
C S I R O P U B L I S H I N G

Australian Journal of Agricultural Research

Volume 49, 1998
© CSIRO Australia 1998



A journal for the publication of original contributions
towards the understanding of an agricultural system

www.publish.csiro.au/journals/ajar

All enquiries and manuscripts should be directed to

Australian Journal of Agricultural Research

CSIRO PUBLISHING

PO Box 1139 (150 Oxford St)

Collingwood

Vic. 3066

Australia

Telephone: 61 3 9662 7628

Facsimile: 61 3 9662 7611

Email: jenny.fegent@publish.csiro.au



Published by **CSIRO PUBLISHING**
for CSIRO Australia and
the Australian Academy of Science



Improved methods for predicting individual leaf area and leaf senescence in maize (*Zea mays*)

C. J. Birch^{AC}, G. L. Hammer^B and K. G. Rickert^A

^A The University of Queensland, Gatton College, Lawes, Qld 4343, Australia.

^B QDPI/CSIRO, Agricultural Production Systems Research Unit, Toowoomba, Qld 4350, Australia.

^C Corresponding author; email: C.Birch@mailbox.uq.edu.au

Abstract. The ability to predict leaf area and leaf area index is crucial in crop simulation models that predict crop growth and yield. Previous studies have shown existing methods of predicting leaf area to be inadequate when applied to a broad range of cultivars with different numbers of leaves. The objectives of the study were to (i) develop generalised methods of modelling individual and total plant leaf area, and leaf senescence, that do not require constants that are specific to environments and/or genotypes, (ii) re-examine the base, optimum, and maximum temperatures for calculation of thermal time for leaf senescence, and (iii) assess the method of calculation of individual leaf area from leaf length and leaf width in experimental work. Five cultivars of maize differing widely in maturity and adaptation were planted in October 1994 in south-eastern Queensland, and grown under non-limiting conditions of water and plant nutrient supplies. Additional data for maize plants with low total leaf number (12–17) grown at Katumani Research Centre, Kenya, were included to extend the range in the total leaf number per plant.

The equation for the modified (slightly skewed) bell curve could be generalised for modelling individual leaf area, as all coefficients in it were related to total leaf number. Use of coefficients for individual genotypes can be avoided, and individual and total plant leaf area can be calculated from total leaf number. A single, logistic equation, relying on maximum plant leaf area and thermal time from emergence, was developed to predict leaf senescence. The base, optimum, and maximum temperatures for calculation of thermal time for leaf senescence were 8, 34, and 40°C, and apply for the whole crop-cycle when used in modelling of leaf senescence. Thus, the modelling of leaf production and senescence is simplified, improved, and generalised. Consequently, the modelling of leaf area index (LAI) and variables that rely on LAI will be improved.

For experimental purposes, we found that the calculation of leaf area from leaf length and leaf width remains appropriate, though the relationship differed slightly from previously published equations.

Additional keywords: corn, leaf area index, modelling.

Introduction

Accurate simulation of leaf area index in crop models is crucial to accurate simulation of light interception and dry matter accumulation. Commonly, simulation models of maize, for example CERES-Maize (Jones and Kiniry 1986), AUSIM-Maize (Carberry *et al.* 1989; Carberry and Abrecht 1991), CORNF (Stapper and Arkin 1980), and a model proposed by Muchow *et al.* (1990; which will be referred to in this paper as the MSB model), use 2 methods of predicting each

of leaf area and leaf senescence, and thus leaf area index (LAI). This paper reports on the successful generalisation of equations for both leaf area and leaf senescence, for a wide range of cultivars that vary in leaf numbers.

Both existing methods use a leaf level approach to predicting individual leaf area, but the equations used differ substantially. One method uses a series of 4 equations that are either linear or curvilinear and are applied to specific ranges of leaf numbers (Eqns

Table 1. Principal equations used in modelling of leaf area and leaf senescence in AUSIM-Maize and the MSB model
 LFNO, leaf number; TLNO, total leaf number; TPLA, total plant leaf area; sc, coefficient of senescence

Eqn	Condition	Equation	Source
<i>(a) Discontinuous equations for individual leaf area (LALF)</i>			
1	Leaves 1–4	$LALF = 9 \cdot 8 * LFNO$	Carberry <i>et al.</i> (1989), Carberry and Abrecht (1991)
2	Leaves 5–12	$LALF = 5 \cdot 45 * LFNO^2$	As Eqn 1
3	Leaves 13 to TLNO – 3	546.6	As Eqn 1
4	Uppermost 3 leaves	$LALF = 520 / (LFNO + 5 - TLNO)^{0.5}$	As Eqn 1
<i>(b) Continuous equation for individual leaf area</i>			
5	All leaves	$LALF = A_{max} * \exp[a(LFNO - x_0)^2 + b(LFNO - x_0)^3]$	Dwyer and Stewart (1986) See also ^A
<i>(c) Discontinuous equations for prediction of senescence of leaf area (SLA)</i>			
6	Emergence to tassel initiation	$SLA = TPLA / 1000$	As Eqn 1
7	Tassel initiation to end of leaf growth	$SLA = TT * TPLA / 10000$	As Eqn 1 See also ^B
8	End of leaf growth to start of linear grain filling	$SLA = TPLA(0.06 + TT / 170 * 0.041)$	As Eqn 1 See also ^B
9	Start of linear grain filling to physiological maturity	$SLA = TPLA[0.09 + sc(TT / P5)^3]$	As Eqn 1 See also ^B
<i>(d) Continuous equation for prediction of the fraction of leaf area that has senesced (FSEN)</i>			
10	Throughout crop life	$FSEN = c * \exp(dTT)$	Muchow <i>et al.</i> (1990) See also ^C

^A A_{max} is area of largest leaf, x_0 is position of largest leaf, $x_0 = 0.46TLNO + 3.53$ (Stapper and Arkin 1980), $a = 0.00731$, $b = -0.0344$, $LFNO = 2.5 * \exp(0.00225TT)$ (Muchow *et al.* 1990).

^B TT is thermal time calculated as in Jones and Kiniry (1986).

^C $c = 0.00161$, $d = 0.00328$ (Muchow *et al.* 1990), TT is thermal time calculated as in Muchow *et al.* (1990).

1–4, Table 1). These equations will be referred to as discontinuous equations and are used to predict individual leaf area in the version of AUSIM-Maize referred to in this paper. The other method also uses a leaf level approach, but uses a single (continuous) function, which describes a modified (slightly skewed) bell curve (Eqn 5, Table 1). It is the method used in the MSB model. The form of Eqn 5 was proposed by Dwyer and Stewart (1986), and the coefficients used in the MSB model are those derived for the cultivar XL82 grown at Katherine, Northern Territory (Muchow and Carberry 1989).

Leaf senescence is an expression of plant ageing, but may be influenced by genotype, cultural factors (e.g. plant population, nutrient status, pest incidence), carbon supply, and the environment in which the crop is grown (Carberry *et al.* 1993). Genetic differences in senescence have been reported for grain sorghum (e.g. Hammer *et al.* 1987), and delayed senescence in maize (the ‘stay green characteristic’) varies with genotype (Wolfe *et al.* 1988; Kaiser *et al.* 1991; Havilah and Kaiser 1994).

There are also 2 common methods of modelling leaf senescence. One approach, as in CERES-Maize and AUSIM-Maize, uses a series of 4 discontinuous equations [Eqns 6–9 (from AUSIM-Maize), Table 1]. These equations predict senesced leaf area (SLA) as a fixed fraction of total plant leaf area (TPLA) present on a day (Eqn 6), or TPLA present and thermal time, as a measure of leaf age (Eqns 7–9). The individual equations only apply for specific phenological intervals. Eqn 9 also has provision to modify the predicted SLA by a coefficient for senescence (sc) in individual genotypes. This capability is present in AUSIM-Maize, and replaces a constant in CERES-Maize.

The second method of predicting leaf senescence uses a single, logistic (continuous) function (Eqn 10) throughout the crop life. Eqn 10 calculates the fraction of leaf area that has senesced (FSEN), rather than leaf area that has senesced. The equation relies only on thermal time as a measure of leaf age and 2 constants derived for the cultivar XL82 grown at Katherine (Muchow *et al.* 1990).

The discontinuous equations for both leaf area and leaf senescence are used in AUSIM-Maize, and the continuous equations are used in the MSB model. Leaf area index is calculated daily from both approaches by adjusting the single plant calculations for a known plant population.

Predicted LAI values from both approaches were unsatisfactory, when predicted and observed LAI were compared over a wide range of environments and genotypes (Birch 1996, 1997). The main errors were underprediction of leaf area of leaves above the 12th leaf, and thus total plant leaf area in AUSIM-Maize, underprediction of total leaf area in the MSB model, and overprediction of senesced leaf area in both models. Further, predictions of LAI from Eqns 5 and 10 were better than from Eqns 1–4 and 6–9 (Birch 1995, 1996, 1997). However, unless total leaf number (TLNO) and area of largest leaf (A_{\max}) can be estimated, there is a major disincentive to using Eqn 5. Also, since the values of the coefficients a and b in Eqn 5 may vary across cultivars, and the coefficients in Eqn 10 may vary, generalising Eqns 5 and 10 would improve modelling of leaf area and leaf senescence.

An alternative and superior method of predicting leaf senescence in grain sorghum has not been evaluated for maize:

$$\text{SLA} = \text{TPLA}_{\max} / \{1 + \exp[-f(\text{TT} - g)]\} \quad (11)$$

where TT is thermal time from emergence, calculated as for Eqn 8, TPLA_{\max} is the maximum total plant leaf area, and f and g are senescence coefficients. Of these, f refers to the steepness of the curve when SLA is plotted against thermal time after emergence, and g to thermal time from emergence until 50% of the leaf area has senesced (Carberry *et al.* 1993).

There are several weaknesses in each of the present approaches to predicting individual leaf area. Firstly, there is no adjustment for reduced leaf size at high or low temperature. Secondly, neither approach has adequate provision to reduce leaf area when inadequate assimilate supply, because of environmental constraints or plant competition, limits leaf area. Both high and low temperatures reduce leaf area of individual leaves (Thiagarajah and Hunt 1982; Hardacre and Turnbull 1986; Reid *et al.* 1990; Grobelaar 1963, cited by Ritchie and Ne Smith 1991). Also, the areas of individual leaves were lower in the high temperature environment at Katherine (Carberry *et al.* 1989; Carberry 1991) than on plants with similar TLNO in the more moderate environment at Gatton (Birch 1989; Karanja 1993). Further, inadequate photosynthate supply may result in smaller leaves (Thiagarajah and Hunt 1982).

The equations for predicting individual leaf area have been derived from a narrow range in TLNO, and thus may be highly specific. For instance, Eqns 1–4 were derived from plants with 18 leaves (Carberry *et al.* 1989), and Eqn 5, as calibrated by Muchow and Carberry (1989), is similarly affected. The original form of Eqn 5, proposed by Dwyer and Stewart (1986), was developed with plants with 18–20 leaves. However, Eqn 5 [with different values of a and b than presented by Dwyer and Stewart (1986) and Muchow and Carberry (1989)] could be used to predict individual leaf area for maize plants with TLNO of 12–17. Also, the values of A_o , x_o , a , and b could be calculated from TLNO (Keating and Wafula 1992). The use of predicted values for A_o , x_o , a , and b reduced precision in prediction of individual leaf area (LALF), but there was improved utility of Eqn 5. However, their generalisations need to be validated, and if necessary, the relationships modified for $\text{TLNO} > 17$.

Calculation of areas of individual leaves

In studies of leaf area in maize, area of individual leaves is usually calculated from leaf length (LL) and the leaf width (at the widest point; LW) as follows (Montgomery 1911):

$$\text{Individual leaf area} = 0.75 * \text{LL} * \text{LW} \quad (12)$$

However, no studies have been conducted recently to reassess the applicability of this equation to the many hybrids of maize now available. Though other workers in maize have used similar values of the coefficient in Eqn 12, e.g. 0.73 (Mc Kee 1964; Dwyer and Stewart 1986) and 0.72 (Keating and Wafula 1992), it is prudent to reassess Eqn 12 because of the changes in genotypes since 1911.

The objective of this paper is to develop improved and generalised equations for predicting LALF and leaf senesced leaf area, and thus LAI in maize. This required the re-examination of the temperature coefficients for calculation of thermal time for leaf senescence, and the coefficient in Eqn 12.

Materials and methods

A field experiment was conducted at The University of Queensland, Gatton College (27° 33' S, 152° 20' E), on a moderately fertile, deep alluvial vertisol (Typic Chromustert) (Powel 1982; Schafer *et al.* 1986) that has moderate water-holding capacity and is well drained. Irrigation and nutrients were applied at rates to ensure that non-limiting conditions were maintained. Specifically, nitrogen was applied at 150 kg N/ha as Nitram (34% N) immediately after planting and incorporated by irrigation. Additional nitrogen (as urea or Nitram) at 50 kg N/ha was applied 4 and 7 weeks after planting and incorporated by irrigation. Zinc was applied as a foliar spray of

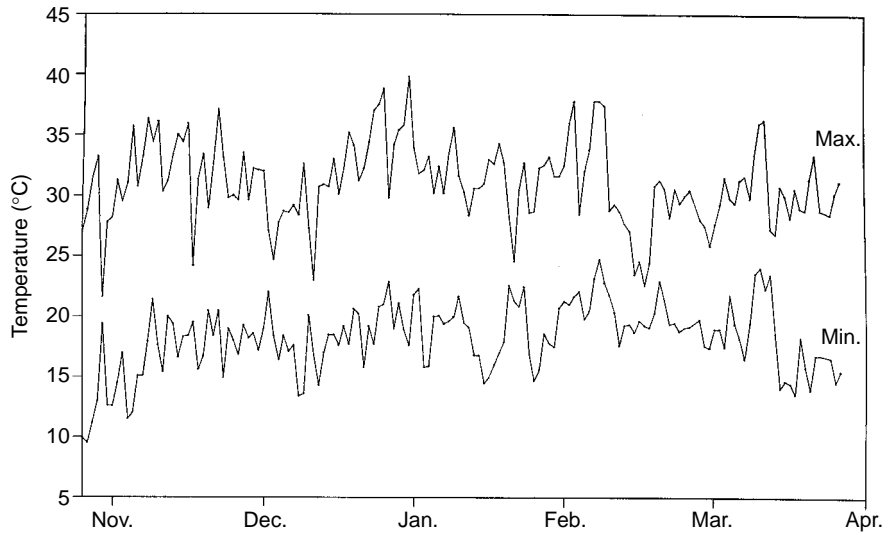


Fig. 1. Daily maximum and minimum temperatures from 25 October 1994 to the completion of the study. The months are shown at the first day of each.

1 kg $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ in 100 L H_2O /ha at 2, 4, and 6 weeks after emergence in each planting. The soil was well supplied with all other nutrients. Irrigation was scheduled by the WATER-SCHED (DPI 1993) technique, and the crop sprinkler irrigated when the accumulated deficit reached, at most, 50 mm. The sprinklers were mounted on risers so that they were above the crop canopy, to ensure satisfactory water distribution. Insects were controlled by the appropriate chemicals, and weeds were controlled chemically or by hand removal.

Experimental design

Five cultivars of maize (Hycorn 42, DK529, XL82, Hycorn 83, and Barker) were planted 5 cm deep on 25 October 1994, after routine land preparation, and thinned to an established population of 70 000 plants/ha at 1 week after emergence. Based on the American Eastern States Relative Maturity System, the cultivars represented relative maturities of 90–105 days (Pacific Hycorn 42, De Kalb DK529), 106–120 days (De Kalb XL82), 121–135 days (Hycorn 83), and >135 days (Barker).

Plots were 12 m long and consisted of 4 rows 0.75 m apart. All data were collected from the central 2 rows of each plot. Three replicates were used in a randomised complete block design.

Data collection

Number of leaves, leaf length, and leaf width

Five randomly located plants in each plot were tagged and used for non-destructive sampling every 7–11 days. Leaf 5 and, after leaf 4 had senesced, leaf 10 were tagged as reference leaves. Total number of leaves and numbers of green and senesced leaves were counted until the last leaf was fully expanded. After that, only the number of senesced leaves was recorded. (A leaf was considered senesced if less than half of its area remained green.) Leaf length (LL; from the junction of the leaf blade and leaf sheath, or in leaves that were not fully expanded, the junction of the expanded part of the leaf and the whorl) and leaf width (LW; at the widest part of the leaf) were measured on each leaf. Senesced leaf area and, by difference, green leaf

area were calculated from the numbers of senesced and green leaves. At 24 and 65 days after emergence, 2 representative plants were removed from each plot, and the area of each green leaf (LALF) was measured with a planimeter. LL and LW of each leaf were also recorded. These data were used to reassess Eqn 12.

Crop ontogeny

Tassel initiation (TI) was not measured, but was estimated to occur at the same thermal time after emergence [i.e. at 208, 270, 254, 270, and 365 degree-days, using the temperature coefficients in Birch (1996) for Hycorn 42, DK529, XL82, Hycorn 83, and Barker] as in the crop planted on 29 October 1993 (Birch 1996).

The times of tasseling and silking were recorded using the 5 tagged plants. Tasseling was recorded on the following scale: 0, tassel present, no anther sacks extruded; 1, up to 25% of the tassel with anther sacks extruded; 2, 25–50% of the tassel with anther sacks extruded; 3, 50–75% of the tassel with anther sacks extruded; 4, 75–100% of the tassel with anther sacks extruded. The presence of cobs was recorded and the stage of silking was recorded on the following scale: 0, cobs present, no silks; 1, silks extruded and green (red-green in Barker); 2, silks colour changed to red or red-brown. When more than half the plants rated reached 2 on the tasseling scale, and 1 on the silking scale, tasseling and silking were deemed to have occurred across the whole crop.

The times of physiological maturity were determined by regularly sampling 2 cobs per plot to assess the presence of black layers at the base of the grain, the black layer indicating that no further accumulation of grain mass is possible (Daynard and Duncan 1969). Grains were removed from the base, middle, and distal end of the cobs. Physiological maturity was taken to have occurred when at least 75% of the removed grains in each plot had black layers.

Weather data

Daily maximum (TMAX) and minimum (TMIN) temperatures (Fig. 1), rainfall, and evaporation were recorded at an automatic weather station 300 m from the site.

Use of additional data

Additional data from Kenya (Keating and Wafula 1992) were added to expand the range in total leaf number when examining prediction of individual leaf area, and from Gatton (Karanja 1993), when examining relationships for leaf senescence. The Kenyan study was conducted at Katumani under mean temperatures (Wafula 1989) that were, as in the present experiment (Fig. 1), near the optimum for leaf expansion (mean 24°C). Thus, any effects of temperature on individual leaf area in these data sets will be minimal. The cultivar used in Kenya was Katumani Composite B (KCB). In the study of Birch (1989), the areas of individual leaves on Katumani Composite B were the same as on 3 other cultivars (De Kalb XL82, Pioneer 6875, and Barker) for leaves 1–12. Above leaf 12, the area of individual leaves differed, because of variation in crop duration, and the number of leaves on the plants. Thus, the data for Katumani Composite B can be added to the data from the present experiment, as this cultivar has the same individual leaf area as the other cultivars.

Data analysis

As an initial step, the observed area of leaves for individual leaves was regressed on leaf length and leaf width to determine the coefficient in Eqn 12 for each cultivar. As there was no significant ($P < 0.05$) difference among these, a single coefficient was determined by regression. Analysis of variance was also carried out on the number of leaves per plant, total plant leaf area, and senesced leaf area for each sampling time, to determine differences among the cultivars. Fitted values of SLA and FSEN were calculated using base, optimum, and maximum temperatures for the life of the crop of 8, 34, and 44°C (as in AUSIM-Maize) and 8, 34, and 40°C (Birch 1996). A base temperature of 0°C after silking (Muchow *et al.* 1990; Birch 1996) was also examined for calculation of thermal time for leaf senescence.

Equations relating the size (A_{\max}) and position (x_0) of the largest leaf to TLNO were derived from the data from this experiment and from Keating and Wafula (1992).

The predictions of LALF by Eqns 1–4 and 5, and of SLA by Eqns 6–9 and FSEN by Eqn 10 (coefficients shown in Table 1), were compared with observed data from this experiment. Since few of the predictions were sufficiently accurate across the range of cultivars used, revised coefficients were calculated for each equation for each cultivar. Only the results for equations that are applied for prediction of senescence through the whole of crop life are reported. An exhaustive exploration of possible relationships between the coefficients and environmental variables (e.g. temperature, expressed as thermal time) and plant characteristics (e.g. TLNO) was carried out. This investigation revealed some potentially useful relationships, especially for the coefficients in Eqns 1, 2, and 5 for prediction of individual leaf area, but not for Eqns 8 and 9 (for SLA), or Eqn 10 (for FSEN). Consequently, the utility of Eqn 11 as a predictor of SLA was investigated using data from this experiment and Karanja (1993). The fitted values from the individual leaf area, SLA, and FSEN were then compared with the observed data from the present trial.

Results

Calculation of leaf area from leaf length and leaf width

Analysis of variance of coefficients for Eqn 12 showed that there were no significant differences among the coefficients for individual cultivars at either sampling

time. Thus, the average coefficient over both samplings (0.79 ± 0.003) was adopted.

Number of leaves per plant

Fig. 2a shows the total number of leaves produced by the 5 cultivars between planting and silking. At all sampling times, Barker had most leaves, whereas other cultivars were generally similar to one another. Differences among all cultivars arose after silking of Hycorn 42, as the slower maturing cultivars had more leaves. Fig. 2b shows the number of senesced leaves in each cultivar from emergence to physiological maturity. In each cultivar, 5–7 leaves senesced prior to silking, and there were few significant differences among cultivars. After silking, the number of senesced leaves increased as the crop aged, but differences among cultivars appeared only after 98 days after emergence. Green leaves persisted for longer on Barker than on other cultivars, but senesced rapidly as maturity approached.

Total plant leaf area and senesced leaf area

There were no differences in total plant leaf area (cm^2/plant) among cultivars until 47 days after emergence (Fig. 2c). Subsequently, differences mirrored crop durations: as duration increased, total plant leaf area increased. Similarly, there were no differences in senesced leaf area (cm^2/plant) until after silking (Fig. 2d). The increase in senesced leaf area after silking was initially slow, but increased rapidly as physiological maturity approached. This pattern was especially pronounced in Barker (Fig. 2d). There were no differences between cultivars in green leaf area (cm^2) until 54 days after emergence. Subsequently, differences in green leaf area followed the pattern of the crop durations of the cultivars used. Maximum green leaf area occurred at silking in all cultivars.

Leaf area distribution

As TLNO increased, the area of the largest leaf (A_{\max}) also increased (Fig. 3). For leaves 1–11, leaf areas were generally the same in all cultivars. However, Barker and Hycorn 83 tended to have smaller and larger leaves, respectively, than other cultivars, although the differences were usually not significant for the first 11 leaves. For higher leaves, Hycorn 42 had the smallest, Barker the largest, and the other cultivars were intermediate. These differences are associated with declining area of upper leaves, and differences in crop duration, that led to differences in total leaf number among cultivars.

Area and position of largest leaf

The relationship between A_{\max} (cm^2) and total leaf number is shown in Fig. 4 for data from the present

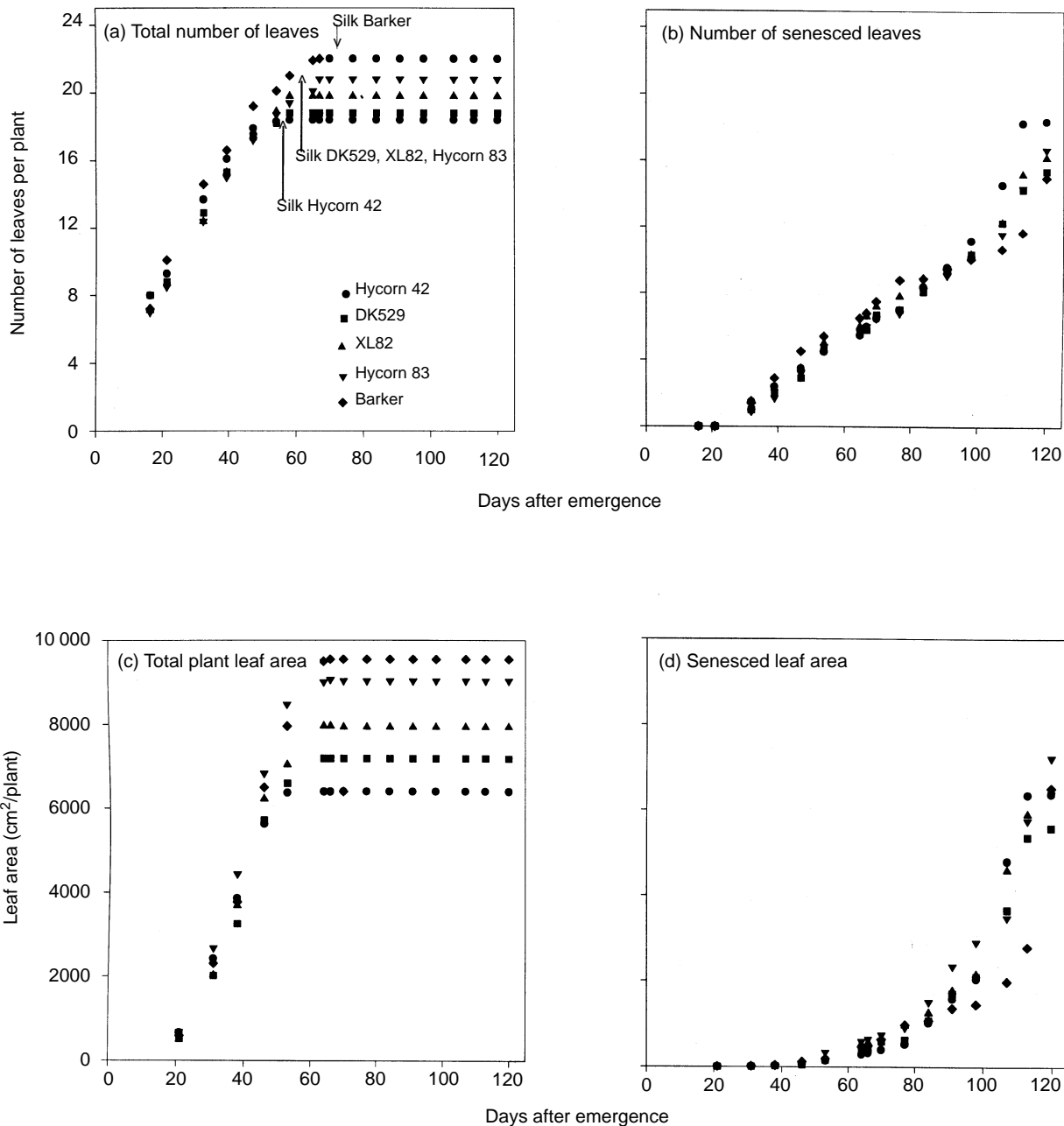


Fig. 2. (a) Total leaf number and (b) number of senesced leaves; and (c) total leaf area and (d) senesced leaf area per plant leaf area in 5 cultivars of maize at various times after emergence.

experiment and the data of Keating and Wafula (1992). A nonlinear regression of A_{max} on total leaf number (TLNO) explained the variation in leaf area, for plants with 12–23 leaves:

$$A_{max} = 1000 \cdot \exp[(-1.17 \pm 0.015) + 0.047(\pm 0.006) \cdot TLNO] \quad (r^2 = 0.82, n = 18) \quad (13)$$

However, this equation can only be used until TLNO = 25; at higher values of TLNO it produces A_{max} in

excess of 1000 cm², for which there is no support in the literature or from the present experiment.

The position of the largest leaf (x_0) was consistently two-thirds of the way up the stem, and related to total leaf number as follows:

$$x_0 = 0.67(\pm 0.01) \cdot TLNO \quad (r^2 = 0.99, n = 11) \quad (14)$$

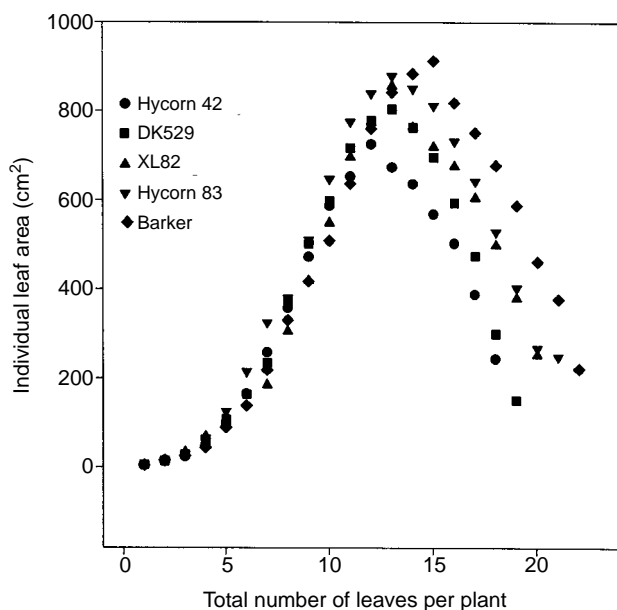


Fig. 3. Mean area of individual leaves *v.* total leaf number per plant in 5 cultivars of maize.

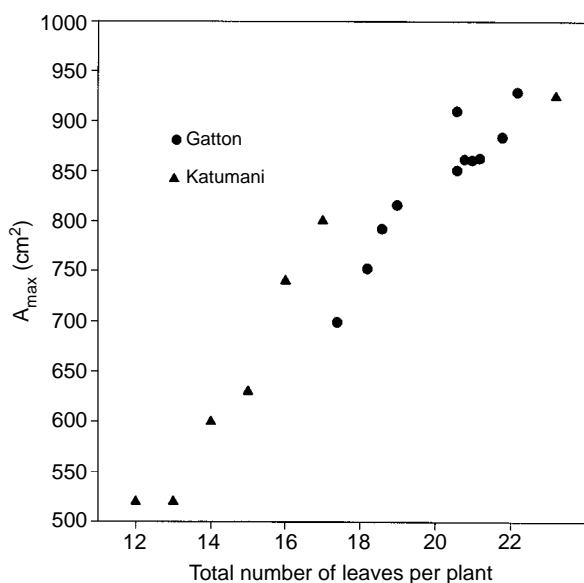


Fig. 4. Relationship between the area of the largest leaf (A_{max}) and total number of leaves per plant (TLNO):

$$A_{max} = 1000 \cdot \exp(-1.17 + 0.47 \cdot TLNO)$$

$$r^2 = 0.82, n = 18$$

Prediction of leaf area by discontinuous equations

A single equation was derived for leaves 1–3 for all cultivars:

$$\text{Leaf area} = 8.35(\pm 0.44) \cdot LFNO$$

$$(r^2 = 0.96, n = 30) \tag{15}$$

where LFNO is leaf number. This equation had a higher r^2 and provided more accurate fitted LALF than Eqn 1 which is used in AUSIM-Maize.

For higher leaves, 3 equations were developed, but again the thresholds for changing from one equation to another differed from those used for Eqns 2–4. A boundary was set at LFNO = 11, because differences occurred among cultivars in individual leaf area for LFNO > 11. The form of the equation for leaves 4–11 was:

$$LALF = \text{constant} \cdot LFNO^2 \tag{16}$$

The values of the constant were $5.53(\pm 0.16)$, $5.68(\pm 0.15)$, $5.35(\pm 0.18)$, $6.13(\pm 0.13)$, and $4.90(\pm 0.11)$ for Hycorn 42, DK 529, XL82, Hycorn 83, and Barker. For all regressions, r^2 was 0.99. As the 10% confidence intervals of coefficients for Hycorn 42, DK529, and XL82 overlapped, the data for these cultivars were combined, the resultant constant being $5.52(\pm 0.09)$ ($r^2 = 0.99$). The coefficient derived across all cultivars was $5.4(\pm 0.09)$ ($r^2 = 0.99$), a value similar to that currently used in AUSIM-Maize.

The leaf area of the largest leaf (A_{max}) was related to the total leaf number (Eqn 13). For leaves above the largest leaf, a single equation was calculated:

$$LALF = 1.58(\pm 0.05) \cdot A_{max} - 2.62(\pm 0.14) \cdot LFNO^2$$

$$(r^2 = 0.94) \tag{17}$$

Comparison of observed and fitted leaf areas from discontinuous equations

The fitted leaf areas of individual leaves calculated from Eqns 13, 15, 16 (with $a = 5.4$, derived for all cultivars), and 17 generally compared favourably to the observed leaf areas (Fig. 5).

Prediction of leaf area by a continuous function

Eqn 5 describes a slightly skewed bell curve, in which the area of the largest leaf (A_{max}) represents the amplitude of the curve, x_o is leaf number at the peak of the curve, and a and b are coefficients, a controlling the breadth and b the skew of the curve. To examine whether a and b varied with cultivar and/or total leaf number, A_{max} and x_o were set at the experimental means for each cultivar, and the coefficients a and b were calculated for each cultivar (Table 2). The a and b coefficients for Hycorn 42 and DK529, and for XL82 and Hycorn 83, were similar, and common coefficients were calculated for these pairs of cultivars (last 2 lines of Table 2). The combination of the data from the present experiment and Keating and Wafula (1992)

(Fig. 6a, b) produced logistic relationships, which can be used to generalise Eqn 5, between a and b , and total leaf number. These relationships were:

$$a = -0.009(\pm 0.004) - \exp[-0.20(\pm 0.007)*\text{TLNO}]$$

$$(r^2 = 0.95, n = 12) \quad (18)$$

and

$$b = 0.0006(\pm 0.0002) - \exp[-0.43(\pm 0.008)*\text{TLNO}]$$

$$(r^2 = 0.91, n = 12) \quad (19)$$

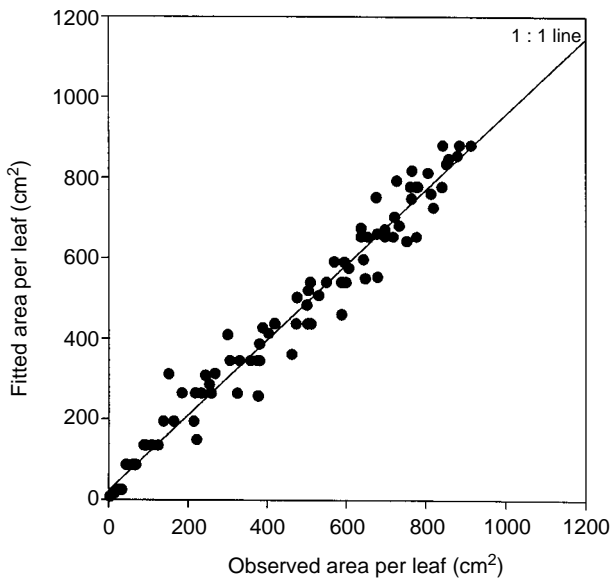


Fig. 5. Fitted *v.* observed areas of leaves: fitted values from discontinuous equations (Eqns 13, 16, 17, and 18):

$$y = 2.9(\pm 18.0) + 0.91(\pm 0.03)*x$$

$$r^2 = 0.97, \text{RMSD} = 50 \text{ cm}^2$$

Table 2. Coefficients in Eqn 2 to predict individual leaf area when the area of the largest leaf (A_{max}) and the leaf number of the largest leaf (x_o) are given

Cultivar	$a \pm \text{s.e.}$	$b \pm \text{s.e.}$
Hycorn 42	-0.0344 ± 0.0012	0.00068 ± 0.00012
DK529	-0.0319 ± 0.0016	0.00052 ± 0.00019
XL82	-0.0283 ± 0.0015	0.00046 ± 0.00008
Hycorn 83	-0.0263 ± 0.0006	0.00053 ± 0.00009
Barker	-0.0229 ± 0.0009	0.00036 ± 0.00008
Hycorn 42 and DK 529	-0.0328 ± 0.0013	0.00073 ± 0.00014
XL82 and Hycorn83	-0.0269 ± 0.0009	0.00063 ± 0.00009

Comparison of observed and fitted leaf areas when using the continuous function

When the area and position of the largest leaf (A_{max} and x_o) were supplied from the experimental data, the fitted individual leaf areas calculated using the a and b

coefficients in Table 2 were very close to the observed data. However, this assessment relied on the provision of A_{max} and x_o , and the revised a and b coefficients for each cultivar. Therefore, 3 further assessments of fitted leaf areas were performed in which the parameters and coefficients were progressively replaced with predictions based on the equations for each parameter and coefficient presented earlier. The replacements were: (a) Eqns 18 and 19 were used to calculate a and b from observed TLNO; (b) Eqns 13, 18, and 19 were used to calculate A_{max} , a , and b from observed TLNO; and (c) Eqns 13, 14, 18, and 19 were used to calculate A_{max} , x_o , a , and b from observed TLNO.

The fitted leaf areas from each of these options were generally very good, and thus the comparison of fitted and observed leaf areas is presented only for (c) above (Fig. 7).

Temperature coefficients for calculation of thermal time for leaf senescence

Fitted values of SLA and FSEN when base, optimum, and maximum temperatures of 8, 34, and 40°C were used for thermal time were at least as accurate as those calculated with base, optimum, and maximum temperatures of 8, 34, and 44°C, and superior to a base temperature of 0°C after silking. Since these findings were consistent over all equations, base, optimum, and maximum temperatures of 8, 34, and 40°C were used in the balance of this paper, and are the same as the critical temperatures for crop ontogeny until silking (Birch 1996).

Prediction of senesced leaf area by discontinuous equations

It was possible to derive discontinuous equations, similar to Eqns 6–9, that provided accurate fitted senesced leaf area for each cultivar. However, it was not possible to generalise the equations. Coefficients specific to each genotype were required for 2 of the equations that were derived, and this renders their use in modelling difficult. Consequently, they are not reported here, as they do not meet the objectives of the study. More broadly applicable equations that do not require coefficients for individual cultivars have been developed, and appear later.

Prediction of the fraction of total plant leaf area that has senesced

The natural logarithm of the observed fraction of leaf area that had senesced (FSEN) was plotted against thermal time from emergence [using base, optimum, and maximum temperatures of 8, 34, and 40°C derived for leaf production (Birch 1996)] to investigate the use of Eqn 10.

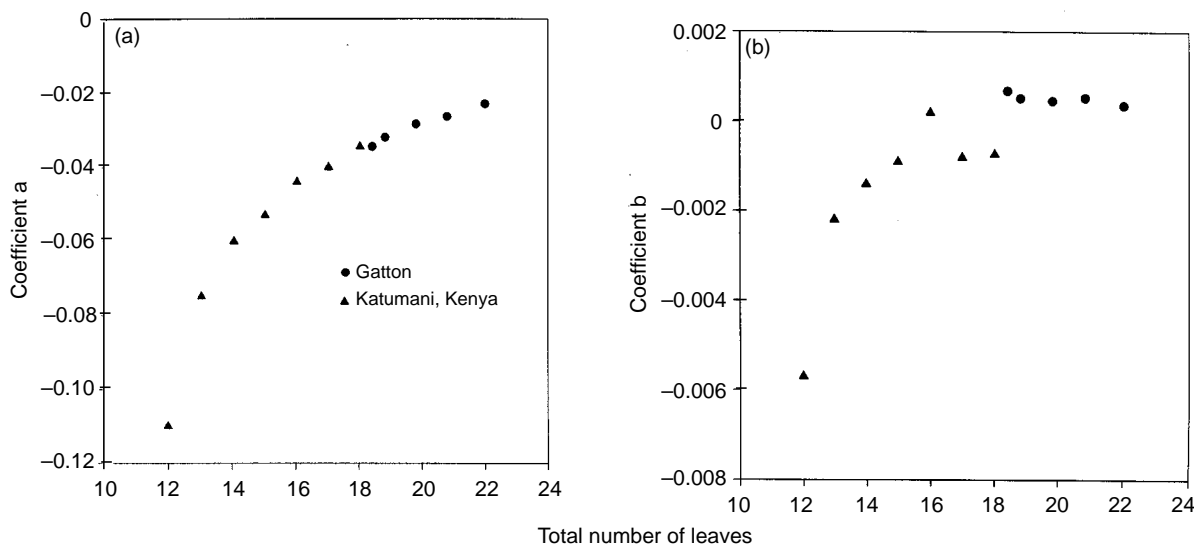


Fig. 6. Relationship between (a) the *a* coefficient or (b) the *b* coefficient in the modified bell curve (Dwyer and Stewart 1986) (Eqn 5) and total leaf number (TLNO) in the present experiment at Gattton and at Katumani, Kenya.

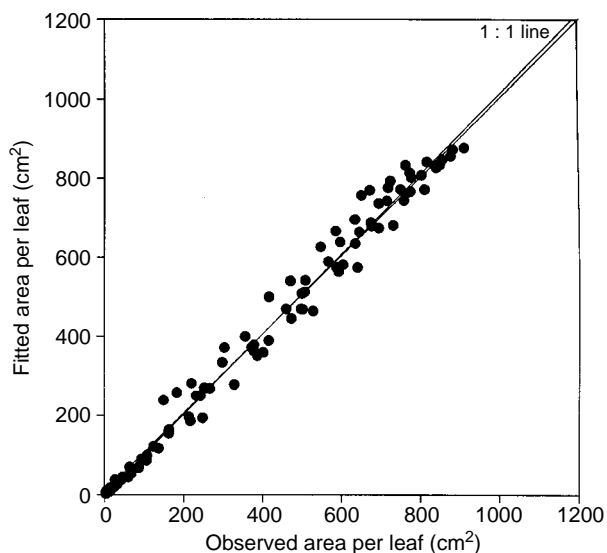


Fig. 7. Comparison of fitted and observed leaf areas: fitted values when A_{max} , x_0 , a , and b in Eqn 5 were fitted from total leaf number (TLNO) by Eqns 13, 16, 17, and 18:

$$y = 0.2 (\pm 6.3) + 1.01 (\pm 0.01) * x$$

$$r^2 = 0.99, \text{RMSD} = 36 \text{ cm}^2$$

There were changes in the slope of the plot of FSEN against thermal time from emergence, for each cultivar. The changes in slope were associated with silking. Before silking, the values of *c* in Eqn 10 were very low and all cultivars were different (Table 3). The *d* coefficients were similar for Hycorn 42, DK 529, and XL82, higher for Hycorn 83 and lowest for Barker. The value for each of *c* and *d* calculated from all data prior to silking (Table 3) provided acceptable fitted values of the proportion of leaf area that had senesced

until silking. After silking, a consistent pattern in both the *c* and *d* coefficients emerged; the value of *c* increased and *d* decreased as crop duration increased. The fitted values of FSEN from values of *c* and *d* that were common to the 5 cultivars before silking and cultivar-specific values after silking (Table 3) were satisfactory (Fig. 8). However, the accuracy of the fitted values declined as the proportion of leaf area that had senesced increased rapidly as physiological maturity was approached.

Table 3. Values of *c* and *d* in Eqn 10 for five cultivars

Cultivar	$a \pm s.e$	$b \pm s.e.$	r^2
<i>Before silking</i>			
Hycorn 42	0.000345 ± 0.000004	0.00475 ± 0.00013	0.99
DK 529	0.000109 ± 0.000006	0.00604 ± 0.00074	0.96
XL82	0.000638 ± 0.000064	0.00434 ± 0.00105	0.85
Hycorn 83	0.000029 ± 0.000001	0.00822 ± 0.00027	0.99
Barker	0.001017 ± 0.000029	0.00359 ± 0.00022	0.98
All	0.000467 ± 0.000028	0.00509 ± 0.00056	0.96
<i>After silking</i>			
Hycorn 42	0.00105 ± 0.000041	0.00349 ± 0.00020	0.98
DK 529	0.00188 ± 0.000065	0.00309 ± 0.00015	0.98
XL82	0.00295 ± 0.000133	0.00277 ± 0.00016	0.98
Hycorn 83	0.000353 ± 0.000115	0.00270 ± 0.00013	0.98
Barker	0.00426 ± 0.000570	0.00230 ± 0.00044	0.82

It was not possible to generalise the equation for the fraction of leaf area that had senesced, and thus, like the discontinuous equations, the utility of Eqn 10 depends on the supply of genotype-specific coefficients. Thus, the approach does not meet the objective of this study.

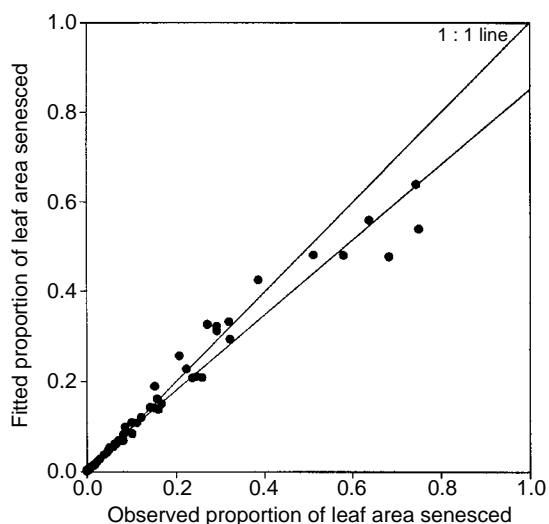


Fig. 8. Comparison of fitted and observed proportion of leaf area that has senesced using Eqn 12, with a and b common before silking and for individual cultivars after silking:

$$y = 0.01(\pm 0.02) + 0.84(\pm 0.02) * x$$

$$r^2 = 0.96$$

Prediction of senesced leaf area on a whole plant basis

Prediction of senesced leaf area on a whole plant basis (Eqn 11) was investigated using a similar approach to that proposed for grain sorghum by Carberry *et al.* (1993). The derivation of the value of the coefficients in Eqn 11, f (the steepness of the curve) and g (the thermal time from emergence to half of the leaf area having senesced), followed the procedures in Carberry *et al.* (1993).

The coefficient g was derived first, and was related to total leaf number:

$$g = 107.9 * TLNO - 327 \quad (r^2 = 0.68, n = 17) \quad (20)$$

Eqn 20 was then used to derive f for individual cultivars, and for all data combined (Table 4).

Table 4. Total leaf number and values of the senescence coefficient f for each cultivar and for all nine cultivars

The coefficients of determination were above 0.95 for all regressions in Table 4

Cultivar	TLNO	$f \pm s.e.$	n
Hycorn 42	18.4	0.0054 ± 0.0002	11
DK 529	18.8	0.0054 ± 0.0002	11
XL82	19.8	0.0043 ± 0.0002	11
Hycorn 83	20.8	0.0040 ± 0.0003	12
Barker	22.0	0.0036 ± 0.0002	13
Hycorn 40 ^A	16.7	0.0055 ± 0.0003	6
Hycorn 50 ^A	16.3	0.0048 ± 0.0006	7
GH5009 ^A	17.8	0.0046 ± 0.0001	6
GH5019wx ^A	19.0	0.0047 ± 0.0004	8
All		0.0048 ± 0.0003	85

^A Cultivars used by Karanja (1993).

The data in Table 4 show that f differed among the cultivars, with a range of 0.0036–0.0055. Values of f for individual cultivars and from all data were used to fit values for senesced leaf area. The fitted values of senesced leaf area differed across cultivars, and were superior when f was based on individual cultivars rather than on all data combined.

The fitted senesced leaf area using f derived for all cultivars in Table 4, to generalise Eqn 11, agreed reasonably well with observed senesced leaf area (Fig. 9a). To compare this approach and that of Eqn 10 (using cultivar-specific coefficients for c and d ; Fig. 8), the proportion of leaf area predicted by the generalisation of Eqn 11 to have senesced is compared with the observed proportion of leaf area that had senesced in Fig. 9b. It is evident that some precision has been lost in the generalisation of Eqn 11. However, it was not possible to generalise Eqn 10, and thus the generalisation of Eqn 11 is preferred for prediction of leaf senescence.

Discussion

Leaf area calculation

The method of calculation of leaf area (Eqn 15) proposed by Montgomery (1911) is sound, although the coefficient for the present trial was 0.79, rather than 0.75 derived by Montgomery and used by some authors, e.g. Bonhomme *et al.* (1982), Muchow and Davis (1988). The coefficient derived here is considered reliable, as it was derived from cultivars with diverse genetic background and maturity.

Leaf area distribution

Sensitivity analysis, in which the values of coefficients and variables were changed that influence prediction of leaf number per plant, individual leaf area, and total plant leaf area, produced conflicting effects on predictions of individual leaf area made by AUSIM-Maize (Birch 1996). These conflicts are probably partly responsible for changes to the CERES-Maize model to produce AUSIM-Maize for semi-arid tropical areas of Australia (Carberry *et al.* 1989; Carberry and Abrecht 1991), and CM-KEN for Kenya (Keating *et al.* 1991). Thus, there is a strong case for developing a single equation that can be generalised for many environments.

The modified bell curve (Eqn 5) requires fewer coefficients than the discontinuous equations (Eqns 13, 15, 16, and 17) and is more generally applicable. A_{\max} and x_0 were related to total leaf number in grain sorghum by Muchow and Carberry (1989), who found that Eqn 5 accounted for more of the variation than did discontinuous equations that were similar to Eqns 1–4.

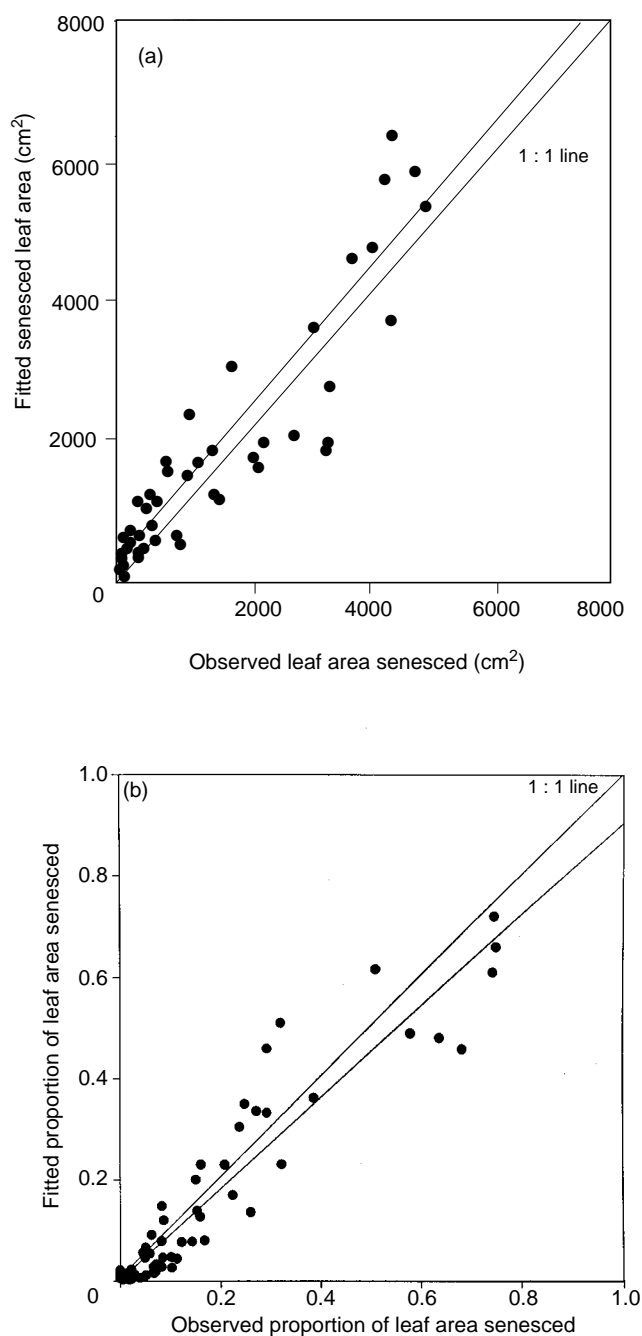


Fig. 9. Comparison of fitted and observed (a) senesced leaf area and (b) proportion of leaf area that has senesced by using Eqn 14, with f and g common to all cultivars. Regression equations for comparisons in (a) and (b) are:

$$\begin{aligned} (a) \quad y &= 109(\pm 159) + 1.03(\pm 0.08) * x \\ r^2 &= 0.90, \text{RMSD} = 510 \text{ cm}^2 \\ (b) \quad y &= 0.0024(\pm 0.005) + 0.90(\pm 0.05) * x \\ r^2 &= 0.98, \text{RMSD} = 0.07 \end{aligned}$$

Also, in maize, values of the parameters A_{\max} and x_o , and the coefficients a and b in Eqn 5, had previously been related to total leaf number (Keating and Wafula 1992), albeit for a limited range in total leaf number

(12–17). Further, Eqn 5 has been successfully used to predict individual leaf area in grain sorghum, and A_{\max} , x_o , a , and b have been related to total leaf number in that crop (Carberry *et al.* 1993).

It was possible to calibrate the coefficients in Eqns 13, 15, 16, and 17, and to produce satisfactory fitted individual leaf areas (Fig. 5). From this assessment, it appears that Eqns 15 and 16 (for leaves 1–12) are generally applicable. Thus, they will be useful in models (such as AUSIM-Maize) that predict leaf area production and crop ontogeny concurrently. These equations may be useful until tassel initiation, when total leaf number is able to be predicted. Fitted individual leaf areas of the lower leaves are similar from Eqns 15 and 16 and the modified bell curve (generalised by Eqns 13, 14, 18, and 19). Thus, either option could be used until tassel initiation, but the use of the generalised Eqn 5 would require separation of modelling of processes of crop development and leaf area production. However, such an approach is not biologically valid and may not be attractive for this reason alone. After tassel initiation, the generalised form of Eqn 5 should be used, as it provides more accurate predictions of the larger leaves produced between tassel initiation and silking.

The modified bell curve (Eqn 5) has been generalised by incorporating the data of Keating and Wafula (1992), which provided a wide range in total leaf number per plant. Thus, a sound basis existed for the equations relating A_{\max} , x_o , a , and b in the modified bell curve to total leaf number (Eqns 13, 14, 18, and 19). These equations mean that only total leaf number needs to be predicted for Eqn 5 to be used. Hence, provided the time of TI can be predicted, TLNO can be predicted from thermal time that accumulates from germination to TI. The time of TI depends on cultivar differences described by genotype constants for the basic vegetative period and photoperiod sensitivity. Hence, accurate data on these 2 genotype characteristics become crucial to the prediction of TLNO and LALF. This aspect has been explored in more detail in Birch (1996).

The use of generalised equations in environments where temperatures differ from the optimum for leaf expansion is likely to overestimate LALF under high or low temperatures. High temperatures result in smaller leaves (e.g. Reid *et al.* 1990), and maize grown in the high temperature environment at Katherine (Carberry 1991) had smaller leaves than the plants with similar total leaf number (18–20 leaves) in the present study. Reduced leaf area and reduced leaf length at mean temperatures above 20–23°C have been reported (Thiagarajah and Hunt 1982; Hardacre and Turnbull 1986; Grobelaar 1963, cited by Ritchie and

Ne Smith 1991). Leaf length of the second leaf of maize was maximised when temperatures were 20–24°C (Nie *et al.* 1992). Also, leaf areas of individual leaves were distributed approximately symmetrically around the optimum temperature for leaf area (Thiagarajah and Hunt 1982; Hardacre and Turnbull 1986; Reid *et al.* 1990). In the present trial, mean daily temperatures rarely exceeded 25°C prior to the full expansion of the largest leaves. Also, field evidence showed that, for plants with 18 leaves, A_{\max} increased until the mean temperature reached 23–25°C, and then declined at higher mean temperatures (Karanja 1993). It is clear that an adjustment to prediction of leaf area is needed to incorporate the effects of temperature. By combining the data from Thiagarajah and Hunt (1982) and Hardacre and Turnbull (1986), and converting them to relative terms (scale 0–1), a quadratic equation to describe the effect of daily mean temperature (TEMPM) on leaf area was derived:

$$\text{Relative leaf area} = 1 - 0.0051^* (\text{TEMPM} - 24)^2 \quad (21)$$

This equation implies that there is no leaf expansion if the daily mean temperature falls below 8°C or exceeds 40°C. An adjustment similar to Eqn 21 will be needed in models to adjust leaf area production for temperature effects, so that the models are not specific to the site and temperature conditions. Further, there may be a need to modify the prediction of leaf area if leaf area is constrained by photosynthate supply. This possibility has been raised by Thiagarajah and Hunt (1982), and is explored in Birch (1996). Detailed studies of photosynthate production and distribution among plant parts are necessary to propose the appropriate equations to account for reduced leaf area because of inadequate photosynthate supply.

Leaf senescence

In the present trial, cultural factors were not limiting, and the environment was common to all cultivars for most of the crop cycle. Hence, the effect of genotype on the senescence coefficients can be assessed.

The prediction of senesced leaf area by the discontinuous equations (Eqns 6–9) in AUSIM-Maize depends on total plant leaf area alone for only part of the crop life, and for the balance, total plant leaf area and thermal time. By contrast, the continuous equation (Eqn 10) used in the MSB model relies on thermal time alone. Both of these approaches are based on data that may be confounded by cultural and environmental variables (Carberry *et al.* 1993), and thus may produce erroneous predictions of leaf senescence.

Neither the discontinuous equations (Eqns 6–9) nor the logistic equation (Eqn 10) for prediction of leaf senescence could be generalised sufficiently to avoid the use of coefficients that were specific to genotype. This was especially true after silking when rapid senescence occurs. However, Eqn 10 was able to be generalised for senescence before silking. Thus, it can be used until total plant leaf area is predicted at silking. This approach will be acceptable in models such as AUSIM-Maize and CERES-Maize that predict leaf expansion and senescence as concurrent processes up to silking. After silking, the method proposed by Carberry *et al.* (1993; Eqn 11) should be adopted. The applicability of this technique had been established for grain sorghum by Carberry *et al.* (1993), and was found in this study to be suitable for maize. However, there were some relatively large errors in fitted senesced leaf area when the generalised form was used. These probably arose because there were differences among cultivars in the senescence coefficients. Since the equation for g (Eqn 20), which had a relatively low r^2 , is used to derive the values of f , there may be errors in the values of both g and f . Nevertheless, the range in values of f for maize is relatively narrow (0.0036–0.0055) when compared with the range for grain sorghum (0.046–0.103) reported by Carberry *et al.* (1993). These authors also reported a low r^2 (0.49) on their equation for g , and their values for f will also be affected by the inherent inaccuracies in calculated values of g . It is clear that the approach described by Eqn 11 holds promise for predicting leaf senescence, but that further refinements are needed to improve its utility. In particular, because of delayed senescence in cultivars with the ‘Stay Green’ characteristic, further investigations are needed to extend the application of this approach. Nevertheless, Eqn 11, with Eqn 20 used to predict the coefficient g , appears to be the most useful of the options examined in this paper, and avoids the use of coefficients for particular cultivars. Thus, a common senescence coefficient (f) (0.0048±0.0003) can be used and the curve steepness coefficient (g) can be calculated from total leaf number (Eqn 11).

Conclusions

This study improved methods of predicting leaf area production and senescence. A logistic equation, in which senesced leaf area is related to total leaf number and thermal time after emergence, was more readily generalised than discontinuous equations, or those based on thermal time alone. Also, all genotype and environment effects on leaf senescence are mediated by total leaf number, and as with individual leaf area, no adjustments for genotype appear to be needed. Thus, in modelling, provided total leaf number can

be predicted accurately, both individual leaf area and leaf senescence can be predicted. These generalised procedures developed here mean that modelling of leaf area production by maize has been simplified. However, the approach needs to be confirmed in independent data sets from different environments, since it does not consider the influence of assimilate limitation on leaf area.

Acknowledgments

Grateful appreciation is extended to Dr P. S. Carberry for provision of a copy of the AUSIM-Maize model and the supporting documentation, Dr R. C. Muchow for a copy of the MSB model, and to Mr R. J. Bell for assistance in collection of the field data, and in general to the University of Queensland, Gatton College, for provision of field resources and equipment, without which this study would not have been possible. Special mention is also made of Dr R. F. Brown, Dr L. M. Bahnisch, Dr K. D. Healy, and Mr P. Morrisson for their valuable comments on the manuscript.

References

- Birch, C. J. (1989). Testing the CERES-Maize model under tropical and sub-tropical Australian conditions. Queensland Agricultural College Research Report, Queensland Agricultural College, Lawes.
- Birch, C. J. (1995). Performance and reliability of two maize simulation models in a range of environments. In 'Proceedings of International Congress on Modeling and Simulation (MODSIM95), 27–30 November 1995, The University of Newcastle, Newcastle, NSW. Volume 1: Agriculture, Catchment Hydrology and Industry'. (Eds. P. Binning, H. Bridgman, and B. Williams.) pp. 344–9. (Modeling and Simulation Society of Australia: Canberra.)
- Birch, C. J. (1996). Modeling crop ontogeny, leaf area and dry matter accumulation and distribution in diverse cultivars of maize. PhD Thesis, The University of Queensland.
- Birch, C. J. (1997). Testing the performance of two maize simulation models with a range of cultivars of maize (*Zea mays*) in diverse environments. *Environmental Software* **11**, 91–8.
- Bonhomme, R., Ruget, F., Derieux, M., and Vincourt, P. (1982). Relations entre production de matière sèche aérienne et énergie interceptée chez différents géotypes de maïs. *C. R. Acad. Sc. Paris*, t. 294 (1982). Serie III, 393–8.
- Carberry, P. S. (1991). Test of leaf-area development in CERES-Maize: a correction. *Field Crops Research*, **27**, 159–67.
- Carberry, P. S., and Abrecht, D. G. (1991). Tailoring crop models to the semi-arid tropics. In 'Climatic Risk in Crop Production'. Proceedings, International Symposium on Climatic Risk in Crop Production: Models and Management for the Semiarid Tropics and Subtropics. Brisbane, Australia, 2–6 July 1990. (Eds R. C. Muchow and J. A. Bellamy.) pp. 157–82. (CAB: Wallingford, UK.)
- Carberry, P. S., Hammer, G. L., and Muchow, R. C. (1993). Modeling the genotypic and environmental control of leaf area dynamics in grain sorghum. III Senescence and prediction of green leaf area. *Field Crops Research* **33**, 329–51.
- Carberry, P. S., Muchow, R. C., and McCown, R. L. (1989). Testing the CERES-Maize simulation model in a semi-arid tropical environment. *Field Crops Research* **20**, 297–315.
- Daynard, T. B., and Duncan, W. G. (1969). The black layer and grain maturity in corn. *Crop Science* **9**, 473–6.
- DPI (1993). WATERSCHED—irrigation scheduling for field crops. Queensland Department of Primary Industries, Brisbane.
- Dwyer, L. M., and Stewart, D. W. (1986). Leaf area development in field-grown maize. *Agronomy Journal*, **78**, 334–43.
- Hammer, G. L., Hill, K., and Schrodter, G. N. (1987). Leaf area production and senescence of diverse grain sorghum hybrids. *Field Crops Research* **17**, 305–17.
- Hardacre, A. K., and Turnbull, H. L. (1986). The growth and development of maize (*Zea mays*) at five temperatures. *Annals of Botany* **58**, 779–87.
- Havilah, E. J., and Kaiser, A. G. (1994). The 'Stay-Green' characteristic and maize silage production. In 'Make it with Maize'. Proceedings Second Australian Maize Conference 6–9 February 1994, The University of Queensland, Gatton College, Lawes. (Eds C. J. Birch, R. J. Fletcher, P. Albury, and A. Andrews.) pp. 209–12. (Maize Association of Australia.)
- Jones, C. A., and Kiniry, J. R. (Eds) (1986). 'CERES-Maize, a Simulation Model of Maize Growth and Development.' (Texas A&M University Press: College Station, TX.)
- Kaiser, A. G., Havilah, E. J., and Colless, J. M. (1991). Characteristics required in Australian Forage Maize Hybrids. In 'Maize in Australia—Food, Forage and Grain'. Proceedings First Australian Maize Conference, Moama-Echuca, 15–17 April 1991. (Ed. J. Moran.) pp. 28–33. (Maize Association of Australia.)
- Karanja, D. R. (1993). The effect of planting date on growth and development of short, medium and long season maize (*Zea mays*) cultivars. MAgSc Thesis, The University of Queensland.
- Keating, B. A., Godwin, D. C., and Watiki, J. M. (1991). Optimising nitrogen inputs in response to climatic risk. In 'Climatic Risk in Crop Production'. Proceedings, International Symposium on Climatic Risk in Crop Production: Models and Management for the Semiarid Tropics and Subtropics. Brisbane, Australia, 2–6 July 1991. (Eds R. C. Muchow and J. A. Bellamy.) pp. 329–58. (CAB: Wallingford, UK.)
- Keating, B. A., and Wafula, B. M. (1992). Modeling the fully expanded area of maize leaves. *Field Crops Research* **29**, 163–76.
- McKee, G. W. (1964). A coefficient for computing leaf area in hybrid corn. *Agronomy Journal* **56**, 240–1.
- Montgomery, E. G. (1911). Correlation studies in corn. 24th Annual Report, Agricultural Experiment Station of Nebraska. pp. 109–59.
- Muchow, R. C., and Carberry, P. S. (1989). Environmental control of phenology and leaf growth in a tropically adapted maize. *Field Crops Research* **20**, 221–36.
- Muchow, R. C., and Davis, R. (1988). Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment. II Radiation interception and biomass accumulation. *Field Crops Research* **18**, 17–30.
- Muchow, R. C., Sinclair, T. R., and Bennett, J. M. (1990). Temperature and solar radiation effects on potential maize yield across locations. *Agronomy Journal* **82**, 338–43.
- Nie, G. Y., Long, S. P., and Baker, N. R. (1992). The effects of development at sub-optimal growth temperatures on photosynthetic capacity and susceptibility to chilling dependent

- photoinhibition in *Zea mays*. *Physiologia Plantarum* **85**, 554–60.
- Powel, B. (1982). Soils of the Gatton Research Station. Queensland Department of Primary Industries Bulletin QB82005. Queensland Department of Primary Industries, Brisbane.
- Reid, J. F., Zur, B., and Hesketh, J. D. (1990). The dynamics of maize canopy development. 2. Leaf area growth. *Biotronics*, **19**, 99–107.
- Ritchie, J. T., and Ne Smith, D. S. (1991). Temperature and crop development. Ch 2. *In* 'Modeling Plant and Soil Systems'. (ASA/CSSA/SSSA: 677 S. Segoe Rd, Madison, WI 53711.)
- Schafer, B. M., Ritchie, A. M., and Strachan, D. B. (1986). Soils of the Queensland Agricultural College farm, Darbalara. Queensland Agricultural College, Technical Paper No. 7.
- 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.)
- Thiagarajah, M. R., and Hunt, L. A. (1982). Effects of temperature on leaf growth in corn (*Zea mays*). *Canadian Journal of Botany* **60**, 1647–52.
- Wafula, B. M. (1989). Evaluation of the concepts and methods of response farming using crop growth simulation models. MAgrSc Thesis, The University of Melbourne.
- Wolfe, D. W., Henderson, T. C., Hsiao, T. C., and Alvino, A. (1988). Interactive water and nitrogen effects on senescence of maize. I Leaf area duration, nitrogen distribution and yield. *Agronomy Journal* **80**, 859–64.

Manuscript received 31 January 1997, accepted 21 October 1997