

Plant development and leaf area production in contrasting cultivars of maize grown in a cool temperate environment in the field.

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## Abstract

Crop models need accurate simulation of the interdependent processes of crop development and leaf area production. Crop development proceeds according to genotype characteristics and environmental influences, specifically temperature and photoperiod. It can be partly described by thermal requirements for development intervals and coefficients that describe genotype adaptation.

The objectives of this study were to (a) quantify (i) time of tassel initiation, tasselling and silking; (ii) thermal intervals for initiation, appearance and expansion of successive leaves (iii) thermal duration from initiation to tip appearance and from tip appearance to collar appearance, and (iv) leaf area and canopy cover as measured by leaf area index (LAI) in contrasting cultivars of maize grown in the field in a cool environment; and (b) relate these to plant characteristics and environmental variables, particularly temperature.

For these purposes, three cultivars of maize were grown in three and four cultivars in two serial plantings from 18 April to 24 June in field experiments at Wageningen, The Netherlands, in 1997, and detailed data on crop development, leaf production and environmental variables were collected. The base temperature ( $T_b$ ) for maize was confirmed as 8°C, but thermal time calculation needs to be re-examined to explore a recovery period after chilling injury. Equations that relate foliar properties to total leaf number and ordinal leaf position were derived. Individual leaf area can be described by the modified bell curve, and differences in temporal increase in LAI were related to parameters of leaf initiation, appearance and expansion.

**Key words:** leaf appearance, leaf initiation, leaf expansion, maize, modelling, phyllochron, temperature, thermal time, *Zea mays*

## List of abbreviations

T – mean temperature (°C)

$T_b$  - base temperature (°C)

TI – tassel initiation

$TT_i$  - thermal interval between initiation of successive leaves (°Cd leaf<sup>-1</sup>)

$TT_a$  - thermal interval between appearance of successive leaf tips (°Cd leaf<sup>-1</sup>)

$TT_c$  - thermal interval between appearance of successive leaf collars (°Cd leaf<sup>-1</sup>)

$TT_{eti}$  - thermal duration from emergence to TI (°Cd)

$TT_{et}$  - thermal duration from emergence to tasselling (°Cd)

$TT_{ej}$  - thermal duration from emergence to the end of the basic vegetative period (°Cd)

$TT_{sm}$  - thermal duration from silking to physiological maturity (°Cd)

$TT_{it}$  - thermal duration from leaf initiation to appearance of the leaf tip (°Cd)

$TT_{tc}$  - thermal duration from appearance of the leaf tip to appearance of leaf collar (°Cd)

$TT_{is}$  - thermal duration from leaf initiation until leaf senescence (°Cd)

$TT_{ts}$  - thermal duration from appearance of leaf tip until senescence (°Cd)

$TT_{ge}$  - thermal duration from germination to emergence (°Cd)

$TT_{tit}$  - thermal duration from tassel initiation to tasselling (°Cd)

PS – photoperiod sensitivity (°Cd h<sup>-1</sup>)

L – individual leaf area (cm<sup>2</sup>)  
A<sub>o</sub> – area of largest leaf (cm<sup>2</sup>)  
x – position of leaf, numbered basipetally  
x<sub>o</sub> – position of largest leaf, numbered basipetally  
TI - - total number of leaves on stem  
Lv – number of leaves (tips visible) present  
L<sub>e</sub> – number of fully expanded leaves (collar present)  
L<sub>s</sub> – number of senesced leaves (more than 50% of L having lost green colour)  
LAI – leaf area index (for green leaves only)  
PA – total leaf area on a plant (cm<sup>2</sup>)

## **Introduction**

Crop development is usually predicted using accumulated thermal time calculated from temperature coefficients for individual crops, photoperiod sensitivity and coefficients describing characteristics of genotypes. Mechanistic models usually use a leaf level approach to simulate plant leaf area, and thus crop canopy production e.g in CERES-Maize (Jones and Kiniry 1986), AUSIM-Maize (Carberry and Abrecht 1991), CORNF (Stapper and Arkin 1980), CERES-Sorghum (SAT) (Birch et al. 1990), and maize models proposed by Birch (1996) and Muchow et al. (1990). However, not all complexity of biological systems can be included (Sinclair and Seligman 2000), and the level included must be resolved in terms of the objectives for which a model was constructed. Further, the ‘domain of relevance’ of the model must be stated, and simplifications of processes that occur at a lower level of hierarchy than that at which the model operates are widely used (Sinclair and Seligman 2000). This paper addresses plant development and leaf area production in contrasting cultivars of maize grown in a cool temperate environment, and examines the use of existing approaches to quantification, thus prediction, of selected aspects of crop development and canopy production in such environments.

Prediction of canopy production and senescence relies on prediction of appearance and duration of expansion of leaves, their individual and cumulative leaf area and senescence of individual leaves. Canopy production and crop development are interrelated, for example flowering in gramineous crops occurs on completion of canopy production.

Parameters are needed for  $TT_i$ ,  $TT_a$  and  $TT_c$ , and usually constant values are used.  $TT_a$  in maize is fairly stable within environments. However, it is lower in the cool temperate environment of The Netherlands (Struik 1983, Hussien 1995, Birch et al. 1998b) than in warm temperate, sub-tropical and tropical environments (Bonhomme et al., 1991, Kiniry and Bonhomme 1991, Birch et al. 1998b). Typically,  $TT_a$  is 30% greater in tropical than in temperate areas (Kiniry and Bonhomme 1991, Birch et al. 1998b), and has been shown to increase linearly with  $T$  before  $TI$  of 12.5 and 25.5 °C (Birch et al. (1998b):

$$TT_a = 6.3 + 1.7 * T \quad (r^2 = 0.76, n = 53) \quad (1).$$

$L$  varies with ordinal position of the leaf. Dwyer and Stewart (1986) proposed a modified bell curve for prediction of individual leaf area ( $L$ ) of maize, which related  $L$  to coefficients for  $A_o$ , width ( $a$ ) and skew ( $b$ ) of the bell curve,  $x$  and  $x_o$ :

$$L = A_o * \exp\{a * (x - x_o)^2 + b * (x - x_o)^3\} \quad (2)$$

$A_o$ ,  $x_o$ ,  $a$  and  $b$  have been related to  $TI$  (Birch et al. 1998a), the equations for the  $a$  and  $b$  being:

$$a = -0.009 - e^{-0.20 * TI} \quad (\text{Birch et al. 1998a}) \quad (3), \text{ and}$$

$$b = 0.0006 - e^{-0.43 * TI} \quad (\text{Birch et al. 1998a}) \quad (4).$$

These approaches, complemented with expressions describing the progress of senescence as a function of thermal time, have proved satisfactory when the objectives of the model are to predict biomass and final crop yield from environmental variables (temperature, radiation, photoperiod), management inputs (e.g. planting date, plant population, water and supply) and genotype characteristics (e.g.  $TT_{ej}$ ,  $PS$ ,  $TT_{sm}$ ). However, they are not suitable for use modelling crop canopy structure, vertical distribution of LAI and light interception, time for expansion and senescence of individual leaves, photosynthetic efficiency and dilution of foliar

applied materials (e.g. pesticides) under a range of environmental and management conditions. For these purposes, models need to be able to predict on a temporal basis the changing architecture of individual plants and the canopy as a whole. For such uses, robust approaches to prediction of appearance, duration of expansion and life cycle of individual leaves, TI, L, and PA are also needed. Also, since internode length influences vertical distribution of leaf area, robust methods of prediction of internode extension are required. Thus, the processes of canopy production need to be more fully quantified than in commonly used models.

The objectives of this study were to (a) quantify (i) time of tassel initiation, tasselling and silking; (ii) thermal intervals for initiation, appearance and expansion of successive leaves (iii) thermal duration from initiation to tip appearance and from tip appearance to collar appearance, and (iv) leaf area and canopy cover as measured by leaf area index (LAI) in contrasting cultivars of maize grown in the field in a cool environment; and (b) relate these to plant characteristics and environmental variables, particularly temperature.

## **Materials and Methods**

A field experiment located at Wageningen Agricultural University (Latitude 51° 58'N, Longitude 5° 40'E), was described in full in Birch et al. (1998b). Briefly, three cultivars of maize, (Lincoln, LG11 and LG22.42, quick, medium and slow maturity respectively) (Anonymous 1997)) were planted on 5 dates (18 April, 6 and 23 May, and 3 and 24 June 1997) in a split-plot design with three replicates. Hycorn 42 from Australia was added in June plantings. Subplots were four rows of 9m length. Established plant population was 10 plants m<sup>-2</sup>, and crops were grown under non-limiting conditions of nutrient and water supply. Pests were rigorously controlled. Maximum and minimum temperatures at 1.50m (Figure 1) were recorded nearby at Wageningen University Meteorological Station.

Tassel initiation was determined by destructive sampling of three plants per sub-plot at 2 to 3 day intervals after plants had four leaves. The apices of the plants were examined under a stereoscopic microscope, and rated according to micrographs of

Moncur (1981), until rating 4 was reached. Ratings were plotted against time (days) from emergence; tassel initiation was recorded when apex rating reached 2.

Other data on crop development were collected from five randomly located, tagged plants in each sub-plot. Tasselling was assessed as follows: 0 (tassel present, no anther sacks extruded), 1 (up to 25% of the individual tassels having extruded anther sacks), 2 (25 - 50%), 3 (50 - 75%), and 4 (75 - 100%). Silking was assessed as 0 (cobs present, no silks), 1 (silks extruded and green), and 2 (silk colour changed to red or red brown). Tasselling and silking were recorded when 50% of plants reached ratings of 2 and 1 respectively.

#### *Leaf production, area and senescence*

The fifth and tenth leaves on the tagged plants were tagged, so that  $L_v$  and  $L$  could be accurately recorded.  $L_v$ ,  $L_e$  and  $L_s$  were recorded regularly (1 to 2 d intervals) until completion of canopy production and then  $L_s$  (2 to 3 day intervals) until final harvest.

$TT_i$  is the quotient of thermal time from germination to TI and the number of leaves initiated (six less than total leaf number, assuming there were six seminal leaves in the embryo (Carberry et al. 1989)). (Germination was assumed to be 20 °C d after planting, rather than one day (15 - 20°C d) as used in CERES-Maize and AUSIM-Maize).  $TT_a$  is the reciprocal of leaf appearance rate, calculated by regressing  $L_v$  on thermal time from emergence, and  $TT_c$  the reciprocal of leaf expansion rate calculated by regression of on thermal time from emergence. However, collars of the last four leaves appeared more quickly than on other leaves, and required different regressions, as in Birch (1996).

$TT_{it}$  (for the first six leaves present in the embryo, germination was treated as initiation), and  $TT_{tc}$  were estimated. The procedure is illustrated in Figure 2, which uses actual data for  $L_v$  and  $L_e$  for Lincoln grown in planting 3. The number of leaves initiated as thermal time from germination increased was estimated using  $TT_i$  calculated as above.  $TT_{it}$  is represented by AB, and  $TT_{tc}$  by BC in Figure 2.

$TT_{is}$  and  $TT_{ts}$  (for leaves that senesced before the trial was terminated by harvest) were determined in a similar manner.

$L$  was determined from leaf length ( $l$ , cm) from the collar to the tip of fully expanded leaves, and from where a leaf could be seen in the whorl of expanding leaves to the tip, and leaf width ( $w$ , cm) at the widest point, as follows:

$$L = l * w * 0.75 \text{ (Montgomery 1911, Birch et al. 1998a)} \quad (5)$$

$L$  was accumulated to calculate PA on each sampling time. Green leaf area was calculated by deducting senesced leaf area from PA, and with plant population, used to calculate LAI. The  $a$  and  $b$  coefficients for Equation 2 were derived by substituting observed values of  $A_o$  and  $x_o$  and calculating  $a$  and  $b$  by nonlinear estimation (Wilkinson 1990). The usefulness of Equations 3 and 4 to predict  $a$  and  $b$  coefficients in Equation 2 was assessed by comparing the values predicted by substituting observed TI in Equations 3 and 4 and observed values.

### Statistical Analysis

Analysis of variance, linear and non-linear regression and fitting of coefficients in functions by non-linear estimation were completed using appropriate procedures in SYSTAT (Wilkinson 1990).

Data on time (d) from emergence to tassel initiation and tassel initiation to silking were also analysed by DEVEL to separate effects of temperature and photoperiod on crop development. DEVEL is an iterative optimization procedure, that uses Simplex optimization routines contains a library of eight options for temperature response and eight for photoperiod response, ranging from linear response to power functions, all of which have been used to describe temperature and photoperiod responses. The program can be used to assess temperature and photoperiod responses by crops either independently or concurrently (Holzworth and Hammer 1992). The user selects an equation to describe the response being investigated and provides initial estimates of coefficients for terms the equation. DEVEL then proceeds to carry out an iterative

optimization that minimizes residual error, and provides optimized estimates of the coefficients (with 90% confidence intervals for each) and an estimate of the proportion of variation explained ( $r^2$ ). The user may then 'fix' the value of one or more coefficients, and repeat the procedure to obtain optimized values for the remaining coefficients. The user repeats the process with alternative functions and selects the function best statistically fits the temperature and photoperiod response.

## **Results**

### *Crop Development*

Emergence in plantings 1 and 2 took 16 and 12 days, and in plantings 3, 4 and 5 (9, 5 and 8 days, except Hycorn 42, which was slower).  $TT_{ge}$  (germination was assumed to be 20 °C d after planting, rather than 1 day) to emergence were more consistent 49, 55, 66, 59 and 54 °C d in plantings 1 to 5 respectively; there were no systematic significant differences among cultivars, except for Hycorn (longer  $TT_{ge}$ ).

TI occurred from 12 to 31 d after emergence, the slowest being in crops planted on 18<sup>th</sup> April and 5<sup>th</sup> May 1997. Optimisation by DEVEL showed little or no photoperiod effect on thermal duration of  $TT_{eti}$ . Consequently, only temperature response for emergence to TI was further investigated.  $T_b$  were 8.2, 8.8 and 7.9 °C for Lincoln, LG11 and LG22.42, and 8.3 °C for all data. These are all close to  $T_b$  of 8 °C found by Birch et al. (1998c), so  $T_b = 8$  °C was retained.  $T_b = 8$  °C was also found for tassel initiation to silking, but could not be determined for post-silking development.

$TT_{eti}$  was calculated for each cultivar in each planting using  $T_b = 8$  °C ranged from 120 to 260 °C d (Figure 3), and in plantings 3 to 5 was similar within cultivar, but as expected higher in later maturing cultivars. For Hycorn 42, it was close to that found in Australia (Birch et al. 1998c).

Time (d) from emergence to tasselling and silking differed substantially between plantings, but thermal times for this interval were more consistent, though longer in plantings 1 and 2 (Figure 3). Tasselling preceded silking in the late June planting only



- in others it coincided with or followed silking. Tasselling and silking occurred later in the later maturing cultivars ( $P = 0.05$ ) in all plantings, but differences were not great, consistent with only small differences in Tl.  $TT_{it}$  were generally proportional to the number of leaves remaining to reach full expansion after tassel initiation (Table 1). Thus, the longer  $TT_{et}$  in plantings 1 and 2 was mostly accounted for by longer  $TT_{eti}$ .

#### *Leaf production, area and senescence*

Our data on  $TT_{it}$ ,  $TT_{tc}$ ,  $TT_{is}$  and L show similar trends in all plantings. Consequently, we present data for planting 4 only in graphical form, since it adequately represents data for Lincoln, LG11, LG22.42 and Hycorn 42 (Figures 4a, 4b, 5, 6).

#### *Total leaf number*

Average Tl was similar in plantings 1 to 4 but slightly lower in planting 5 (Table 1). LG22.42 had more leaves in each planting and on average than Lincoln and LG11 (which were usually similar), but less than Hycorn 42.

#### *Thermal intervals for initiation of leaves and between appearance of leaf tips and of leaf collars*

In the results that follow, standard errors were all smaller than  $\pm 5\%$  for  $TT_i$ ,  $TT_a$  and  $TT_c$  in Lincoln, LG11 and LG22.42, but larger in Hycorn 42 (up to  $\pm 12.5\%$ ).  $TT_i$  was higher in plantings 1 and 2 (average 32.3 and 29.3  $^{\circ}\text{C d leaf}^{-1}$ ) than in plantings 3, 4 and 5 (23.3, 20.6 and 22.3  $^{\circ}\text{C d leaf}^{-1}$ ). In LG22.42 in plantings 1 and 2,  $TT_i$  was shorter (27.4  $^{\circ}\text{C d leaf}^{-1}$  in both) than in Lincoln (35.8 and 30.7  $^{\circ}\text{C d leaf}^{-1}$ ) and LG11 (33.6 and 30.0  $^{\circ}\text{C d leaf}^{-1}$ ), but in plantings 3, 4 and 5, all were in the range 20.3 to 24.5  $^{\circ}\text{C d leaf}^{-1}$ . Overall, mean  $TT_i$  was shorter in LG22.42 (23.8  $^{\circ}\text{C d leaf}^{-1}$ ) than in Lincoln and LG11 (26.7 and 26.1  $^{\circ}\text{C d leaf}^{-1}$ ). Hycorn 42 had the shortest  $TT_i$  (average 17.1  $^{\circ}\text{C d leaf}^{-1}$ ).

Data on  $TT_a$  have been reported in Birch et al. (1998b), and are not repeated here.  $TT_c$  within and among plantings and cultivars showed some small but significant ( $P < 0.05$ ) differences. LG22.42 had shorter  $TT_c$  in planting 1 ( $40.0 \text{ }^\circ\text{C d leaf}^{-1}$ ) than other cultivars (Lincoln  $46.3 \text{ }^\circ\text{C d leaf}^{-1}$ , LG11  $43.5 \text{ }^\circ\text{C d leaf}^{-1}$ ). In other plantings, it had similar or shorter ( $P < 0.05$ )  $TT_c$  ( $38.5$  to  $41.7 \text{ }^\circ\text{C d leaf}^{-1}$ ) than Lincoln and LG11 ( $38.5$  to  $43.5 \text{ }^\circ\text{C d leaf}^{-1}$ ). Hycorn 42 had longer intervals ( $45.5$  and  $50.0 \text{ }^\circ\text{C d leaf}^{-1}$ ).

*Thermal durations from estimated time of leaf initiation to leaf tip appearance and leaf tip to collar appearance.*

$TT_{it}$  (Figure 4a) could be related to  $x$  by cubic polynomials:

$$TT_{it} = h*x + i*x^2 + j*x^3 \quad (6),$$

and  $TT_{ic}$  (Figure 4b) was related to  $x$  using quadratic equations:

$$TT_{ic} = n*x + p*x^2 \quad (7).$$

The mean values of  $h = 46$  (range 44 to 49) and  $i = -4.4$  (range -4.2 to -4.7) were retained as they did not differ in regressions for total leaf numbers of 13 to 16. However, the value of  $j$  declined as total leaf number increased (Table 2), and for total leaf number = 15, was lower in LG22.42 than in Lincoln and LG11, consistent with the lower thermal interval between appearance of successive leaf tips in LG22.42 (Figure 4a). The value of  $h$  ( $53 \pm 1.6$ ) for plants with 17 leaves (Hycorn 42) differed from  $h$  for plants with 13 to 16 leaves, so a separate equation with values of  $i$  ( $-3.9 \pm 0.2$ ) and  $j$  ( $0.15 \pm 0.01$ ) was retained.

The value of  $n$  decreased and of  $p$  increased as TI increased (Table 2) for plants with 13 to 16 leaves (Lincoln and LG11). However, both  $n$  (41.1) and  $p$  (-2.19) for LG22.42 with 15 leaves were higher and lower than for Lincoln and LG11 with 15 leaves ( $n = 34.8$ ,  $p = -1.95$ ). They were also lower and higher respectively for TI = 16 in LG22.42 ( $n = 30.8$ ,  $p = -1.41$ ) than in this cultivar with 15 leaves.

### *Thermal duration from leaf tip appearance to leaf senescence of individual leaves*

$TT_{ts}$  of individual leaves could only be determined for the lower leaves in each planting, because the trial was terminated at the time of harvest for silage production. The leaves low on the stem had short  $TT_{ts}$  of 300 to 400 °C d leaf<sup>-1</sup>, increasing to 800 - 1000 °C d leaf<sup>-1</sup> for leaf 5 and above, though at most only 8 leaves had senesced by harvest (Figure 5). The pattern was generally consistent among plantings, though there was some evidence of difference among cultivars. Lower leaves on slower maturing cultivars that had more leaves senesced earlier, probably because of higher LAI (see later), resulting in lower light intensity, and thus earlier senescence of lower leaves.

### *Individual leaf area*

L did not differ among cultivars until above leaves 9 or 10, when slower maturing cultivars had larger leaves than Lincoln and LG1, and in LG22.42 and Hycorn 42, the largest leaf occurred at a higher ordinal leaf position (Figure 6).

L could be described by the modified bell curve (Dwyer and Stewart 1986) (Equation 2).  $A_0$  and  $x_0$  in each cultivar and planting and the coefficients  $a$  and  $b$  in Equation 2 are presented in Table 3.  $A_0$  varied among cultivars and plantings, being generally lower in plantings 3 and 4 than in other plantings. Within plantings,  $a$  (Table 3) was higher for plants with higher TI (Table 1), while  $b$  had mostly positive values in plantings 1, 2 and 5, and mostly negative values in plantings 3 and 4, but was not consistently related to TI.

With two exceptions (LG11 and LG22.42 in planting 1), values of  $a$  predicted by Equation 3 were within 15% of the observed value for the relevant number of leaves (Table 3). Observed values of  $b$  ranged from -0.0049 to +0.0064, and predictions of  $b$  by Equation 4 were unsatisfactory.

### *Total and senesced leaf area and green Leaf Area Index*

PA was greater on LG22.42 (and Hycorn 42, Planting 4) than on Lincoln and LG11 in all plantings. There was only small difference in PA among cultivars until after 300 °C from emergence in all plantings, after which PA in slower maturing cultivars was higher. PA reached a maximum near 5000 cm<sup>2</sup> in LG22.42 in all plantings, and Hycorn 42 in planting 4, but in Lincoln and LG11 ranged from 3500 to 4400 cm<sup>2</sup>.

Leaf senescence was absent or very minor until 400 °Cd after emergence in all plantings for all cultivars (data not presented). In subsequent samplings, differences among cultivars within plantings occurred but the pattern was not consistent. LAI exceeded 4.0 for extended periods in LG22.42 in all plantings and Hycorn 42 but not at all or for brief periods only in the other cultivars (Figure 7).

### Discussion

#### *Crop Development*

The lack of photoperiod response in Lincoln, LG11 and LG22.42 may be due to (i) lack of sensitivity to photoperiod, or (ii) photoperiods prior to tassel initiation of 17.2, 17.6, 18.1, 18.3 and 18 hours (plantings 1 to 5, respectively, calculated as in Jones and Kiniry (1986). The photoperiods experienced were close to or above the ceiling photoperiod for maize (Bonhomme et al. 1991). Hycorn 42 had similar TT<sub>eti</sub> as at Gatton, Australia (latitude 27° 33' S, longitude 152° 20' E), with photoperiods ranging from 12.5 to 16.5 h (Birch et al.1998c), confirming little, if any, photoperiod response in this cultivar. T<sub>b</sub> for crop development was confirmed at 8°C from emergence to tasselling and silking.

The longer TT<sub>eti</sub> in all cultivars in plantings 1 and 2 than in later plantings may be due to the several occasions when minimum temperature was below T<sub>b</sub>, and even below 0

°C, and maximum temperatures below 15 °C, with high daily radiation. These conditions can cause chilling injury (Schapendonk et al. 1994), thus delaying crop development. The procedure used for calculating thermal time accumulates thermal time only for the part of the day when temperature is above  $T_b$  (by using 3 hour interpolated temperatures (Jones and Kiniry 1986)), as advocated by Bonhomme (2000), our findings highlighting the importance of adequate definition of the domain to which a model or its components are applied (Sinclair and Seligman 2000). We propose that a recovery period during which reduced or no thermal time accumulation occurs may be necessary after chilling injury. Thus  $TT_{eti}$  would be lower than reported here. The reasonably consistent proportional relationship across planting times and cultivar between  $TT_{it}$  and number of leaves remaining to fully expand after TI (Table 1) indicates that the long  $TT_{eti}$  in plantings 1 and 2 was due to the assumptions inherent in thermal time calculation, and that these are invalid for crops established under low temperature conditions. For these reasons, calculations that rely on  $TT_{eti}$  in plantings 1 and 2 will not be used extensively in the balance of this paper.

#### *Leaf number and the dynamics of canopy production*

$TT_i$  in plantings 3 to 5 were similar and comparable to those used in CERES-Maize (25 °Cd leaf<sup>-1</sup>), AUSIM-Maize (23.2 °Cd leaf<sup>-1</sup>), and found by Birch et al. (1998d) (25 °Cd leaf<sup>-1</sup>). The first of these values is an average from numerous trials in the United States, and the latter derived for a range of cultivars in tropical and sub-tropical environments in Australia. The similarity of the values indicates that  $TT_i$  is fairly consistent across environments. The exception appears to be where low temperature conditions occur, as in plantings 1 and 2. The longer  $TT_i$  in plantings 1 and 2 suggest that  $TT_i$  is increased at low temperature and supports the re-examination of thermal time calculation when chilling occurs.

$TT_a$  in the present study were similar to values calculated from data in Struik (1983) and (Hussen 1995), and 25 to 40% shorter than in sub-tropical and tropical environments (Kiniry and Bonhomme 1991, Bonhomme et al.1991, Birch et al. 1998d). There was some evidence that LG22.42 had shorter  $TT_c$  and  $TT_c$  for Hycorn 42 than in other cultivars. The shorter  $TT_c$  in Lincoln, LG11 and LG22.42 than occur

in warmer environments, where  $TT_c$  often exceed  $50\text{ }^\circ\text{Cd leaf}^{-1}$  (e.g. Gatton, Australia (Karanja 1993, Birch et al. 1998d), Temple, USA (Birch and Kiniry 1997, unpublished) indicates that constant values for this parameter cannot be used across cultivars and environments.

$TT_a$  found in the present study formed part of the data set used to relate  $TT_a$  to  $T$  prior to  $TI$  (Birch et al. 1998b). Other factors may need to be added to account for 24% of the variation in  $TT_a$  that remained unexplained in that study e.g. genotype differences (Tollenaar et al. 1984, Bonhomme et al. 1991) and photoperiod (Warrington and Kanemasu 1983).

#### *Thermal duration from leaf initiation to leaf tip appearance, leaf tip collar appearance*

A family of curves for  $TT_{it}$  plotted against leaf position were described by cubic polynomial equations (Equation 6, coefficients in Table 2). The different coefficients for Hycorn 42 than for plants with 13 to 16 leaves is consistent with longer thermal intervals for appearance of leaf tips and leaf collars (later) and is probably because Hycorn 42 was grown at lower temperatures than for which it was selected.

Our data show a consistent pattern of increased  $TT_{tc}$  as leaf size increases to the maximum and then declines as leaves become smaller near the top of the plant.  $TT_{tc}$  was related to ordinal leaf position (Equation 7, coefficients in Table 2). The trends in the relationship between the linear and quadratic coefficients and  $TI$  indicate that further research with a wider range in  $TI$  is needed to confirm the utility of the trends that have been found here.

#### *Leaf area of individual leaves*

By supplying values of  $A_0$  and  $x_0$  to the modified bell curve (Equation 2), observed values of the coefficients  $a$  and  $b$  were calculated. Predicted values of  $a$  (by Equation 3) were usually close to the observed values of  $a$ , thus Equation 3 shows promise for

predicting  $a$  in both cool and warm environments (e.g. Australia), but Equation 4 failed to reliably predict  $b$ .

Keating and Wafula (1992) using nonlinear relationships of a different form from Equations 3 and 4, investigated the use predicted values for  $a$  and  $b$  and concluded no real advantage was gained in predictions of individual leaf area using separate values of  $b$  for cultivars with 12 to 18 leaves. Fournier and Andrieu (1998) also investigated prediction of  $x_0$ ,  $a$  and  $b$  in Equation 2 using linear relationships between these parameters and Tl and data from published sources. Coefficients of determination ( $r^2$ ) for equations relating  $a$  and  $b$  to Tl were low (0.54 and 0.55). However, these authors were able to reproduce the areas of leaves of plants used in the development of the equations, but did not test their equations on independent data.

The ability to predict these parameters and apply them to different cultivars grown in a wide range of environmental conditions is important to the use of Equation 2 in modeling, by reducing the number of parameters that have to be supplied (Keating and Wafula 1992). The failure of Equation 4 to predict  $b$  may be due to the skew of the curve being particularly sensitive to environmental and/or genetic factors, or it may be that  $b$  does not vary greatly with total leaf number across a wide range of cultivars and thus no advantage accrues from predicting  $b$ . It is evident that further research is needed to investigate prediction of  $a$  and  $b$ , to determine the appropriate form/s of equations to use and to determine whether or not a single value of  $b$  is adequate for modeling purposes, and will require very detailed data, probably from controlled environment studies.

*Total plant leaf area, senesced leaf area and green leaf area index.*

Since leaf area index did not exceed 4.0, producing estimated light interception of  $\geq 85\%$ , using light extinction coefficient = 0.46 (Birch et al. 1999) in all cultivars and plantings, full light interception would only have occurred for brief periods. Thus, plant population may need to be increased to hasten reaching LAI of 4 or above and retain it for an extended period. However, the increase would only be small, as more recent evidence from Wageningen does not support a large increase in plant

population (Wageningen Agricultural University, unpublished data, 1999). Alternatively, cultivar selection may improve light interception. The more rapid appearance and expansion of leaves, and larger individual leaf size (above leaf 9 or 10) in LG22.42 resulted in higher LAI early in crop life in this cultivar. Thus, radiation interception would have been greater leading to higher yield. The shorter thermal intervals between appearance of successive leaves in LG22.42 contributed to faster expansion the crop canopy. LG22.42 also had higher total plant leaf area (an extra 300 to 1000 cm<sup>2</sup>/plant) and higher LAI (Figure 7), near 400 °C d after emergence in all plantings. These characteristics mean it is the type of maize cultivar required in cool environments (Giauffert et al. 1990). The slower production of leaf area by Hycorn 42 than other cultivars in Planting 4 because slower leaf appearance and expansion show that this cultivar is clearly less well adapted to cool environments than occur in Australia.

#### *Implications for Modelling*

Our data show that relationships exist between measures of production of leaf canopies, environmental characteristics (e.g. temperature) and plant characteristics (e.g. Tl). They also show that coefficients in at least some of the equations developed here may be related to plant characteristics e.g. Tl. Thus, in modelling the central importance of accurate prediction of leaf number (Birch et al. 1998c) is reinforced. Further studies of the development of leaves, involving dissection and measurement of dimensions of unfurling leaves, careful examination of plant apices and the identification of vegetative and reproductive structures are necessary. Also needed are studies of the effects of environmental stresses and supplies of resources such as nutrients on the development, final size and life cycle duration of leaves. These would increase understanding of processes of leaf and canopy production to a level where the information could be incorporated in models of crop canopy architecture. From this, distribution of light within canopies, location and dilution of applied chemicals and the like could be examined using models, and thus advance the applications of models in scientific investigation and crop management.



## **CONCLUSIONS**

This study confirmed the base temperature ( $T_b$ ) for maize at 8°C, suggesting  $T_b$  is the same across environments. Dimensions of leaves of maize show some variation across environments and cultivars, but are essentially conservative – in that maize produces large leaves rapidly, even in cool environments. The relatively slow production of leaves by Hycorn 42 confirms substantial differences in leaf production among cultivars from different regions, and emphasises the need for care in extrapolating parameters developed with specific groups of cultivars to other cultivars or areas outside their zone of adaptation.

This study has provided insight into the processes of canopy production by maize in a cool temperate environment, and provides guidance on relating foliar properties to total leaf number and ordinal leaf position. There is sufficient evidence of difference among genotypes in canopy production to justify further research to develop appropriate modelling techniques that use the approach of relating thermal intervals from leaf initiation to tip and leaf tip to collar appearance to leaf position. Individual leaf area can be described by the modified bell curve, but methods of predicting the values of coefficients in it need to be refined.

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## Figure captions

Figure 1. Maximum and minimum temperatures at Wageningen, during the experimental period in 1997.

Figure 2. Illustration of the approach to determining thermal time from leaf initiation to leaf tip appearance and leaf tip to leaf collar appearance.

Figure 3. Crop development intervals in four cultivars (1 = Lincoln, 2 = LG11, 3 = LG22.42 and 4 = Hycorn 42) of maize grown at Wageningen in 1997: (a) emergence to tassel initiation, (b) tassel initiation to silking and (c) silking to tasselling (where silking preceded tasselling). 'T' indicates tasselling where tasselling preceded silking.

Figure 4. Thermal duration from estimated initiation to (a) leaf tip appearance and (b) leaf collar in three or four cultivars of maize in five plantings at Wageningen in 1997. (Standard errors are all less than 5% of the thermal durations for individual leaves in each cultivar).

Figure 5. Thermal duration of individual leaf life cycles, from estimated time of initiation to senescence (<50% of leaf area green). (Standard errors are all less than 5% of the thermal durations for individual leaves in each cultivar).

Figure 6. Leaf area of individual leaves in several cultivars of maize planted on five dates at Wageningen in 1997. (Standard errors are all less than 5% of individual leaf areas in each cultivar, for leaves above leaf 5, and less than 8% for leaves 1 to 5.).

Figure 7. Green leaf area index in serial measurements in three maize cultivars grown in five plantings, and a fourth cultivar grown in one planting at Wageningen.

Table 1. Total number of leaves, number of leaves remaining to fully expand after tassel initiation (TI) and thermal time from tassel initiation to tasselling in four cultivars of maize planted on 5 dates in 1997 at Wageningen.

Planting date	Cultivar	Total leaf number	Leaves to fully expand after TI	Thermal time from TI to Tasselling (°Cd)
18 April 1997	Lincoln	13.6	9.6	409
	LG11	14.5	10.5	454
	LG22.42	16.9	12.9	481
	Planting date mean (1)	15.0	-	-
6 May 1997	Lincoln	14.4	10.4	418
	LG11	14.9	10.9	401
	LG22.42	16.5	11.5	445
	Planting date mean(1)	15.2		
23 May 1997	Lincoln	14.4	10.4	394
	LG11	14.5	10.5	414
	LG22.42	16.4	12.4	486
	Planting date mean(1)	15.1		
3 June 1997	Lincoln	14.2	10.7	418
	LG11	14.8	11.3	440
	LG22.42	16.2	11.7	464
	Hycorn 42	17.5	12.5	493
	Planting date mean(1)	15.1(a) 15.7(b)		
25 June 1997	Lincoln	13.7	10.7	416
	LG11	14.1	11.1	425
	LG22.42	15.3	11.3	425
	Hycorn 42	16.7	11.7	490
	Planting date mean(1)	14.4(a) 15.0(b)		

(1) For total leaf number only

(a), (b) mean for three or four cultivars, excluding and including Hycorn 42, respectively.

Final leaf number: lsd ( $P = 0.05$ ), planting date mean = 0.5, lsd ( $P = 0.05$ ), cultivar mean (excluding Hycorn 42) = 0.6.

Table 2. Coefficients and their standard errors, and coefficients of determination ( $r^2$ ) in equations relating thermal duration of development intervals of leaves to ordinal leaf position ( $x$ ) in several maize cultivars grown in 3 of 5 plantings at Wageningen in 1997: (a)  $j$  in  $TT_{it} = 46*x - 4.3*x^2 + j*x^3$ , where  $TT_{it}$  = thermal time from estimated time of leaf initiation to leaf tip appearance, and (b)  $n$  and  $p$  in  $TT_{tc} = n*x + p*x^2$  where  $TT_{tc}$  = thermal time from tip appearance to collar appearance.

Total leaf number	Cultivars	$j$	se of $j$	$r^2$	$n$	se of $n$	$p$	se of $p$	$r^2$
		<i>(a) Thermal duration from leaf initiation to leaf tip appearance</i>			<i>(c) Thermal time from tip appearance to collar appearance</i>				
13	Lincoln, LG11	0.21	0.004	0.97	43.1	2.7	-2.51	0.26	0.88
14	Lincoln, LG11	0.195	0.002	0.96	39.2	1.13	-2.35	0.10	0.89
15	Lincoln, LG11	0.190	0.002	0.98	34.8	1.11	-1.95	0.10	0.90
15	LG22.42	0.180	0.002	0.97	41.1	2.80	-2.19	0.10	0.88
16	LG22.42	0.170	0.001	0.97	30.8	1.00	-1.41	0.08	0.93
17	Hycorn 42	*	*	*	39.2	1.13	-1.94	0.09	0.9

- For Hycorn 42 Thermal duration from leaf initiation to leaf tip appearance =  $53.2 (\pm 1.6) - 3.9(\pm 0.2) * x^2 + 0.15 (\pm 0.01) * x^3$   $r^2 = 0.99$

Table 3. Observed values of  $x_o$ ,  $A_o$  and the coefficients  $a$  ( $\pm se$ ) and  $b$  ( $\pm se$ ) and predicted  $a$  and  $b$  (from equations 3 and 4) in the modified bell curve for three cultivars of maize grown in five plantings, and an additional cultivar grown in one planting at Wageningen in 1997. The coefficients of determination for observed  $a$  and  $b$  exceeded 0.90, except for Lincoln ( $r^2 = 0.82$ ) and LG11 ( $r^2 = 0.86$ ) planted on 25 June 1997.

Planting date	Cultivar	$x_o$	$A_o$	Observed $a \pm se$	Predicted $a$	Observed $b \pm se$	Predicted $b$
18 April	Lincoln	10	581	-0.077 $\pm$ 0.007	-0.075	-0.0045 $\pm$ 0.0009	-0.0023
	LG11	10	574	-0.09280.004 $\pm$	-0.064	-0.0048 $\pm$ 0.0006	-0.0014
	LG22.42	11	670	-0.055 $\pm$ 0.003	-0.043	+0.0037 $\pm$ 0.0005	-0.0001
6 May	Lincoln	9	621	-0.075 $\pm$ 0.010	-0.065	+0.0064 $\pm$ 0.0015	-0.0015
	LG11	9	635	-0.066 $\pm$ 0.006	-0.060	-0.0028 $\pm$ 0.0008	-0.0010
	LG22.42	11	622	-0.047 $\pm$ 0.002	-0.046	+0.0012 $\pm$ 0.0004	-0.0002
23 May	Lincoln	9	530	-0.058 $\pm$ 0.007	-0.065	+0.0041 $\pm$ 0.0010	-0.0015
	LG11	9	540	-0.058 $\pm$ 0.007	-0.064	-0.0030 $\pm$ 0.0008	-0.0014
	LG22.42	10	585	-0.042 $\pm$ 0.003	-0.047	+0.0024 $\pm$ 0.0004	-0.0003
3 June	Lincoln	10	552	-0.067 $\pm$ 0.009	-0.067	-0.0041 $\pm$ 0.0009	-0.0016
	LG11	10	515	-0.063 $\pm$ 0.004	-0.061	-0.0030 $\pm$ 0.0005	-0.0012
	LG22.42	12	613	-0.042 $\pm$ 0.003	-0.048	-0.0014 $\pm$ 0.0002	-0.0003
	Hycorn 42	12	753	-0.045 $\pm$ 0.001	-0.039	+0.0002 $\pm$ 0.0001	-0.0001
25 June	Lincoln	9	582	-0.072 $\pm$ 0.001	-0.74	-0.0049 $\pm$ 0.0001	-0.0022
	LG11	9	605	-0.070 $\pm$ 0.001	-0.069	-0.0046 $\pm$ 0.0010	-0.0017
	LG22.42	10	623	-0.051 $\pm$ 0.003	-0.056	+0.0025 $\pm$ 0.0004	-0.0008
	Hycorn 42	Insufficient data					















