 0.76x$, $r^2 = 0.70$, RMSD = 3.8 d
Table 1. Sources of independent observations on leaf number used in comparisons against predicted leaf number by equations and parameters developed in this study.

<table>
<thead>
<tr>
<th>Cultivars</th>
<th>Genetic Coefficients*</th>
<th>Observed time of emergence available</th>
<th>Observed time of TI available</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>De Kalb XL82, Barker</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Gatton</td>
<td>Birch 1989</td>
</tr>
<tr>
<td>De Kalb XL82 and Barker</td>
<td>Yes</td>
<td>Most</td>
<td>Yes</td>
<td>Katherine</td>
<td>Carberry et al. 1989, Muchow and Carberry 1989, Carberry and Abrecht 1991</td>
</tr>
<tr>
<td>Hycorn 40, Hycorn 50 GH5009, GH 5019wx</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Gatton</td>
<td>Karanja 1993</td>
</tr>
<tr>
<td>De Kalb XL82, Barker</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>KatherineDouglas-Daly Kununurra Walkamin</td>
<td>Carberry 1993 pers. comm.</td>
</tr>
<tr>
<td>De Kalb XL82</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Gatton</td>
<td>Muchow 1990, Muchow, pers. comm. 1994</td>
</tr>
<tr>
<td>De Kalb XL82, De Kalb DK529, Hycorn 42, Hycorn 83, Barker</td>
<td>Yes</td>
<td>Yes</td>
<td>**</td>
<td>Gatton</td>
<td>Birch, unpublished data</td>
</tr>
</tbody>
</table>

* Experimentally determined genetic coefficients for thermal duration of emergence to the end of the juvenile stage, and photoperiod sensitivity available from Birch et al. (1998).

** assumed to be same thermal time after germination as in sowing on comparable date in 1993 (Birch 1996)
Table 2. Regressions of the number of leaf tips present on thermal time after emergence calculated from $T_b$, $T_{opt}$ and $T_{mx}$ of 8, 34 and 40 °C, using equation 2, where $a =$ number of leaf tips at emergence, $b =$ leaf appearance rate (leaves (°Cd)$^{-1}$) and se = standard error.

<table>
<thead>
<tr>
<th>Sowing</th>
<th>$a$</th>
<th>se of $a$</th>
<th>$b$</th>
<th>se of $b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.92</td>
<td>0.11</td>
<td>0.021</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2</td>
<td>2.80</td>
<td>0.23</td>
<td>0.020</td>
<td>0.002</td>
</tr>
<tr>
<td>3</td>
<td>3.10</td>
<td>0.28</td>
<td>0.024</td>
<td>0.001</td>
</tr>
<tr>
<td>4</td>
<td>3.42</td>
<td>0.42</td>
<td>0.021</td>
<td>0.001</td>
</tr>
<tr>
<td>5</td>
<td>3.14</td>
<td>0.26</td>
<td>0.020</td>
<td>0.001</td>
</tr>
<tr>
<td>6</td>
<td>2.40</td>
<td>0.20</td>
<td>0.025</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>7</td>
<td>3.27</td>
<td>0.27</td>
<td>0.020</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Lsd (P = 0.05), for sowings 1 to 7:

- Sowings 1, 2, 4, 5 and 7: 2.80, 0.13, 0.020, 0.001
- Sowings 3 and 6: 2.64, 0.27, 0.024, 0.001
- All data: 3.00, 0.15, 0.021, 0.001

The coefficient of determination exceeded 0.95 for all regressions.
Table 3. Regressions of the number of fully expanded leaves, until the fifth last leaf, on thermal time after emergence calculated from $T_b$, $T_{opt}$ and $T_{mx}$ of 8, 34 and 40 °C for (a) sowings and (b) cultivars, using Equation 3, where $a = \text{rate of full leaf expansion (leaves \,(°\text{Cd})^{-1})}$ and $se = \text{standard error.}$

<table>
<thead>
<tr>
<th></th>
<th>$a$</th>
<th>se of $a$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>(a) Sowing</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.017</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>2</td>
<td>0.018</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>3</td>
<td>0.021</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>4</td>
<td>0.018</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>5</td>
<td>0.018</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>6</td>
<td>0.021</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>7</td>
<td>0.020</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>lsd (P = 0.05)</td>
<td>0.0007</td>
<td></td>
</tr>
<tr>
<td><strong>(b) Cultivar</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hycorn 42</td>
<td>0.020</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DK 529</td>
<td>0.019</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>XL82</td>
<td>0.019</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Hycorn 83</td>
<td>0.018</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Barker</td>
<td>0.019</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>lsd (P=0.05)</td>
<td>0.0008</td>
<td></td>
</tr>
</tbody>
</table>

The coefficient of determination exceeded 0.95 for all regressions.
Table 4. Optimum rate of development of five cultivars of maize from silking to physiological maturity, expressed as rate of progress (d⁻¹), real time (d) and thermal time (°Cd), with base, optimum and maximum temperatures of 0, 34 and 40 °C.

<table>
<thead>
<tr>
<th></th>
<th>Hycorn 42</th>
<th>DK 529</th>
<th>XL 82</th>
<th>Hycorn 83</th>
<th>Barker</th>
</tr>
</thead>
<tbody>
<tr>
<td>Optimum rate of development (d⁻¹)</td>
<td>0.029</td>
<td>0.029</td>
<td>0.025</td>
<td>0.025</td>
<td>0.024</td>
</tr>
<tr>
<td>10% confidence interval</td>
<td>0.028-0.029</td>
<td>0.028-0.029</td>
<td>0.025-0.026</td>
<td>0.025-0.026</td>
<td>0.023-0.024</td>
</tr>
<tr>
<td>Minimum chronological duration (d)</td>
<td>35</td>
<td>35</td>
<td>40</td>
<td>40</td>
<td>42</td>
</tr>
<tr>
<td>Minimum thermal duration (°Cd)</td>
<td>1190</td>
<td>1190</td>
<td>1360</td>
<td>1360</td>
<td>1430</td>
</tr>
</tbody>
</table>