

A Simple Quantitative Model to Predict Leaf Area Index in Sorghum

Sruthi Narayanan,* Robert M. Aiken, P. V. Vara Prasad, Zhanguo Xin, George Paul, and Jianming Yu

ABSTRACT

Leaf area index (LAI) is a widely used physiological parameter to quantify the vegetative canopy structure of crops. Over the years, several models to estimate LAI have been developed with various degrees of complexity and inherent shortcomings. The LAI simulation models proposed so far for sorghum [*Sorghum bicolor* (L.) Moench] either lack details of the leaf area dynamics of expanding leaves or demand exhaustive measurements. The objective of this study was to develop a simple quantitative model to predict the LAI of sorghum by introducing a new method for simulation of the leaf area of expanding leaves. The proposed model relates LAI to thermal time. It calculates LAI from an algorithm considering the total number of mature leaves, the area of mature leaves, the area of expanding leaves, and plant density. The performance of the model was tested using LAI data collected using a nondestructive method under field conditions. The slope of the regression of modeled LAI on observed LAI varied for photoperiod-sensitive and -insensitive genotypes in 2010. The coefficients of determination (R^2) between modeled and observed LAI were 0.96 in 2009 and 0.99 (photoperiod insensitive) and 0.95 (photoperiod sensitive) in 2010. The inclusion of expanding leaves in the model improved its accuracy. The model provides an accurate estimate of LAI at any given day of the vegetative growing season based only on thermal time and making use of default coefficients demonstrated in this research.

Leaf area index, defined as the total leaf area per unit ground area, is commonly used to quantify vegetative canopy structure (Welles and Norman, 1991). Leaf area index influences photon capture, photosynthesis, assimilate partitioning, growth, and yield formation (Rajcan and Tollenaar, 1999; Yin et al., 2000; Launay and Guérif, 2003; Rosenthal and Vanderlip, 2004; Tsiatas and Maslaris, 2008). Thus, accurate quantification of LAI is important for crop growth and development models.

Early attempts to simulate the leaf area in sorghum used the relationship between the area of a single leaf and the total leaf area of the whole plant (Bueno and Atkins, 1981). This relationship is largely influenced by genotype, location, and plant density and is not sufficient for estimating leaf area with crop development. Arkin et al. (1983) developed a leaf area model for sorghum consisting of five component processes of leaf growth to estimate

daily increments in leaf area using leaf appearance and expansion rates with considerations for leaf senescence. Although all the component processes of individual leaf growth were simulated in the sorghum leaf area model proposed by Arkin et al. (1983), the model required detailed inputs, and its predictions were not accurate considering the intensive measurements needed to use the model (Muchow and Carberry, 1990).

Rosenthal et al. (1989) developed the grain sorghum growth simulation model SORKAM, a derivative of the SORGF model (Arkin et al., 1976), to calculate individual leaf area based on maturity classes. The SORKAM model used the leaf appearance rate, leaf expansion rate, and leaf expansion duration to simulate leaf area dynamics. The leaf expansion rate ($\text{cm}^2 [\text{heat unit}]^{-1}$) was a function of leaf number in SORKAM. Rosenthal and Vanderlip (2004) further modified SORKAM to make it independent of maturity class or duration. Muchow and Carberry (1990) developed a leaf area model for a tropical grain sorghum hybrid considering the component process of leaf initiation as a function of photoperiod and thermal time. They considered fully expanded and expanding leaf areas separately but used a common equation to simulate them, assuming that the area of expanding leaves at a given time was equal to the fully expanded area of the next 1.6 sequential expanding leaves. Hammer et al. (1993) modeled genotypic and environmental control of leaf area dynamics for unculm and tillering grain sorghum at the whole plant and individual leaf levels and incorporated leaf area senescence into their approaches; however, they did not separate the total leaf area

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Abbreviations: ALG_x, apparent age of an expanding leaf; cGDD, cumulative growing degree days; DAP, days after planting; GDD, growing degree days; LAI, leaf area index; TLN, total number of mature leaves.

Table 1. Observed plant density (mean \pm standard deviation) of sorghum genotypes grown at Colby, KS, in 2009 and 2010.

Genotype	Photoperiod sensitivity	Plant density†	
		2009	2010
TX 7000	normal	6 \pm 0.85	7 \pm 1.2
TX 2862	normal	4 \pm 0.64	7 \pm 1.0
PI 584085	normal	4 \pm 0.93	–‡
Liang Tang Ai	normal	6 \pm 1.3	8 \pm 1.5
TX 7078	normal	5 \pm 1.5	6 \pm 0.47
TX 399	late flowering	4 \pm 0.90	6 \pm 0.40
IS 27150	late flowering	6 \pm 1.2	7 \pm 1.5
IS 27111	photoperiod sensitive	7 \pm 0.92	9 \pm 1.4

† Observations on plant densities were made 14 d after planting (DAP) in 2009 and 33 DAP in 2010. Plant counts included only main culms.

‡ Observations on plant density were not recorded for PI 584085 in 2010 because it had <20% plant density.

into mature and expanding leaf areas. The predictive power of a leaf area production model decreases when the contribution of expanding leaves to the total leaf area is not considered (Muchow and Carberry, 1990). Taken together, the LAI simulation models proposed so far for sorghum either lack the details of leaf area dynamics of expanding leaves or demand exhaustive measurements. Thus, the objectives of this study were to (i) develop a simple quantitative model to predict LAI in sorghum and (ii) introduce a new method for the simulation of the leaf area production of expanding leaves.

MATERIALS AND METHODS

Field Experiments

Field studies were conducted in 2009 and 2010 at the Kansas State University Northwest Research-Extension Center, Colby, KS (39°24' N, 101°4' W, 963 m asl). Eight sorghum genotypes (TX 7000, TX 399, TX 2862, PI 584085, Liang Tang Ai, TX 7078, IS 27150, and IS 27111) were planted in 6.1- by 6.1-m plots on 25 June 2009 and in 6.1- by 3.0-m plots on 28 May 2010. These genotypes represented a range of plant height, vegetative canopy structure, and photoperiod sensitivity (Z. Xin and R. Aiken, personal communication, 2000). Genotypes IS 27150 and IS 27111 were tall statured (Narayanan et al., 2013). All genotypes except IS 27111 were photoperiod insensitive. Genotypes TX 399 and IS 27150 were late flowering (Table 1). Plots were arranged in a randomized complete block design in 2009. Due to a planting error in 2010, some blocks did not receive all the genotypes. Therefore, the plots were arranged in an incomplete block design in 2010. There were five blocks in both years. Sorghum was maintained as well watered and fertilized throughout the experiment. Supplemental in-season irrigation was provided during mid-vegetative growth (38 mm) and just before anthesis (25 mm). Nutrient application included 102 kg N ha⁻¹ and 34 kg P ha⁻¹ banded before planting. Other details of the experiments were given by Narayanan et al. (2013). The observed plant density of the genotype PI 584085 was <20% in 2010.

Measurements

Periodic phenological development was recorded at approximately biweekly intervals for two representative plants in each plot (10 samples per genotype). Plants were at about the eight-leaf stage in 2009 and the 10-leaf stage in 2010 when these observations were started. Observations included the total

number of mature leaves (TLN) and the length (L , length of midrib from leaf tip to ligule or collar) and maximum width (W , measured at about two-thirds of the final blade length from the ligule or collar) of all even-numbered mature leaves on the main culm. A leaf was considered mature or fully expanded when its ligule or collar became completely visible above the leaf sheath. Measurements of L and W were taken only on intact, unshredded leaves. These observations of individual leaves were used to develop genotype-specific and generic coefficients required for the LAI estimation model.

To derive the relationships among L , W , and area (A_m) of mature leaves, we harvested the youngest four even-numbered mature leaves from plants that were not tagged for periodic phenological observations. Two plants per genotype were sampled for these measurements. Leaves were cut at the leaf collar, placed in sealable plastic bags, and transported to the laboratory in a portable cooler. Measurements of A_m , L , and W of these leaves were made at the laboratory. A leaf area meter (Model CI 203, CID Bio-Science) was used to measure A_m .

To derive the equations for calculating the leaf area of expanding leaves, the whole-plant whorl was detached from the plant by making a cut just below the collar of the top mature leaf and taken to the laboratory. The expanding leaves were numbered starting from the leaf that was one node above the top mature leaf, and cut at the point where the two edges of the leaf lamina touch each other. The area of each cut portion was measured by a CI 203 leaf area meter and was denoted as the current area of expanding leaves.

The LAI was measured by a plant canopy analyzer (LI-COR LAI-2000, LI-COR Biosciences) approximately biweekly beginning from 35 d after planting (DAP) in 2009 and approximately weekly beginning from 40 DAP in 2010. Plants were at about the eight-leaf stage in 2009 and the 12-leaf stage in 2010 when LAI measurements were started. Leaf area index was measured using the procedure outlined by Welles and Norman (1991). Measurements were taken between 0800 and 0900 h, mainly on days with overcast sky conditions. We used a 90 or 180° view cap for the instrument sensor, which helps to remove direct sunlight from the sensor's view. While taking measurements, the instrument sensor was shaded by the shadow of the operator. This was to ensure low sun angles and to meet the manufacturer's specification of taking measurements in diffused solar radiation (avoiding exposure to direct sunlight). Other details of the LAI measurements were given by Narayanan et al. (2013). These nondestructive field measurements of LAI were used to evaluate the predictive accuracy of the LAI estimation model.

Theory and Model Parameterization

Overview of the Leaf Area Index Estimation Model

The LAI was calculated from an algorithm (Fig. 1) considering TLN, A_m , the area of expanding leaves, and plant density. The area of mature leaves was calculated from L , W , and a leaf shape factor (F_s). The area of expanding leaves was calculated as proportional to their expected mature area [$E(A_{x_m})$] using a new method introduced by the model (see below).

Total Number of Mature Leaves

The total number of mature leaves in sorghum was computed using the phyllochron (P , °C d) which is the interval between

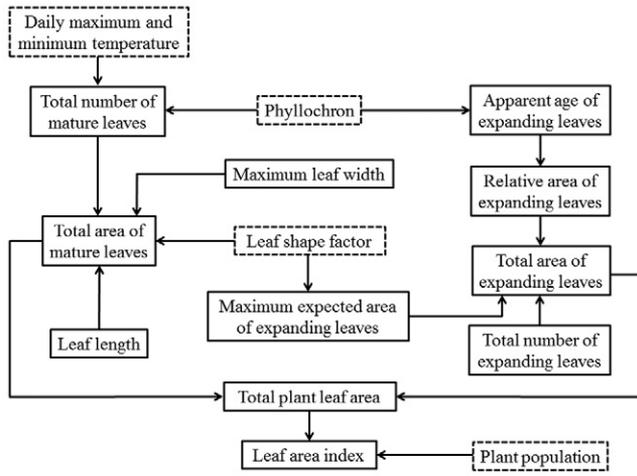


Fig. 1. Flowchart showing scheme of leaf area production model. Dashed boxes indicate inputs for the model. Arrows connect the derived variables (toward which they point) and the variables needed to derive them (from which they start).

the appearance of successive leaves on the same culm. The phyllochron is an input for the proposed leaf area production model. It was computed from the following relationship between the TLN and cumulative growing degree days (cGDD):

$$TLN = P^{-1}cGDD \quad [1]$$

The slope, P^{-1} in the above equation, is the rate of leaf appearance (leaf °C d⁻¹), the inverse of which is P . Growing degree days (thermal time; GDD) was calculated as (Arkin et al., 1983; Ritchie and NeSmith, 1991)

$$GDD = \frac{T_{min} + T_{max}}{2} - T_b \quad [2]$$

where T_{min} is the daily minimum temperature and T_{max} is the daily maximum temperature. The lower limit of T_{min} is restricted to a base temperature (T_b) of 7°C (Muchow and Carberry, 1990), while the upper limit of T_{max} is restricted to 42°C (Alagaraswamy et al., 1986). Cumulative growing degree days was computed beginning from the day of planting.

Leaf Area Index

The leaf area production model presented here calculates the LAI of sorghum genotypes at j DAP as

$$LAI_j = (TMA_j + TXA_j) \text{ plant density} \quad [3]$$

where TMA_j is the estimated area of mature leaves and TXA_j is the estimated area of expanding leaves at j DAP. The estimate of $(TMA_j + TXA_j)$ in Eq. [3] is the leaf area per plant.

Area of Mature Leaves

The total area of all mature leaves on a plant at j DAP (TMA_j) was calculated as

$$TMA_j = \sum_{k=1}^{TLN_j} L_k W_k F_s \quad [4]$$

where TLN_j is the total number of mature leaves on the main culm at j DAP for the i th genotype with a phyllochron P_i and was calculated using Eq. [1], with fractions of TLN in Eq. [1] truncated (Rosenthal et al., 1989); L_k and W_k denote the length of the k th leaf and the maximum width of the k th leaf, respectively, and were computed as

$$L_k = f(LN_k), \text{ and}$$

$$f(LN_k) = b_1(LN_k) \text{ when } LN_k < c_b \quad [5a]$$

$$f(LN_k) = (c_b b_1) + b_2(LN_k - c_b) \text{ when } LN_k \geq c_b \quad [5b]$$

$$W_k = f(L_k), \text{ and}$$

$$f(L_k) = a_w(L_k)^3 + b_w(L_k)^2 + c_w(L_k) + d_w \quad [6]$$

where LN_k is the leaf sequence number of the k th leaf, b_1 and b_2 are the slopes of the first and second line segments, c_b is the break point, and $a_w, b_w, c_w,$ and d_w are fitted coefficients. The break point was determined using a least-squares nonlinear regression procedure developed for bilinear functions (Ryan and Porth, 2007).

The leaf shape factor in Eq. [4] is an input required for model calibration. For mature sorghum leaves, F_s was calculated as (Arkin et al., 1983)

$$F_s = \frac{A_{mk}}{LW} \quad [7]$$

where A_{mk} is the observed area of the k th leaf (see above for details on $A_{mk}, L,$ and W).

Area of Expanding Leaves

The total area of expanding leaves at j DAP (TXA_j) was calculated as

$$TXA_j = \sum_{r=1}^{Nx} RAX_r E(Ax_{mr}) \quad [8]$$

where Nx , a user-defined constant, is the maximum number of expanding leaves expected in the whorl such that $TLN + Nx \leq$ flag leaf number; r will be 1 for the expanding leaf at one node above the top mature leaf; RAX_r denotes the relative area of the r th expanding leaf and is estimated as the ratio of the observed area of the r th expanding leaf (see above) to $E(Ax_{mr})$. The expected mature area of an expanding leaf denotes its area when it attains the status of a mature leaf (when its ligule becomes completely visible above the leaf sheath). The expected mature area of the r th expanding leaf was calculated by solving for A_{mk} in Eq. [7]. For this purpose, the value of k needs to be modified to $TLN + r$ because the leaf sequence number of r th expanding leaf is $TLN + r$. The term RAX_r in Eq. [8] was calculated as

$$RAX_r = c_q(ALGX_r) + d_q \quad [9]$$

where c_q and d_q are the slope and intercept, respectively, and ALGx refers to the apparent age of an expanding leaf, which is a new concept introduced by this model. The apparent age of the r th expanding leaf at a given point of time indicates the time elapsed from the tip appearance of the r th expanding leaf in the whorl, and is expressed as a fraction of P . The concept of ALGx is based on the fact that it takes one P for a leaf to expand completely (Wilhelm and McMaster, 1995). The apparent age of the r th expanding leaf for the i th genotype ($ALGx_{ir}$) was calculated as

$$ALGx_{ir} = \left(\frac{N_x - r}{N_x} \right) + \left\{ C - \left\lfloor \frac{\text{Integer}(C N_x)}{N_x} \right\rfloor \right\} \quad [10]$$

where C is defined as

$$C = \left(\frac{cGDD}{P_i} \right) - \text{Integer} \left(\frac{cGDD}{P_i} \right) \quad [11]$$

and the term *Integer* indicates that the fractions are truncated.

Generic Parameterization of Leaf Area Production Model

Fitted parameters are required for Eq. [1], [5], [6], [7], and [9] to implement them in the leaf area production algorithm. A least-squares approach was used for each genotype in each year for the specified parameters in the original model. A generic parameterization of the leaf area production model was also performed by fitting a single set of generic coefficients in these equations using data pooled across genotypes and years. This approach simplified the model and provided ready-to-use coefficients for future applications.

Model Evaluation

Model evaluation was performed using independent field data collected on LAI (see above). However, the same plots were used to collect data on leaf dimensions to build the model and on LAI to evaluate the model. Model performance was evaluated using standard regression and error index statistics (Moriyas et al., 2007; Paul et al., 2013). The error indices root mean square error (RMSE) and mean bias error (MBE) indicate error in the units of the constituent of interest. The error index RMSE can also be expressed as the percentage deviation from the mean (%RMSE). The goodness of fit was quantified by the coefficient of determination (R^2). Predictive bias was identified by RMSE, %RMSE, MBE, and percentage bias (PBIAS; Paul et al., 2013):

$$RMSE = \left[\frac{\sum_{i=1}^n (M_i - O_i)^2}{n} \right]^{0.5} \quad [12]$$

where n is the total number of observations and O_i and M_i are the observed and predicted values, respectively, at each comparison point.

$$MBE = \frac{1}{n} \sum_{i=1}^n (M_i - O_i) \quad [13]$$

$$\%RMSE = \frac{RMSE}{\left(\sum_{i=1}^n O_i \right) / n} 100 \quad [14]$$

$$PBIAS = \frac{\sum_{i=1}^n (M_i - O_i)}{\sum O_i} 100 \quad [15]$$

Statistical Analyses

Analysis of variance on the genotypes was performed using the MIXED procedure in SAS (Version 9.1.3, SAS Institute) for plant density and leaf dimension variables at the 0.05 probability level. Least square means and standard errors of L and W of the genotypes were estimated using the LSMEANS statement of the MIXED procedure in SAS. Analysis of covariance was performed using the MIXED procedure in SAS to: (i) compare P among genotypes (cGDD as covariate); (ii) test the significance of the fitted coefficients a_w , b_w , c_w , and d_w in the prediction equations of W (Eq. [6]; third-, second-, and first-order terms of L as covariates) and compare them among genotypes; (iii) test the significance of the fitted coefficients c_q and d_q in the prediction equation of RAX (Eq. [9]; ALGx as covariate) and compare them among genotypes; and (iv) compare F_s among different genotypes or LN (product of L and W as covariate). The NLIN procedure in SAS was used to estimate the fitted coefficients in the bilinear equation between L and LN of mature leaves (Eq. [5]). Linear and bilinear relationships between L and LN were compared based on R^2 and RMSE (Prasad et al., 2011). Genotype was treated as a fixed effect, and block was treated as a random effect. The probability threshold level (α) was 0.05 for all statistical analyses. Model evaluation was performed by regressing the modeled LAI on the observed LAI using the REG procedure in SAS; the intercept and slope of the linear regression equations were tested for significant departure from zero using a t -test (Aiken, 2005; Paul et al., 2013). The slope was tested for a significant departure from one using the TEST statement of the REG procedure in SAS (Aiken, 2005; Paul et al., 2013).

RESULTS

Data on observed plant density are presented in Table 1. Because plant density for genotype PI 584085 was <20% in 2010, that genotype was excluded from the LAI measurements by plant canopy analyzer in 2010. Analysis of covariance reported significant differences among genotypes for P ($Pr > F$ for the effect of the genotype \times cGDD interaction on TLN was 0.0009 and <0.0001 in 2009 and 2010, respectively). Among genotypes, P varied from 58 to 66°C d in 2009 and from 58 to 69°C d in 2010 (Table 2). The phyllochron was estimated as 61°C d for data pooled across genotypes and years (Table 2). The observed TLN per plant (least square mean \pm SE) at the flag leaf stage varied from 17 \pm 0.41 to 20 \pm 0.41 in 2009 and from 19 \pm 0.44 to 20 \pm 0.39 in 2010 among genotypes ($Pr > F$ for the effect of genotype on TLN was <0.0001 in 2009 and 2010). Data on the observed L and W of genotypes are presented in Fig. 2 and 3.

Table 2. Estimates of fitted coefficients for different prediction equations in the leaf area production algorithm.

Genotype	Year	Phyllochron °C d	b_1 (Eq. [5])	b_2 (Eq. [5])	c_b (Eq. [5])	a_w (Eq. [6])	b_w (Eq. [6])	c_w ‡ (Eq. [6])	d_w (Eq. [6])
TX 7000	2009	62	5.48†	-4.12†	14.5†	ns	-0.0012†	0.2177***	-0.7664*
	2010	62	4.89†	-4.86†	15.6†	0.00011*	-0.0028***	0.2758†	-1.459**
TX 2862	2009	58	5.00†	-4.18†	15.1†	ns	-0.0016†	0.2177***	-1.253***
	2010	59	4.74†	-6.31†	17.3†	0.00011*	-0.0028***	0.2758†	-2.027†
PI 584085	2009	60	5.29†	-14.9†	16.9†	ns	-0.0012†	0.2177***	-1.370***
	2010	59	4.81†	-2.69†	16.8†	0.00011*	-0.0028***	0.2758†	-1.146*
Liang Tang Ai	2009	65	5.38†	-6.82†	13.0†	ns	-0.0009†	0.2177***	-1.470†
	2010	62	4.98†	-9.65†	15.4†	0.00011*	-0.0028***	0.2758†	-0.7515*
TX 7078	2009	66	5.02†	-6.84†	13.4†	ns	-0.0012†	0.2177***	-0.3473*
	2010	62	4.82†	-9.76†	15.3†	0.00011*	-0.0028***	0.2758†	-1.5575***
TX 399	2009	59	4.56†	-3.73†	16.9†	ns	-0.0011†	0.2177***	-0.5095*
	2010	59	4.53†	-5.60†	17.7†	0.00011*	-0.0028***	0.2758†	-0.9091*
IS 27150	2009	62	5.59†	-1.50†	13.7†	ns	-0.0013†	0.2177***	-1.687†
	2010	58	5.24†	-6.10†	15.1†	0.00011*	-0.0028***	0.2758†	-2.162†
IS 27111	2009	65	5.34†	-9.63†	16.6†	ns	-0.0015†	0.2177***	-1.353***
	2010	69	5.40†	-6.85†	16.5†	0.00011*	-0.0028***	0.2758†	-2.881†
Generic coefficients§		61	5.03†	-3.77†	15.1†	ns	-0.0010†	0.1803†	-

* Significant at the 0.05 probability level; ns, not significant.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Significant at the 0.0001 probability level.

‡ Coefficient c_w in Eq. [6] did not vary among genotypes in 2009 ($Pr > F$ for the effect of genotype \times leaf length interaction on maximum leaf width was 0.3346). Similarly, coefficients a_w , b_w , and c_w in Eq. [6] did not vary among genotypes in 2010 ($Pr > F$ for the effect of genotype \times [leaf length]³, genotype \times [leaf length]², and genotype \times leaf length interactions on maximum leaf width were 0.5535, 0.5791, and 0.4995, respectively).

§ Generic coefficients were estimated using data pooled across genotypes and years.

The bilinear equation gave the highest R^2 and smallest RMSE for the relationship between L and LN for all genotypes compared with first-, second-, and third-order linear equations in 2009, 2010, and data pooled across genotypes and years. Thus, L was quantified as a bilinear function of LN in the model (Fig. 2). Maximum leaf width was a third-order linear function of L in 2010, whereas it was a second-order linear function of L in 2009 (Fig. 3) and for data pooled across genotypes and years. The leaf shape factor did not vary with genotype or LN ($Pr > F$ was >0.05 for the effects of interactions among genotype, LN, and the product of L and W on A_m). The value of F_s (\pm SE) was 0.73 ± 0.01 in 2009, 0.81 ± 0.01 in 2010 (Fig. 4), and 0.76 ± 0.01 for the data pooled across genotypes and years. In the case of expanding leaves, RAx increased with ALGx in a linear fashion (Fig. 5). No genotypic difference was observed for this relationship ($Pr > F$ for the effect of a genotype \times ALGx interaction on TLN was 0.5069 and 0.3018 in 2009 and 2010, respectively). The slope and intercept (c_q and d_q , respectively; Eq. [9]) for the relationship between RAx and ALGx were 1.22 ± 0.04 and -0.13 ± 0.02 for the data pooled across genotypes and years.

Model Evaluation

The adequacy of the general framework was verified by simulating the LAI of sorghum with time using the prediction equations. Testing of this model was done on independent data collected by actual LAI measurements in the field. The slope of the regression of modeled LAI on observed LAI varied for photoperiod-sensitive and -insensitive genotypes in 2010, but this trend was absent in 2009. Therefore, the results for photoperiod-sensitive and -insensitive genotypes are given separately for 2010 but not for 2009 in Table 3. Model evaluation parameters are presented in Table 3. A good correlation ($R^2 \geq 0.95$) was found between the modeled and observed LAI in 2009, 2010, and for data pooled across genotypes and years in the generic model (Fig. 6; Table 3). The observed LAI for the sorghum genotypes considered in this study ranged from 0.52 to 3.12 $m^2 m^{-2}$ in 2009, 1.20 to 4.14 $m^2 m^{-2}$ for photoperiod insensitive genotypes in 2010, and 1.82 to 3.58 $m^2 m^{-2}$ for the photoperiod sensitive genotype in 2010. Predictive accuracy was retained when the input data were pooled among genotypes and years (generic model; Table 3). The

Table 3. Slope, number of observations (n), coefficient of determination (R^2), standard error (SE), root mean square error (RMSE), percentage RMSE (%RMSE), mean bias error (MBE), and percentage bias (PBIAS) of modeled vs. observed values of sorghum leaf area index from emergence to maximum leaf production at Colby, KS, in 2009 and 2010.

Year	Model†	Slope‡	SE (slope)	n	R^2	RMSE $m^2 m^{-2}$	%RMSE %	MBE $m^2 m^{-2}$	PBIAS %
2009	original	0.8162	0.027	40	0.96	0.352	18.7	-0.33	-17.8
	generic	0.9748§	0.035	40	0.95	0.452	24.0	-0.03	-1.38
2010 (photoperiod insensitive)	original	0.8768	0.019	27	0.99	0.302	10.5	-0.38	-13.3
	generic	0.7915	0.022	27	0.98	0.377	12.4	-0.66	-22.0
2010 (photoperiod sensitive)	original	1.044§	0.115	5	0.95	0.783	26.3	0.03	0.84
	generic	1.093§	0.089	5	0.97	0.609	20.4	0.19	6.45

† Original model was produced by fitting specific coefficients in Eq. [1], [5], [6], [7], and [9] for genotype and/or year and implementing them in a leaf area production algorithm; generic model was produced by fitting common coefficients in Eq. [1], [5], [6], [7], and [9] using data pooled across genotypes and years and implementing them in a leaf area production algorithm.

‡ Slopes were different from zero at the 0.05 probability level.

§ Not different from one at the 0.05 probability level.

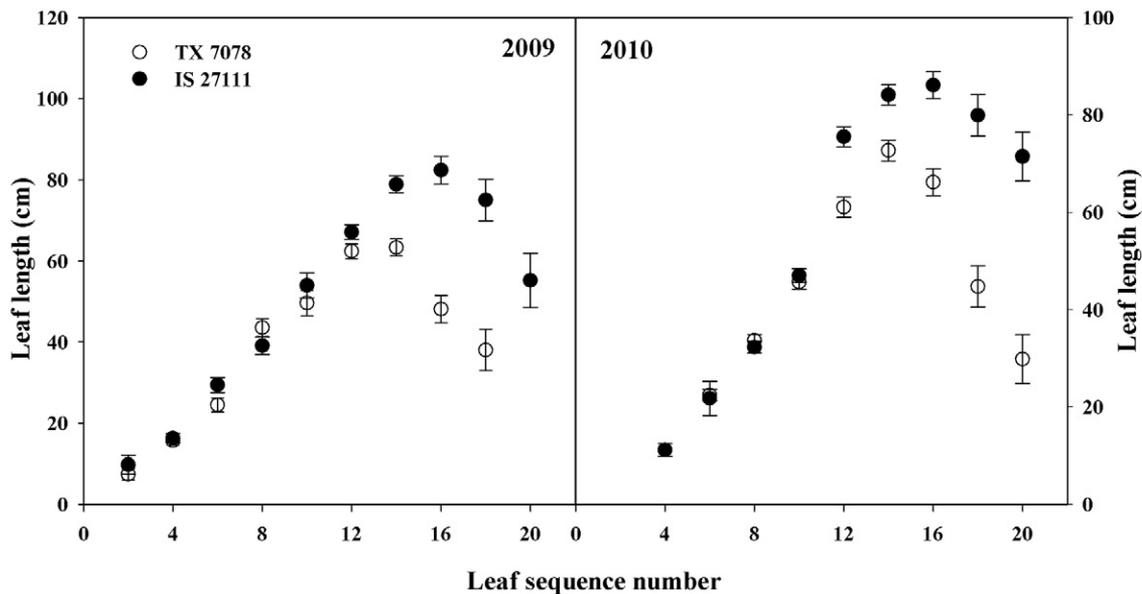


Fig. 2. Length (least square mean \pm standard error) of different even-numbered mature leaves for sorghum genotypes with longest leaves (IS 27111) and shortest leaves (TX 7078) grown at Colby, KS, in 2009 (left) and 2010 (right). Leaf sequence number refers to the leaf position on the culm.

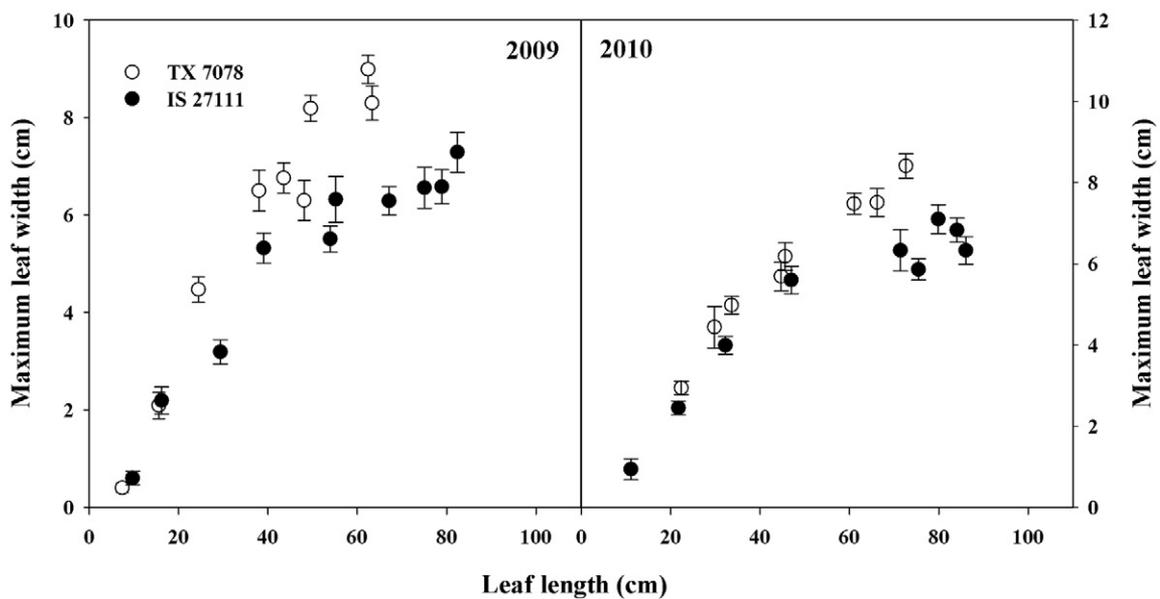


Fig. 3. Maximum width (least square mean \pm standard error) of mature leaves as a function of leaf length for sorghum genotypes with long, narrow leaves (IS 27111) and short, wide leaves (TX 7078) grown at Colby, KS, in 2009 (left) and 2010 (right).

estimated error in the predicted LAI ranged between 12 and 24% (RMSE) when the generic model was utilized (Table 3).

DISCUSSION

The model presented here predicts leaf area under optimum environmental conditions. It can be used to quantify the LAI at any given day of the vegetative growing season based only on GDD and making use of generic coefficients demonstrated in this work (Table 2). The model calculates the area of expanding leaves using a different algorithm than that used for mature leaves in order to incorporate the dynamics of leaf expansion into the model. The prediction range of this model is from emergence to the flag leaf stage.

The generic form of the leaf area production model produced by fitting common coefficients for data pooled across genotypes and

years predicted the LAI with similar accuracy to the original form of the model with specific coefficients for genotypes and years (Table 3). This implies that if the model is parameterized with the generic coefficients provided by this study, the only inputs required by this model to simulate the LAI of sorghum are T_{\min} and T_{\max} during the growing season. Thus, the generic parameterization of the leaf area production model reduces the amount of inputs required by the model, provides default coefficients for its further use, and makes it independent of field measurements.

The advantage of the model presented here over the existing leaf area prediction models is the introduction of a new method for calculating the area of expanding leaves. The model presented here calculates the area of expanding leaves using a different algorithm than that used for mature leaves to accommodate the details of leaf area dynamics by expanding leaves. Most of the leaf

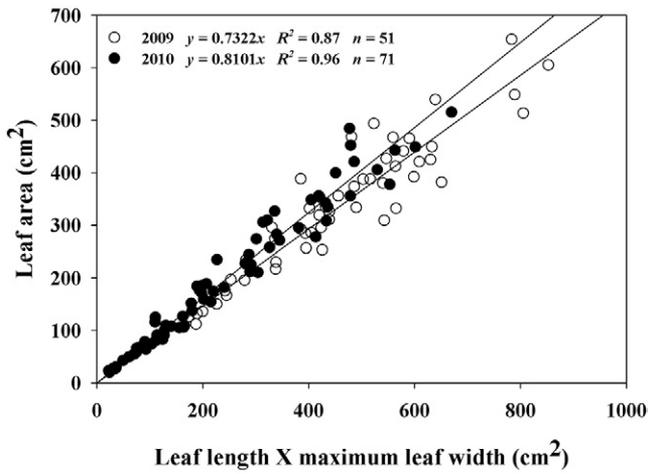


Fig. 4. Depiction of leaf shape factor in sorghum. The shape factor was derived as the slope of the regression of the observed area of mature leaves on the product of the observed values of length and maximum width of mature leaves with a suppressed intercept (because the intercept was not different from zero at the 0.05 probability level). Each symbol in the graph corresponds to a particular leaf.

area models for sorghum use common equations to simulate leaf area production by mature and expanding leaves or to estimate the total leaf area per plant without separating mature and expanding leaf areas (Arkin et al., 1983; Hammer et al., 1987, 1993; Rosenthal et al., 1989; Muchow and Carberry, 1990; Carberry et al., 1993; Arkebauer et al., 1995; Rosenthal and Vanderlip, 2004). In the model presented here, leaf expansion in sorghum is described using the concept of self-proportionality and leaf geometry. In other words, leaf expansion is quantified in the model based on the facts that (i) the dimensions of expanding leaves in the whorl are proportional to the expected dimensions at maturity and (ii) the leaf geometry can be deduced by a triangular tip and a rectangular base. The model considers leaf expansion as a process driven by thermal time (see Eq. [10–11]). Because the expanding leaves are the most erect leaves in the upper canopy of the plant, they probably influence the

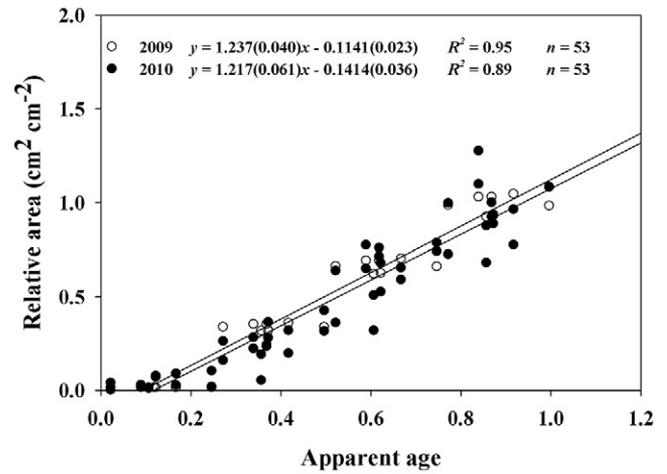


Fig. 5. The relative area of expanding sorghum leaves as a function of their apparent age. The relative area is the ratio of the area of the portion of the expanding leaf lamina that had unwound from the whorl to the expected area of that leaf at ligule formation. The apparent age of expanding leaves denotes the time elapsed from their tip appearance and is expressed in terms of a fraction of the phyllochron. Each symbol in the graph corresponds to a particular leaf. The equation reports the slope (\pm SE) and the intercept (\pm SE) of the regression of relative area on the apparent age of expanding leaves.

distribution of radiation within the plant canopy. Because this model accurately predicts the area of expanding leaves, it could also have applications in canopy light distribution studies.

The model was evaluated using field LAI data collected using a plant canopy analyzer (see above). An underestimation (up to 40%) of LAI is expected if measurements are taken in direct sun conditions by the plant canopy analyzer (Welles and Norman, 1991). To avoid this, LAI measurements were taken in diffused solar radiation in the present study. Under this condition, the plant canopy analyzer estimates LAI with a resolution $>3\%$ and error $<15\%$ (Welles and Norman, 1991).

The performance statistics in Table 3 verify the adequacy of the model. The model accurately predicted sorghum LAI with $R^2 \geq 0.95$ and $RMSE \leq 0.783$ (26%). The performance statistics

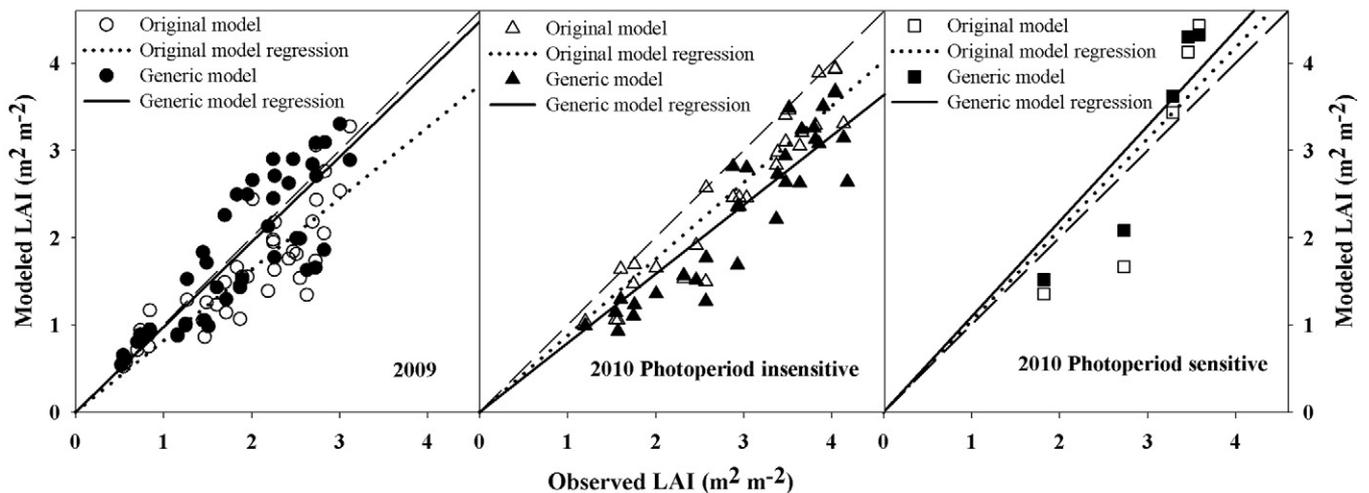


Fig. 6. Modeled vs. observed leaf area index (LAI) in sorghum. The original model was produced by fitting specific coefficients in Eq. [1], [5], [6], [7], and [9] for genotype and/or year and implementing them in a leaf area production algorithm. The generic model was produced by fitting common coefficients in those equations using data pooled across genotypes and years. The broken line is the 1:1 line. The slope of the fitted regression line was different for photoperiod-sensitive and -insensitive genotypes in 2010, whereas this difference was absent in 2009 ($Pr > F$ for the effect of photoperiod sensitivity by observed LAI interaction on modeled LAI was 0.0011 and 0.8293 in 2010 and 2009, respectively). Intercept of the fitted regression lines was not different from zero at the 0.05 probability level in all cases.

MBE and PBIAS (Table 3) indicate error in the predicted LAI in units of LAI or as a percentage error, respectively. A value of zero or close to zero for MBE and PBIAS indicates accurate performance of the model. Negative values of MBE and PBIAS in 2009 and 2010 (photoperiod insensitive) indicate that the model slightly underestimated the sorghum LAI. This may be due to the exclusion of the tiller leaf area in the model.

The difference in the slopes of regression of predicted LAI on observed LAI for photoperiod-sensitive and -insensitive genotypes in 2010 and the absence of this trend in 2009 may be a result of delayed planting in 2009 compared with 2010; the 30-d earlier start of crops in 2010 compared with 2009 might have magnified the effect of day length on leaf expansion (Cookson et al., 2007).

The model presented here has not estimated the area of senesced leaves and tiller leaves, and it compared the genotypes in only one location for 2 yr under water- and nutrient-sufficient conditions. Therefore, the model can be improved with incorporation of the area of tiller leaves and senesced leaves and the effects of environmental factors such as water, nutrients, and solar radiation on leaf area production. Data on LAI used to evaluate the model were collected from the same plots that were used to collect data on leaf dimensions to build the model. Thus, even though the model was evaluated using independent data collected by actual LAI measurements in the field, it was not in independent locations. Further research is needed to evaluate the model with different genotypes in different regions. Modifications in the estimates of fitted coefficients might be needed to maintain the predictive accuracy of the model when used at different locations or environments because leaf area development in sorghum may vary under different growing conditions. However, this model provides a general, useful, and simple reference framework for simulation studies on leaf area.

CONCLUSIONS

The model presented here relates LAI to thermal time. It predicts the LAI of sorghum using an algorithm considering TLN, A_m , the area of expanding leaves, and plant density. Using this model, the total leaf area per plant with a known P and F_s can be calculated given inputs of T_{max} , T_{min} , and the coefficients required for model calibration and can be extended to LAI with the knowledge of plant density. The generic parameterization of the model provides default coefficients for use, which makes it independent of field measurements. The major contribution of this study is the introduction of a new and detailed method to calculate the area of expanding leaves. Future research could evaluate the model with different genotypes at different locations.

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