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Modelling the fully expanded area of maize leaves

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ABSTRACT

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Crop simulation models used for research or management, frequently require the development of leaf area to be mathematically described. This work examined, for maize, the relationship between the fully expanded area-per-leaf and leaf position, in an attempt to identify appropriate functions for use in such models.

The slightly skewed bell-shaped function of the form $LA_n = Y_0 * \exp(a*(xn-X_0)^2 + b*(xn-X_0)^3)$, was used to relate area-per-leaf (LA_n) to leaf position (xn). The amplitude of the curve (Y_0) represents the size of the largest leaf (at position X_0). Plants varied in total leaf number (TLNO) from 12 to 17 and this variation had a major bearing on the total leaf area per plant (TLA). Both Y_0 and X_0 were linearly related to TLNO (r^2 of 0.94 and 0.99 respectively). The parameter which controls the width of the bell-shaped curve (a), was non-linearly related to TLNO ($r^2=0.99$), while the parameter that controls the degree of skewness (b), varied little with TLNO.

Use of the bell-shaped curve in combination with the functions relating its parameters (Y_0, a, X_0) to TLNO, resulted in a root mean standard deviation (RMSD) of estimates of total leaf area per plant (TLA) of 176 cm^2 for plants varying in TLNO from 12 to 17 and in TLA from 2839 to 6925 cm^2. Bell-shaped functions were successfully fitted to independent area-per-leaf data from plants whose TLNO ranged from 13 to 26. The parameters developed in this study allowed area-per-leaf and TLA to be modelled accurately when non-limiting cultural conditions maximized leaf size. Under such circumstances, the bell-shaped curve with parameters linked to TLNO was shown to be a simple and flexible model of the potential area of individual leaves in maize. Resource constraints (such as those that can develop under high plant population) were shown to limit leaf size to less than that predicted by this model. Future work needs to examine the use of the bell-shaped curve in a simulation model context to address these constraints.

INTRODUCTION

The biomass produced by a crop is a function of the accumulated radiation intercepted and the efficiency with which radiant energy is converted to dry matter (Monteith, 1977; Muchow, 1989). Intercepted radiation is in part a

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function of the pattern and extent of leaf area development. Leaf area is thus an important determinant of crop growth. Crop growth models are being used increasingly in research and management and their performance will be strongly influenced by the accuracy of the leaf area predictions.

Two distinct approaches have been used in the simulation of leaf area development in cereals. In the regression approach, leaf area increase is the differential of the regression of total leaf area per plant on some indicator of crop development (i.e., calender time, thermal time, leaf number etc.). This approach is exemplified by the CERES-Maize simulation model (Jones and Kiniry, 1986) in which leaf area increase is a discontinuous non-linear function of the number of leaf tips, which in turn is a linear function of thermal time. A similar approach is used in current sorghum models (Arkin et al., 1983; Hammer et al., 1987).

A more mechanistic approach has been proposed by Muchow and Carberry (1989a,b) which deals with the expansion of individual leaves and involves the following steps:
(1) Describe the rate of appearance of fully expanded leaves as a function of thermal time.
(2) Describe the fully expanded area of each leaf (LA_n) as a function of leaf number up the stem (xn).
(3) Estimate the contribution to leaf area per plant from still expanding leaves.
(4) Estimate loss of leaf area through senescence as a function of thermal time.

This paper is concerned with step (2), and two approaches have been used to describe the fully expanded area of cereal leaves. Dwyer and Stewart (1986) used a slightly skewed bell-shaped function to describe the area-per-leaf profile of a range of maize crops:

$$LA_n = Y_0 * \exp(a * (xn - X_0)^2 + b * (xn - X_0)^3) \quad (1)$$

where the amplitude (Y_0) represents the size of the largest leaf, the point of inflection (X_0) is the leaf number (xn) of the largest leaf, and a and b are constants.

Muchow and Carberry (1989) examined this function for maize but rejected it in favour of a series of four discontinuous linear and non-linear functions. Subsequently, Muchow and Carberry (1990) found the bell-shaped function accounted for a higher proportion of the variation in leaf area in sorghum plants than could be achieved with discontinuous functions. These authors refined the bell-shaped model by relating two of its parameters (Y_0 and X_0) to total leaf number (TLNO).

The purpose of this paper is to assess the wider applicability of the bell-shaped function by examining it over a much wider range of leaf number than was used by Muchow and Carberry (1990). Both our own and other workers' published data will be used to maximize the range in TLNO. The biological meaning of the model's parameters is also considered.

MATERIALS AND METHODS

Cultural details

The leaf size data for model development (Experiment 1) were collected at Katumani Research Station, Kenya (lat. 1°35'S, long. 37°14'E, altitude 1601 m) on a chromic Luvisol (Gicheru and Ita, 1987). The open-pollinated composite maize cultivar, Katumani Composite B (KCB), was sown in 0.75-m rows on 28 October 1985 and thinned to 2.2 plants m^{-2} 15 days from sowing. Rainfall and irrigation provided in the period up until silking was such that no water limitation occurred. The experiment was replicated twice in a split plot design and a nitrogen treatment effectively increased the replication to four when the high inherent fertility of the experimental field masked any nitrogen response. Meteorological conditions throughout the experimental period were given by Wafula (1989).

Measurements

The length and breadth of all leaves on a sample of four plants per plot were recorded at approximately weekly intervals from thinning to silking. Leaf numbers 6 and later 10 were marked to avoid confusion as lower leaves senesced. The lamina area of both fully expanded and expanding leaves was calculated as length×breadth×0.72 (F.K. Lenga, pers. commun., 1988). Data for each plant were processed separately and the maximum area of each leaf (LA_n, where n is the number of the particular leaf from the base of the plant, excluding the coleoptile) identified, along with TLNO produced by the plant at silking.

Characteristics of the bell-shaped curve

The bell-shaped curve (Eq. 1) has four parameters and they can all, to varying degrees, be interpreted in a biologically meaningful way. This is most obvious with Y_0 and X_0 which are the area and position (leaf number from the base of the plant) of the largest leaf on a plant (Fig. 1a and b). The parameter, a, can be interpreted as the 'breadth' of the area-per-leaf profile. Low values of a result in area-per-leaf profiles that rise sharply and fall sharply (Fig. 1c). As a increases, a broader area-per-leaf profile results. The parameter b controls the degree of skewness in the area-per-leaf profile. Negative values of b are associated with area-per-leaf profiles that are skewed towards the left (i.e., towards leaf numbers less than X_0) (Fig. 1d). Positive values of b result in profiles that are skewed towards the right (i.e., $xn > X_0$). A value of zero for b means that the area-per-leaf profile is symmetrical about X_0.

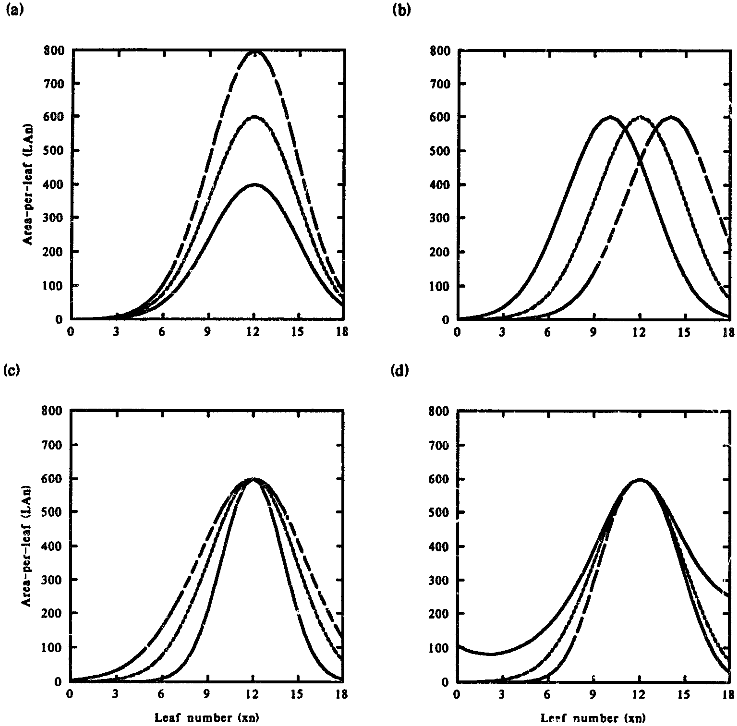

Fig. 1. Characteristics of the slightly skewed bell-shaped function $LA_n = Y_0 * \exp(a * (xn - X_0)^2 + b * (xn - X_0)^3)$
Parameters common to all curves unless stated below: $Y_0 = 600$, $X_0 = 12$, $a = -0.06$, $b = -0.0005$.
(a) Effects of varying Y_0: 400 —; 600 ------; 800 – –.
(b) Effects of varying X_0: 10 —; 12 ------; 14 – –.
(c) Effects of varying a: -0.12 —; -0.06 ------; -0.04 – –.
(d) Effects of varying b: -0.004 —; -0.0005 ------; 0.006 – –.

Data analysis

For each category of TLNO, mean lamina area-per-leaf and leaf number were related using the bell-shaped function and the NONLIN routines of SYSTAT (Wilkinson, 1988). The parameters of the bell-shaped function were related to TLNO using the same routines. The statistic root mean standard deviation (RMSD) was calculated to compare n pairs of predicted (P) and observed (O) parameters, i.e.,

$$\mathrm{RMSD} = [(\mathrm{Sum}(\mathrm{O}-\mathrm{P})^2)/n]^{0.5}$$

The RMSD is calculated either on an individual leaf basis ($\mathrm{RMSD_L}$) or total leaf area basis ($\mathrm{RMSD_T}$) and is a measure of the accuracy of the prediction representing an average weighted difference between observed and predicted data.

Validation data

Area-per-leaf data were available from another experiment (referred to as Experiment 2) with the cultivar KCB at Katumani planted 3 November 1986. The crops were grown at two populations, 22 000 and 66 000 plants ha^{-1} and water supply was non-limiting during canopy development.

Data on the area-per-leaf versus leaf number relationship were also obtained from Cooper (1979), Thiagarajah and Hunt (1982), Dwyer and Stewart (1986) and Muchow and Carberry (1989). Cooper's data relate to a long maturity maize hybrid (H6302) grown at three altitudes (1268, 1890, 2250 m) in western Kenya. The data of Dwyer and Stewart come from three hybrids grown over four years in Ottawa, Canada. The data of Muchow and Carberry (1989) are for the hybrid Dekalb XL82 grown in a hot semi-arid tropical environment in northern Australia. The data of Thiagarajah and Hunt concern the effect of temperature in controlled environments on leaf growth of the maize hybrid A498×CG10.

RESULTS AND DISCUSSION

Area-per-leaf profiles as influenced by TLNO

The composite genetic background of the KCB cultivar means that it exhibits a wide variation in TLNO, ranging from 12 to 17. The distribution of TLNO was approximately normal with a mean of 14.7 leaves/plant.

The relationship between leaf size and leaf number for plants differing in TLNO is shown in Fig. 2. The area of the largest leaf (Y_0) is clearly correlated with its position (X_0) (i.e., $Y_0 = -477 + 106X_0$, $r^2 = 0.93$, $n = 6$), both increasing as TLNO increases. The bell shaped function (Eq. 1) provided a good description for all values of TLNO (Fig. 2) with coefficients of determination greater than 0.99 for all curves (n in the range 12 to 17).

Sensitivity to curve parameters

Whilst the bell-shaped function fitted the observed data well, the need to measure (in the case of X_0 ad Y_0) or estimate (in the case of a and b) four parameters for its application is likely to be a disincentive to its use. Dwyer and Stewart (1986) have suggested that it is possible to normalize the functions shown in Fig. 2 in terms of Y_0 and in doing so, estimate average values of the parameters X_0, a and b, which can be used for all leaf profiles. Muchow

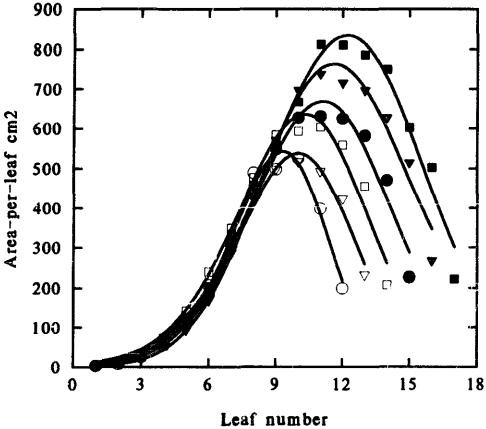

Fig. 2. Fully expanded area-per-leaf of the cultivar KCB grown at Katumani at low population in the absence of water deficits and fitted bell-shaped curves for each value of TLNO ($r^2=0.99$ in all cases, n varies from 12 to 17):
○ TLNO=12; $Y_0=542.8$, $a=-0.110$, $X_0=9.3$, $b=-0.0057$;
▽ TLNO=13; $Y_0=537.7$, $a=-0.075$, $X_0=10.0$, $b=-0.0020$;
□ TLNO=14; $Y_0=635.4$, $a=-0.060$, $X_0=10.3$, $b=-0.0014$;
● TLNO=15; $Y_0=668.2$, $a=-0.052$, $X_0=11.1$, $b=-0.0009$;
▼ TLNO=16; $Y_0=763.0$, $a=-0.044$, $X_0=11.6$, $b=-0.0007$;
■ TLNO=17; $Y_0=835.1$, $a=-0.041$, $X_0=12.2$, $b=-0.0007$.

and Carberry (1990) found they could use common values of a and b, but had to retain individual values of X_0 for each sorghum leaf profile in their dataset.

We examined four options by fitting the bell-shaped function to the normalized dataset (i.e., LA_n/Y_0 for all six curves shown in Fig. 2) progressively replacing parameters common to the entire dataset with fitted values specific to each curve. In Method 1, common values of X_0, a and b were derived from the relationship between normalized LA_n and xn. In Method 2, common values of a and b were obtained while only a common value of b was estimated in Method 3. Method 4 utilizes individual fitted values for all parameters.

The effects of using common values of the bell-shaped curve parameters (X_0, a and b) on the precision of the estimates of LA_n and total leaf area per plant (TLA) are examined in Table 1. The error associated with estimates of individual sizes (LA_n) declined progessively as parameters common to all curves were replaced by individual parameters specific to each curve (Table 1). The errors associated with estimates of TLA actually increased as a common value of X_0 was replaced by specific values of X_0 fitted for each curve

TABLE 1

Observed values of TLA (cm^2) compared with those predicted using the bell-shaped function with parameters derived in four ways. Root mean squared deviation of individual leaf area ($RMSD_L$) and total leaf area ($RMSD_T$) are also shown

TLNO	Observed TLA	Method 1		Method 2		Method 3		Method 4	
		TLA	$RMSD_L$	TLA	$RMSD_L$	TLA	$RMSD_L$	TLA	$RMSD_L$
12	2839	3172	101	3580	77	2723	28	2855	17
13	3268	3587	64	3640	38	3206	18	3271	14
14	4324	4686	69	4502	30	4312	26	4374	26
15	4856	5316	54	4786	27	4859	25	4887	25
16	5923	6429	75	5583	40	6085	32	5897	28
17	6928	7355	105	6191	65	6974	30	6981	30
$RMSD_T$			407		480		88		34

Method 1: Y_0-fitted, $X_0 = 10.59$, $a = -0.0379$, $b = 0.00257$, $r^2 = 0.90$.
Method 2: Y_0 and X_0 fitted, $a = -0.0530$, $b = -0.00032$, $r^2 = 0.95$.
Method 3: Y_0, X_0, and a all fitted, $b = -0.00067$, $r^2 = 0.99$.
Method 4: Y_0, X_0, a, and b all fitted as per Fig. 2.

(cf. Method 1 and 2 in Table 1). This apparently contradictory result occurred because compensatory errors in estimates of LA_n in Method 1 resulted in more accurate estimates of TLA, than did the more accurate estimates of LA_n of Method 2. The use of fitted values of a for each curve markedly improved the estimates of TLA ($RMSD_T = 88$ cm^2), and a further small improvement was associated with replacing a single common estimate of b by fitted values for each curve ($RMSD_T = 34$ cm^2).

Estimation of the bell-shaped curve parameters

Muchow and Carberry (1990) observed that two of the function's parameters, Y_0 and X_0, could be simply estimated from TLNO. Similar relationships were found with maize in this study (Fig. 3 a,b) and in addition, non-linear relationships were found to exist between TLNO and the bell-shaped function parameters, a and b (Fig. 3 c,d) i.e.:

$$Y_0 = -235 + 62 * \text{TLNO}, \; r^2 = 0.94 \tag{2}$$

$$X_0 = 2.42 + 0.574 * \text{TLNO}, \; r^2 = 0.99 \tag{3}$$

$$a = -0.0183 + 0.0146 / (1 - 0.0966 * \text{TLNO}), \; r^2 = 0.99 \tag{4}$$

$$b = 0.0004 + 0.00037 / (1 - 0.0883 * \text{TLNO}), \; r^2 = 0.98 \tag{5}$$

The effects on the precision of the estimates of LA_n and TLA, of replacing the fitted values of Y_0, X_0, a and b (from Fig. 2), with estimates from the functions based on TLNO (Fig. 3), are examined in Table 2. Some precision

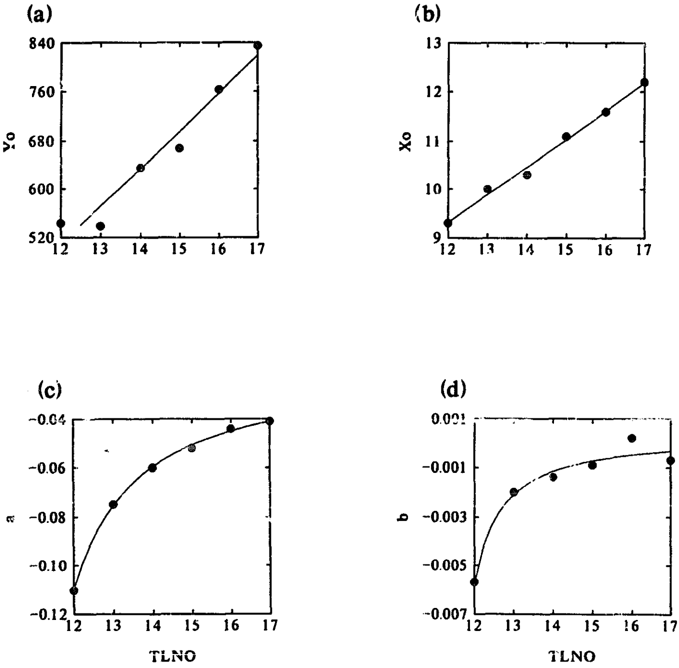

Fig. 3. Relationships between the parameters of the bell-shaped function and TLNO for the cultivar KCB grown at Katumani at low population in the absence of water deficits.
(a) $Y_0 = -235 + 62 * \mathrm{TLNO}$, $r^2 = 0.94$, $n = 6$.
(b) $X_0 = 2.42 + 0.574 * \mathrm{TLNO}$, $r^2 = 0.99$, $n = 6$.
(c) $a = -0.0183 + 0.0146/(1 - 0.0966 * \mathrm{TLNO})$, $r^2 = 0.99$, $n = 6$.
(d) $b = 0.0004 + 0.00037/(1 - 0.0883 * \mathrm{TLNO})$, $r^2 = 0.98$, $n = 6$.

was lost when the parameters of the bell-shaped curve were estimated from TLNO, but this is compensated for by the enhanced utility of the technique. Total leaf area varied from 2839 to 6928 cm^2 and this variation could be estimated with an $RMSD_T$ of 176 cm^2 through the use of the bell-shaped function (Eq. 1) with the Y_0, X_0, and a parameters estimated from TLNO (Eqs. 2, 3 and 4), and a value of b common to all values of TLNO (-0.0007). No real advantage was gained by estimating separate values of the skewness parameter, b (Table 2).

TABLE 2

Observed values of TLA (cm^2) compared with those predicted using the bell-shaped function with parameters derived in four ways. Root mean squared deviation (cm^2) of individual leaf area ($RMSD_L$) and total leaf area ($RMSD_T$) are also shown

TLNO	Observed TLA	Method 1		Method 2		Method 3		Method 4	
		TLA	$RMSD_L$	TLA	$RMSD_L$	TLA	$RMSD_L$	TLA	$RMSD_L$
12	2839	2988	92	3355	64	2547	35	2675	26
13	3268	3823	77	3898	56	3410	24	3493	26
14	4324	4681	67	4446	33	4249	33	4311	29
15	4856	5540	66	4994	30	5086	31	5127	31
16	5923	6388	76	5538	41	5931	29	5946	29
17	6928	7222	106	6076	69	6782	33	6770	33
$RMSD_T$			452		512		176		172

Method 1: Y_0 estimated according to Fig. 3a.
Method 2: Y_0 and X_0 estimated according to Fig. 3 a,b.
Method 3: Y_0, X_0 and a estimated according to Fig. 3 a,b,c.
Method 4: Y_0, X_0, a and b estimated according to Fig. 3 a,b,c,d.
Other parameters the same as for Table 1.

Validation data

The observed area-per-leaf profiles from Experiment 2 were compared with those predicted on the basis of the relationships between TLNO and the bell-shaped curve parameters developed in Experiment 1. Simulated LA_n and TLA were accurate (RMSD of 44 and 175 cm^2 respectively) under low plant population (Fig. 4a), but overestimates of areas of the larger leaves (Fig. 4b) increased errors under high plant population (RMSD of 55 and 395 cm^2 respectively, Table 3). Over both populations, TLA was estimated with an $RMSD_T$ of 305 cm^2 (Fig. 4c).

Comparisons with other studies

Equation 1 was also successfully fitted to area-per-leaf data from those studies reported by Cooper (1979) and Thiagarajah and Hunt (1982) (r^2 in the range 0.98 to 0.99). The bell-shaped curves obtained, together with those reported by Dwyer and Stewart (1986) and Muchow and Carberry (1989) for water non-limiting situations, are compared with the curve for TLNO = 15 from the present study (Fig. 5). The leaves studied by Muchow and Carberry (1989) and, to a lesser extent, Dwyer and Stewart (1986), were smaller than would have been expected on the basis of the present study. Our data most closely resemble those reported by Thiagarajah and Hunt (1982).

The parameters developed in this study were used to predict area-per-leaf and TLA of these other studies (Table 4). Good precision was obtained when cultural conditions were similar to those used to develop the bell-shaped curve

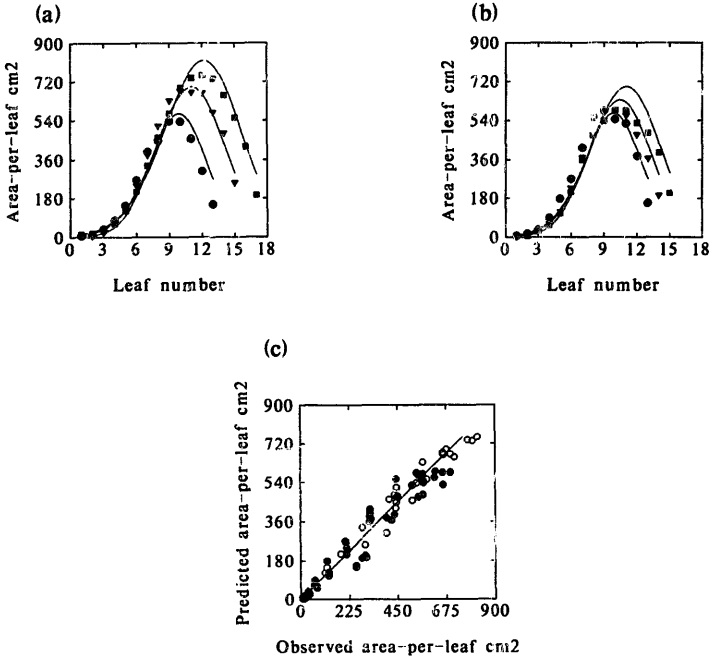

Fig. 4. Fully expanded area-per-leaf (LA_n) observed in Experiment 2 (symbols) and predicted (lines) from the bell-shaped function and parameters developed in Experiment 1.
(a) Low plant population for TLNO=13 (●), 15 (▼), 17 (■).
(b) High plant population for TLNO=13 (●), 15 (▼), 17 (■).
(c) Predicted LA_n versus Observed LA_n at low (○) and high (●) populations.

parameters (e.g., low plant populations and moderate temperature regimes studied by Thiagarajah, 1982), but errors increased under markedly different cultural conditions (e.g. high plant populations in the high temperature environment studies by Muchow and Carberry, 1990).

TABLE 3

Estimation of LA_n and TLA (cm^2) in experiment 2 using the parameters of the bell-shaped curve estimated from Experiment 1. Root mean squared deviation (cm^2) of individual leaf area ($RMSD_L$) and total leaf area ($RMSD_T$) are also shown

Treatment	TLNO	Observed TLA	Predicted TLA	$RMSD_L$
Low population	13	3379	3995	52
	15	5314	5128	36
	17	6561	6770	44
High population	14	4055	4312	43
	15	4549	5128	62
$RMSD_T$				305

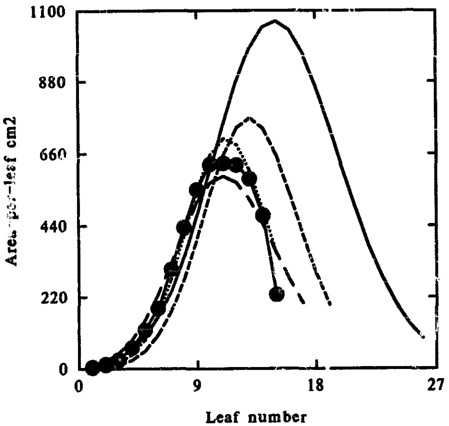

Fig. 5. Fully expanded area-per-leaf (LA_n) described by the bell-shaped function for a number of studies with maize:
(i) Cooper (1979), data from Kitale (—)
$LA_n=1068*\exp(-0.223*(xn-14.9)^2+0.00021*(xn-14.9)^3)$; $r^2=0.99$, $n=26$;
(ii) Dwyer and Stewart (1986), data from clay in 1981 (—)
$LA_n=768*\exp(-0.0396*(xn-13.0)^2-0.00099*(xn-13.0)^3)$, $r^2=0.99$, $n=19$;
(iii) Thiagarajah and Hunt (1982), data from 25/20°C (······)
$LA_n=708*\exp(-0.0504*(xn-11.2)^2+0.00060*(xn-11.2)^3)$, $r^2=0.99$, $n=15$:
(iv) Muchow and Carberry (1989), data from February sowing (– –)
$LA_n=590*\exp(-0.0344*(xn-11.0)^2+0.00073*(xn-11.0)^3)$, $r^2=0.98$, $n=17$;
(v) Symbols (●—●) refer to TLNO=15 in the current study.

TABLE 4

Estimation of LA_n and TLA (cm^2) of other workers' data sets using the parameters of the bell-shaped curve estimated from Experiment 1. Root mean squared deviation (cm^2) of individual leaf area ($RMSD_L$) and total leaf area ($RMSD_T$) are also shown

Treatment	TLNO	Observed TLA	Predicted TLA	$RMSD_L$
Cooper (1979)	26	12471	14350	283
Dwyer and Stewart (1986)	19	6798	8436	122
Thiagarajah and Hunt (1982)	15	5090	5127	34
Muchow and Carberry (1990)	17	5314	6771	144
$RMSD_T$				1444

GENERAL DISCUSSION

Total leaf area for plants ranging in TLNO from 12 to 17 was simulated with an $RMSD_T$ of 34 cm^2 using the bell-shaped curve and fitted parameters for each value of TLNO. The parameters could be estimated from TLNO with an acceptable loss of precision ($RMSD_T = 172$ cm^2) and there was little loss ($RMSD_T = 176$ cm^2) associated with the use of a fixed value of b (-0.00067). The bell shaped curve (Eq. 1), together with the relationships between the parameters of this curve (Y_0, a, and X_0) and TLNO (Eqs. 2, 3 and 4), provide a relatively simple and attractive model of expanded leaf area in maize.

An examination of our own and others' data indicates that the bell-shaped curve is a very robust descriptor of the area-per-leaf profile in maize. While the curve is empirical, its parameters can all be ascribed some biological meaning and two of them can be easily measured directly in the field. While it is outside the scope of this paper, there are good physiological reasons why a curve of this general shape should describe area-per-leaf profiles in cereals. Carbon supply to the growing point during the period of leaf primordium initiation and possibly leaf expansion will increase curvilinearly as assimilate supply from lower expanding leaves becomes increasingly available. Some maximum will be imposed by competition for assimilates from other sinks (stem growth, tassel initiation and growth etc.) after which time, leaf size would be expected to decrease.

Within a cultivar under non-limiting conditions of light, water and nutrients, the parameters of the bell-shaped curve can be simply related to TLNO and this greatly enhances the value of the relationships for simulation modelling. Total leaf number is easily measured and generally already estimated by such models.

While the bell-shaped curve has been shown in this work to be applicable to an extremely wide range of germplasm, we have not had data from such a range of germplasm grown under non-limiting conditions to isolate genetic differences in the relationships between TLNO and the parameters of the bell-shaped curve. Such differences are likely, although it is our hypothesis that they will be small once the dominant effect of TLNO on the area-per-leaf profile has been quantified by the model presented here.

This paper has shown that growth conditions can alter the parameters of the bell-shaped curve and their relationships with TLNO. Dwyer and Stewart (1986) had previously shown that Y_0 will vary in field grown maize in response to site and season variation. Little variation in X_0, a and b was observed by Dwyer and Stewart (1986) and they were successful in developing a model which combined normalized values of these parameters with values of Y_0 predicted from a seasonal water balance. This work has shown that TLNO has a major influence on Y_0, a and X_0, but in a manner that is predictable, at least under non-limiting conditions. Plants with more leaves will exhibit larger maximum leaf size (Y_0), at a higher leaf position (X_0). A similar result was obtained by Muchow and Carberry (1990) for sorghum and our work with maize suggests that it may be more generally applicable. In addition, this work has shown that such plants will have a broader leaf profile (i.e., less negative values of a). It follows therefore, that if the bell-shaped function is to be of value for describing fully expanded leaf area across diverse genotypes and environments, its parameters must be related to TLNO.

The dependence of the parameters of the bell-shaped curve on growth conditions is to be expected, given the known magnitude of environmental and cultural conditions on leaf area. This imposes a constraint on the use of the function to predict leaf area outside a simulation modelling context. Within a simulation model, this function can be used to predict the potential fully expanded lamina area-per-leaf, and either assimilate supply or the water and nutrient stress indices applied to discount this potential under limiting conditions.

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