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Original article

Simulation of individual leaf areas in grain sorghum

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Abstract – Most crop simulation models that incorporate environmental conditions estimate leaf area development. The grain sorghum growth simulation model, SORKAM, calculates individual leaf area based on leaf number and maturity class. The objective of this study was to generalize present leaf growth routines in SORKAM to be independent of maturity since there are no generally accepted maturing classes. Modified relationships between leaf number and leaf growth parameters were developed from existing studies and were tested against independent detailed leaf growth data sets. The revised relationships improved the r^2 between simulated and actual individual leaf areas from 0.80 to 0.88, reduced the bias from 32 cm^2 to 9 cm^2, and the RMSE from 80 cm^2 to 52 cm^2. With the improved simulation, estimated leaf area index through the season was also improved from the original SORKAM estimate (RMSE decreased from 0.77 to 0.63; RMSE: root mean square error). Although simulation of individual leaf areas was improved, total leaf area produced over the season was not.

grain sorghum / leaf area / modeling

1. INTRODUCTION

Leaf area development is critical to determining photosynthetic activity that produces biomass and grain yield [20, 22]. A critical period in accurately estimating leaf area is during early growth before canopy closure [24]. This period is important for determining rates of transpiration and evaporation, and in determining biomass. For crops such as sorghum and wheat, an accurate leaf area estimate is also important in determining the number of tillers produced. In crop models, leaf area has been simulated either on a total plant [4, 9] or individual leaf basis [27]. Carberry et al. [4] found that either method could be accurate, depending on the application of the estimate. Applications of leaf area information include the implementation timing of various management practices, such as fertilizer and pesticide applications and assessments of leaf damage. These assessments can be important in deciding whether to remove the stress affecting leaf damage, replant and/or in deciding future planting dates, plant populations, or maturity combinations [10, 29].

The grain sorghum (Sorghum bicolor L. Moench) growth model, SORKAM, simulates individual leaf areas and their consequential effects on light interception, biomass, and grain yield [27]. The model operates on a daily time step and incorporates weather, plant, and soil information and simulates crop growth, development, and yield. The model has been used in making crop management decisions, such as determining optimum planting dates [8], maturity [8, 26, 29], ratooning [7] and assessing climate variability on yield [11]. In SORKAM [27], as in modifications to CERES-Maize [17], individual leaf development is simulated with components of leaf appearance rate (LAR), leaf expansion rate (LER), and leaf expansion duration (LED).

LAR and LED are linear functions of leaf number [15,17]. Previously, Arkebauer et al. [1] showed that LER could be described by an exponential function of leaf number. In SORKAM, LER is an exponential function of leaf number with separate coefficients for early (16 or fewer leaves), medium (17 or 18 leaves), and late (19 or greater leaves) maturity hybrids. These equations can potentially produce unrealistic leaf area simulations. For example, given the relationships of LER and LED with leaf number (leaf position) and if the wrong maturity class was chosen, one could have a 21-leaf plant with intermediate leaves having an increasing area (per single leaf) with leaf position, then decreasing with higher leaf position due to a decreasing LER, followed by another area increase per leaf due to a constant LER and increasing LED [27]. Such a bimodal distribution is unlikely as found by Lafarge et al. [16] and Lizaso [17] for sorghum and corn (*Zea maize* L.) individual leaf area. In addition, recent literature [6, 14] indicates the coefficients for leaf expansion rate can be characterized using only leaf number. This could provide more variability in leaf area

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Table I. Leaf expansion rate coefficients in SORKAM [27].

		Coefficients		
Maturity	# of leaves	A	B	C
Early	≤ 16	2.155	–0.038	12.653
Medium	17–18	2.305	–0.029	12.608
Late	≥19	2.446	–0.038	12.423

within maturity classes, which may or may not be realistic. Also, Zewdie [30] found that the duration from emergence to flowering was overestimated with the present SORKAM model perhaps because of problems with simulated leaf appearance rate. Consequently, our objective was to (a) develop generalized (i.e. applicable across maturity classes) relationships between leaf appearance rate, leaf expansion rate, or leaf expansion duration and leaf number, (b) incorporate these relationships into the SORKAM model, and (c) test them on independent data. These simplifications would eliminate the need to specify maturity class and could improve leaf area estimates by SORKAM because the problems mentioned above would be avoided.

2. MATERIALS AND METHODS

2.1. Leaf appearance rate

Leaf appearance rate (LAR) is defined as the thermal period between the appearance of successive leaf tips in the whorl (inverse of the phyllochron interval). Currently, the first leaf tip requires 10 growing degree units (GDU, base temperature 7 °C) to appear after emergence. All subsequent leaf tips require 50 GDU [28]. Leaf appearance rate was re-analyzed using data collected by Rosenthal et al. [25] from plants in a glasshouse study. Leaf appearance data (growing degree units) were combined across treatments and averaged for the first 14 leaves that emerged.

2.2. Leaf expansion rate

Leaf expansion rate (LER) is the rate of individual leaf development (cm^2/GDU) from leaf tip appearance in the whorl to ligule appearance (maximum leaf size) [21]. SORKAM (original version) calculates LER as:

$$LER = A * \exp[B * (J - C)^2] \quad (1)$$

where A, B, and C are coefficients that vary with maturity class (Tab. I), J is leaf number, and C is the leaf number with maximum expansion rate and is constant with maturity class. Table I lists the derived coefficients for SORKAM. For late maturing plants, LER is a constant 1.6 cm^2/GDU for leaf numbers greater than 16. Figure 1 shows the derived distribution for early maturing varieties. The relationships were derived from a glasshouse and mini-lysimeter study [25]. From that study, simulated water stress has no effect on leaf growth when the amount of plant available water is greater than 50% of maximum. For conditions of root zone plant available water (PAW)

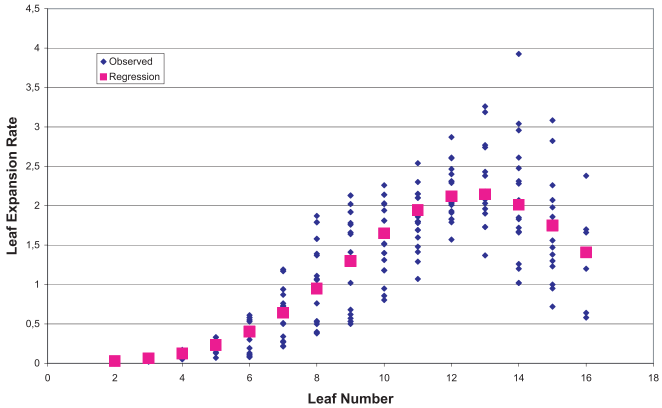

Figure 1. Early maturing leaf expansion rates as a function of leaf number as determined within SORKAM. Data was collected from a water deficit study [25].

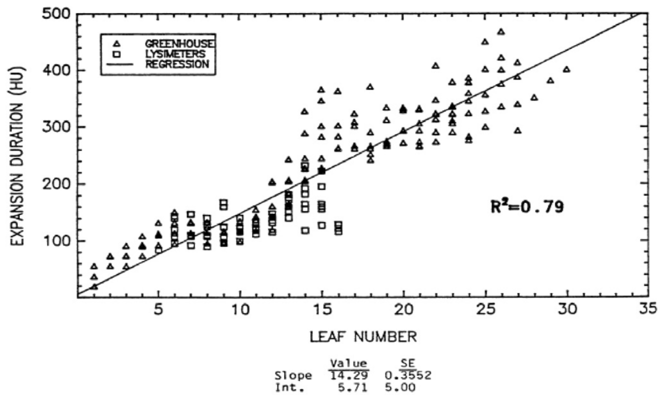

Figure 2. Leaf expansion duration from SORKAM. Data were collected from a water deficit study [25].

of less than 50%, percent expansion rate reduction is %reduction = PAW/2.

To remove the effect of leaf number on LER and therefore obtain an equation applicable across classes of maturity, leaf number was normalized based on the total number of leaves (J/J_{max}) where J_{max} is the total number of leaves. An extensive list of exponential equations was then examined using TableCurve [13] to determine the equation giving the lowest RMSE (root mean square error).

2.3. Leaf expansion duration

Leaf expansion duration (LED) is defined as the thermal period from leaf tip appearance in the whorl to maximum size. Leaf expansion duration in the original SORKAM is a linear function of leaf number [27] (Fig. 2):

$$LED = (14.29 * J) + 5.71 \; (r^2 = 0.79; se_{a.} = 0.3552; se_{b.} = 5.0). \quad [2]$$

Consequently, leaf expansion duration was re-evaluated with combined maturity class individual leaf area data sets, collected

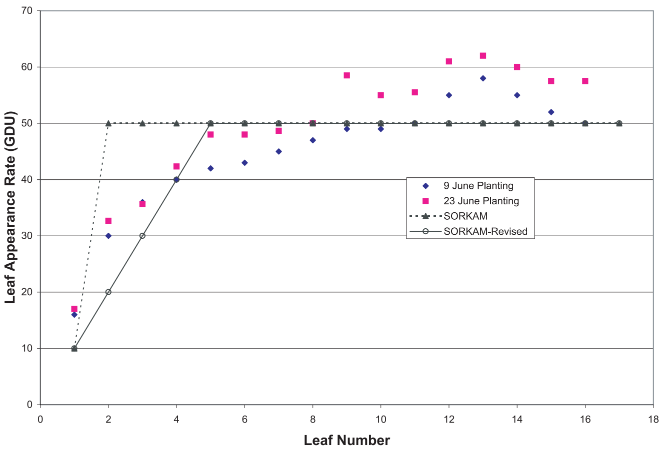

Figure 3. Leaf appearance rate as a function of leaf number from the original and revised SORKAM and data collected by Zewdie [30].

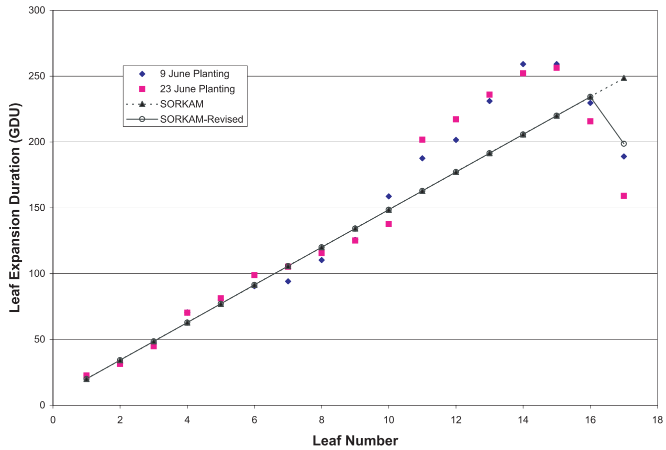

Figure 4. Simulated and measured (from Zewdie [30]) leaf expansion duration for a 17-leaf hybrid.

by Rosenthal et al. [25] and an unpublished population study in the original SORKAM validation [27], and compared to results from Zewdie [30] and Arkin et al. [2].

2.4. Testing of revised leaf model

Modifications to LAR, LER, and LED were incorporated into SORKAM and the resulting simulations from the revised model were compared with original SORKAM simulations of independent test data sets. Zewdie's [30] observed data on leaf development was used to evaluate the changes in leaf appearance rate, leaf expansion rate, and leaf expansion duration.

Independent data sets included individual leaf areas and total plant leaf area from irrigated field experiments at Rocky Ford, CO in 1972 [18]; St John, KS in 1978 [3]; Manhattan, KS in 1978 [12, 28] and a dryland experiment at Manhattan, KS in 1965 [23]. Leaf area simulations were then compared between the original and revised versions of the leaf model of SORKAM and with available measured leaf area and leaf area index. Leaf expansion rate was reduced when the simulated available plant available water was less than 50% of maximum. Such a reduction would decrease individual leaf area as described earlier.

Individual leaf areas and total plant leaf area and leaf area index from all experiments simulated with the SORKAM and the revised SORKAM models were statistically compared with available measured data using linear regression, root mean square error (RMSE), and bias defined as the average percentage difference between simulated and observed data. A similar term, delta, is defined as the percentage relative difference between the revised SORKAM and original SORKAM model estimates. Since the current data set lacks observed yield components (tiller number, seed number, seed weight, total dry weight per shoot, etc.), a comparison between SORKAM and the revised SORKAM models estimates is done to determine what affect the revised leaf equation has on simulating yields and yield components. A separate paper will describe the actual, and simulated estimates from SORKAM and the revised model with a larger data set containing observed yield and yield components.

3. RESULTS AND DISCUSSION

Analysis of leaf growth data collected from a glasshouse study [25] indicated that leaf appearance rate (LAR) (GDU, Base temperature 7 °C) for the first four leaves was less than for leaves five and above. This relationship can be given by

$$LAR = 10 * J \qquad \text{for } J < 5 \tag{3}$$

$$LAR = 50 \qquad \text{for } J \geq 5 \tag{4}$$

where J is leaf number. The revised relationship is compared to field data from Zewdie [30] in Figure 3. The revised version more closely follows actual leaf appearance up to about leaf 9, however, both the original and revised LAR values are less (faster appearance) than measured values for the upper leaves. Zewdie's results are within the range observed of the original data (data not shown). The faster rates may be attributed to the dependence of appearance rate on meristem temperature. Lafarge et al. [15] found that the meristem temperature was approximately 2 °C greater than daytime air temperature for leaf growth before stem elongation. The higher meristem temperature would thus reduce the GDU thermal requirement for appearance. The faster appearance will also increase total leaf area and leaf area index compared to the original SORKAM. Such development could affect the number of tillers and their development. Crauford et al. [5] found similar LAR values (57 GDU; base temperature 8 °C) for upper sorghum leaves. Our LAR values (50 GDU) implies the LAR is constant over the same growth period.

Leaf expansion duration in the original SORKAM was a linear function of leaf number (Fig. 4). Arkin et al. [2] found that leaf expansion duration decreased by approximately 50 GDU for the last (flag) leaf (data not shown). Thus, the only change made in LED was to reduce duration for the flag leaf by 50 GDU from the previous leaf. This is shown for a 17-leaf plant in Figure 4 along with data comparisons from Zewdie [30]. Agreement is quite good up through the 10th leaf, above which LED is underestimated except for the final two leaves. Zewdie's

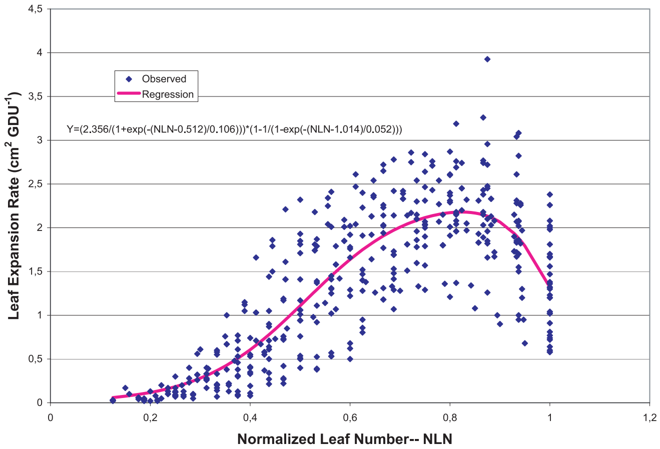

Figure 5. Revised leaf expansion rate as a function of normalized leaf number.

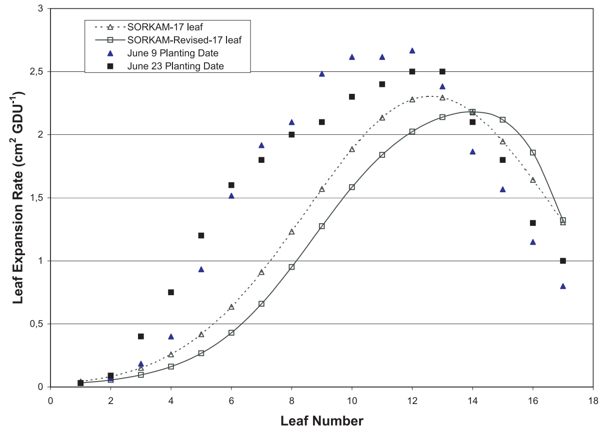

Figure 6. Revised leaf expansion rates compared to data collected by Zewdie [30].

results supports reducing the LED for not only the flag leaf but also the second leaf from the top. However, other published data from the original SORKAM data sets suggest the revised model should have only the flag leaf with a reduced LED (data not shown).

To remove the effect of leaf number and therefore of maturity on LER, leaf number was normalized by the equation

$$NLN = J/J_{max} \quad (5)$$

where J is leaf number and J_{max} is total number of leaves. Combining all original data used to develop the relationships for SORKAM [27], a new relationship between LER and NLN was determined (Fig. 5). The relationship is given by

$$LER = (2.356/(1 + \exp(-(NLN - 0.513)/0.106))) \times (1 - 1/(1 + \exp(-NLN - 1.13)/0.052))) \quad r^2 = 0.71. \quad (6)$$

Original and revised LER rates are compared with measured rates from Zewdie [30] for a 17-leaf hybrid (Fig. 6). Zewdie's results indicate that the simulated LER is less than observed but within the variability shown in Figure 5.

Using the above relationships, simulated leaf areas (SORKAM and revised-SORKAM) were compared with actual leaf area for the data sets in Table II. Selected data sets that include a range of total leaf numbers (16 to 21) and unstressed and water-stressed conditions are shown in Figure 7. In the Reeves (Manhattan, KS) and Luebbe (Rocky Ford, CO) comparisons, an improvement in leaf area estimation, particularly for lower leaves, was observed. In the Jaiyesimi (Manhattan, KS) data, the great differences in LER for later maturity (greater total leaf number) hybrids is evident. The revised SORKAM leaf area simulation was much better for all leaves compared to observed. The Schaffer (Manhattan, KS)

Table II. Hybrid, planting date, and plant population variables in the experiments used for model comparison. Starred treatments correspond to the leaf area and leaf number comparisons (Fig. 7).

Location and year (Source)	Hybrid (leaf No.)	Planting date	Plant population, pl ha^{-1}
Rocky Ford, CO 1972	NB505 (17)*	15 May	83 000*; 166 000
[18]	RS610 (18)		
St. John, KS 1978	RS626 (18)	10, 17, 31 May	120 500
[3]	RS671 (20)	14 June	
Manhattan, KS 1965	RS610 (16)*	17 May	96 900
[23]	RS650 (18)		
	RS701 (20)		
Manhattan, KS 1978	RS626 (18)	27 April	73 000
[12]	C42Y+ (21)*	15*, 30 May	
		9, 26 July	
Manhattan, KS 1978	RS626 (18)*	26 April	120 500
[28]	RS671	15, 25 May*	
	RS702	9, 26 June	

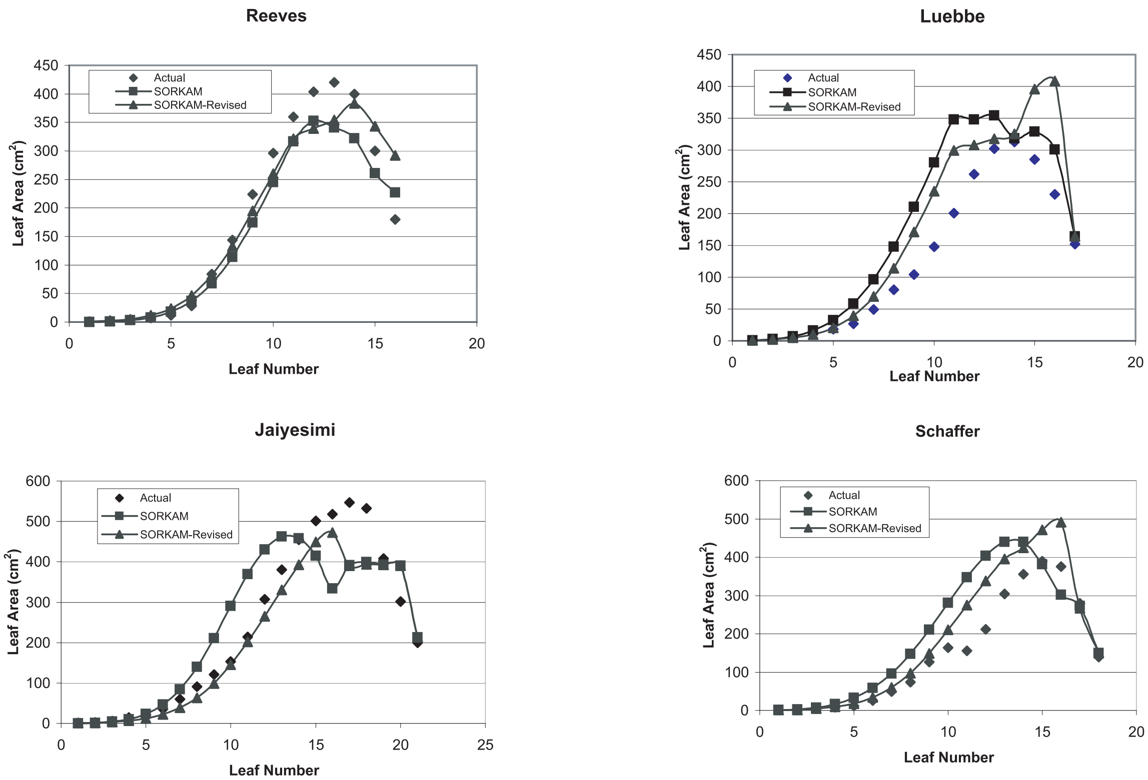

Figure 7. Actual and revised SORKAM estimates of individual leaf area for Manhattan, KS, 1978 [12, 28], Manhattan, KS, 1965 [23], and Rocky Ford, CO, 1972 [18]. The starred treatments in Table II correspond to these graphs.

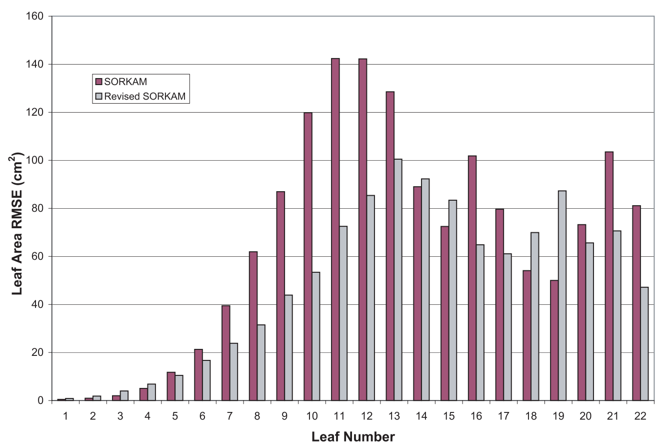

Figure 8. Comparison of SORKAM and revised SORKAM RMSE of leaf area by leaf number.

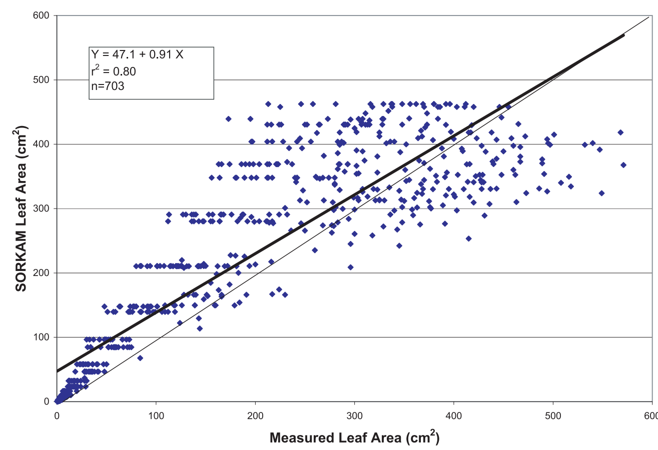

Figure 9. Comparison of simulated SORKAM and measured individual leaf areas for the 37 data sets.

observed leaf expansion data were overestimated by both the SORKAM and revised SORKAM models. Schaffer [28] indicated water stress likely occurred during the growth of leaves 10–13 which could consequently reduce leaf area (leaf 11 was smaller than leaf 10). This stress was not apparent in the simulations as detected by the exponential function of total leaf area with leaf number. However, overall the model significantly reduced the RMSE for individual leaves as compared to SORKAM (Fig. 8). This was especially evident in leaves 7–13, which grow during the period when the panicle initiates. RMSE for later emerging leaves were not very different from the SORKAM estimate.

Simulated individual leaf areas from SORKAM and the revised SORKAM models were regressed on actual data (Figs. 9, 10*)*. This is the general way to compare simulated and observed data. Deviations over the entire leaf area range can then be determined. For the original SORKAM, the slope and intercept are 0.91 and 47.1 ($se_a = 0.02$, $se_b = 72.5$)*,* while for

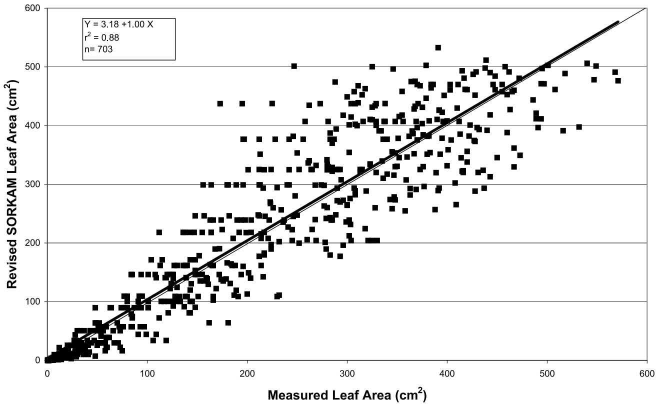

Figure 10. Comparison of the simulated revised SORKAM and measured individual leaf areas for the 37 data sets.

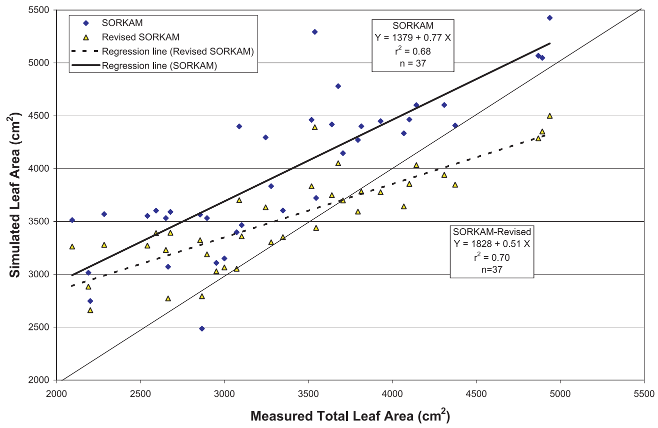

Figure 11. Comparison of measured and simulated (SORKAM and revised SORKAM) total plant leaf area.

the revised SORKAM, the slope and intercept is 1.00 and 3.2. ($se_a = 0.01$, $se_b = 3.2$), respectively. With either model the intercept is not significantly different from 0 but the slope with the original SORKAM model is significantly less than 1. Use of the revised model increased the r^2 from 0.80 to 0.88, reduced the bias from 32 cm^2 to 9 cm^2, and reduced the RMSE from 80 cm^2 to 52 cm^2.

Figure 11 compares the simulated and actual total sum of individual leaf areas for all 37 data sets. Overall, the revised SORKAM has a shallower slope (0.51 [se_a = 0.06] vs. 0.77 [se_a = 0.09]) and a higher intercept (1828 [se_b = 192] vs. 1379 [se_b = 307] cm^2). The r^2 value also increased from 0.68 to 0.70 for the revised model. Thus, although in many cases individual leaf areas were more accurately simulated with the revised SORKAM, simulation of total leaf area was not significantly improved. However, several points should be considered. First, these are comparisons of total leaf area not defined as total leaf area really observed at given times but as the total produced during the whole season (i.e. the sum of surface areas reached of each leaf when it was fully expanded and not leaf area at any

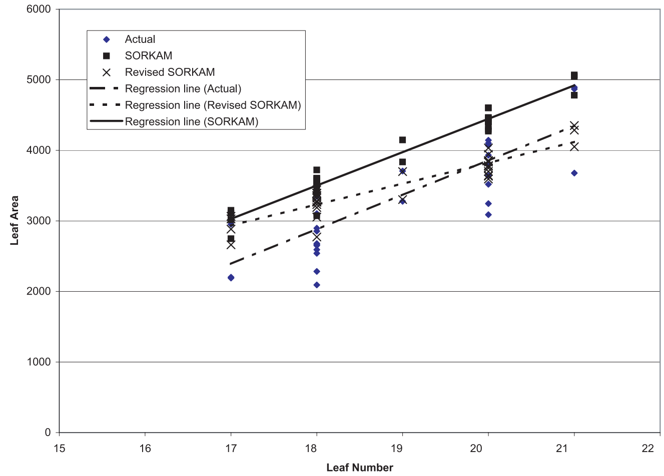

Figure 12. Comparison of total plant leaf area and total leaf number for measured, and simulated SORKAM, and revised SORKAM.

particular time during plant development). The revised version of SORKAM may therefore have improved the simulation of total leaf area with time without improving total leaf area produced. Second, overestimation of total leaf area by SORKAM was greatly reduced by the revision and bias was reduced from 607 cm^2/plant to 169 cm^2/plant.

Simulation of total leaf area also can be considered on a hybrid maturity (total leaf number) basis. With total number of leaves per plant ranging from 17 to 21, common leaf numbers as determined by Miller [19], the revised SORKAM simulated total leaf area is not significantly different from actual total leaf area considering the regression of simulated total leaf area on measured total leaf number (Fig. 12). Again, the slope of the regression of total leaf area (209) on total leaf number was shallower for the total areas simulated with the revised model than for those calculated with the original SORKAM (472) or for actual leaf areas (409) (Fig. 12). The standard errors for slope for the actual (58.4) and SORKAM (19.1) estimate were such that the two are not significantly different. However, the standard error of the intercept were such that the intercepts are significantly different (actual se = 1107; SORKAM se = 362). For the leaf areas simulated by the revised model, the estimate of slope and intercept of the regression on leaf number were significantly different (se_a = 22.6; se_b = 428) from the corresponding estimate obtained using actual values of leaf areas. However, the average total leaf area for plants with 17–21 leaves was 3326 cm^2 (Actual), 3933 cm^2 (SORKAM), and 3501 cm^2 (SORKAM-Revised). Therefore, revised SORKAM is within 180 cm^2 of actual total leaf area. However, using data from plants with 17–21 leaves, which covers the common range of current hybrids [20], the revised SORKAM simulated leaf areas were not significantly different ($P = 0.30$; n = 37) from actual leaf area while the SORKAM simulated leaf areas were significantly different ($P = 0.0008$; n = 32) as determined in a paired t-test.

Comparisons of simulated leaf area index with the revised and original SORKAM indicate that the revised model improved

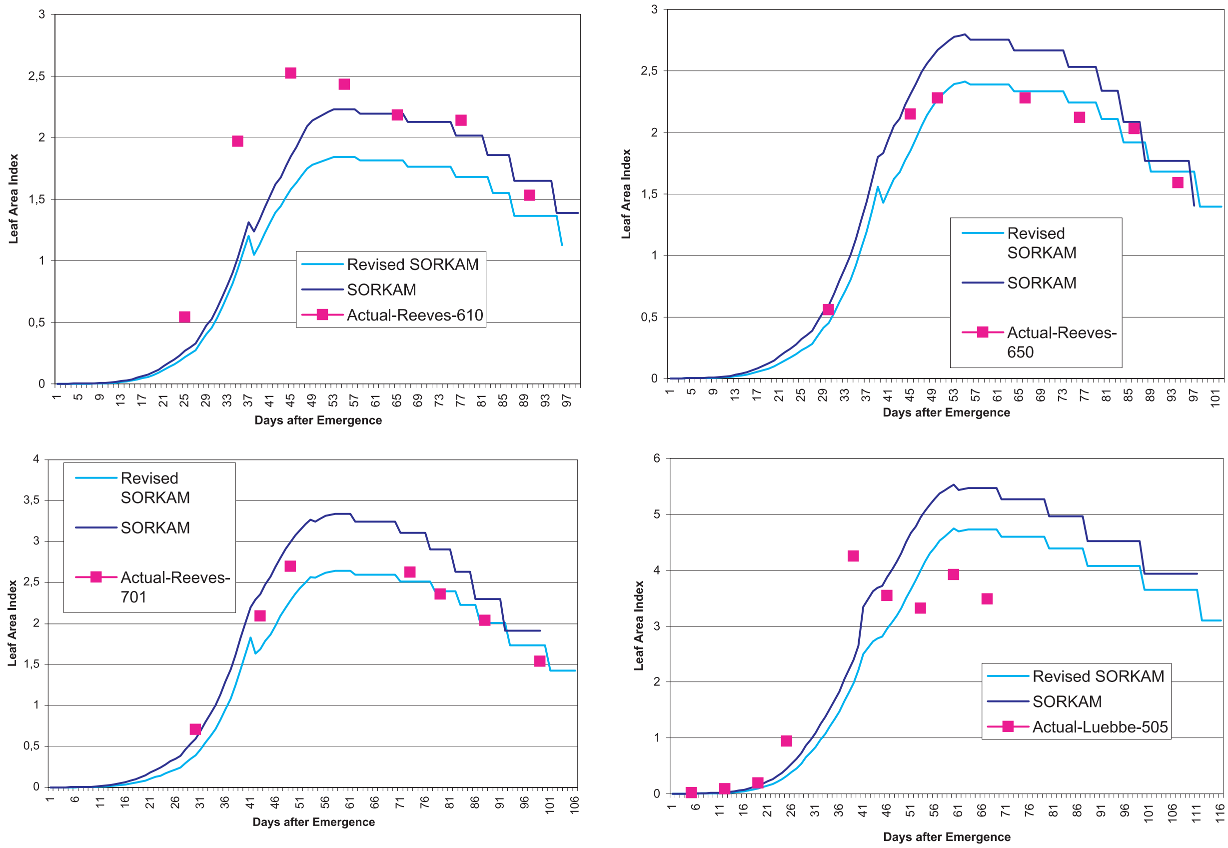

Figure 13. Comparison of measured and simulated (revised SORKAM and SORKAM) leaf area index for Manhattan, KS [23] and Rocky Ford, CO [18].

the estimate of leaf area index (Fig. 13). The comparisons were made over a range of maturities and two locations. The RMSE decreased from 0.77 for SORKAM to 0.63 for the revised SORKAM. (SORKAM t = 0.19, Rev. SORKAM t = 0.07, n = 30 paired t-test). Although both estimates are still significantly different from the observed leaf area index, the revised SORKAM does provide a closer estimate.

Simulating accurate total leaf area index is important in modeling since it is used to calculate light interception. This is particularly important during incomplete canopy cover. During this period, an accurate estimate of leaf area index can determine the fraction of solar radiation intercepted and thus photosynthesis; the proper proportion between transpiration and evaporation; and dry matter produced which has a resulting effect on yield components (e.g. tiller and seed number, and seed weight).

Heiniger et al. [10] identified simulation of tiller number as the weakest yield component in SORKAM. Furthermore, the improvement (reduction) in early leaf area should reduce simulated transpiration rates and under moisture limiting conditions delay simulation of moisture stress effects. Comparing SORKAM and revised-SORKAM estimates of yield components, the new leaf development relationships caused the simulated tiller number to be reduced and this reduction may be associated to the reduction of simulated leaf area for the early

Table III. Effect of the revised leaf growth model on tiller number, seed number, seed weight, and total dry weight. A linear relationship between the revised SORKAM and SORKAM estimate is given by [Revised SORKAM Estimate = a + b* (SORKAM Estimate)]. DELTA is the average percentage difference between the revised and SORKAM estimate (DELTA = [Revised Estimate – SORKAM estimate]/SORKAM estimate * 100).

Variable	a	b	R^2	Delta (%)
Yield (kg ha^{-1})	–69.6	0.94	0.94	–413 (–6.9)
Tiller number	0.07	0.76	0.88	–0.17 (–16.8)
Seed weight, (g 1000^{-1})	–0.32	0.98	0.98	0.11 (–0.5)
Seed number $head^{-1}$	–80	1.15	0.95	343 (12.4)
Seed m^{-2}	2856	0.78	0.75	–2986 (–11.0)
Dry matter $plant^{-1}$	–26.2	1.34	0.94	27.2 (8.1)
Dry matter ha^{-1}	520.5	0.90	0.93	–1013 (–6.9)

leaves, lower simulated dry matter per plant (Tabs. III and IV) ($t = 7 \times 10^{-16}$; n = 37 paired t-test, and thus lower crop growth. The new leaf development relationships also increased simulated seed number compared with the original estimates because

Table IV. Comparison of simulated SORKAM and revised SORKAM in estimating yield components. Standard errors are in parentheses.

Variable	Average SORKAM (se)	Revised SORKAM (se)
Yield (kg ha^{-1})	5954 (277)	5540 (269)
Tiller Number	1.02 (0.03)	0.85 (0.03)
Seed Weight (g 1000^{-1})	21.8 (0.8)	21.7 (0.8)
Seed Number $head^{-1}$	2769 (81.1)	3111 (96.0)
Seeds m^{-2}	27096 (576)	24110 (522)
Dry matter $plant^{-1}$	149.8 (4.6)	177.0 (6.4)
Dry matter ha^{-1}	14715 (378)	13702 (350)

of the reduced simulated tiller number resulting in more radiation intercepted per shoot later in the season after tiller and seed numbers are determined. Seed weights as calculated in SORKAM and the revised SORKAM are essentially the same ($t = 0.64$; $n = 37$ paired t-test). Dry matter (g $plant^{-1}$) calculations using the new relationships were greater than the original estimates by approximately 34% ($t = 6 \times 10^{-15}$; $n = 37$ paired t-test). The increased simulated dry matter is associated with less simulated early leaf area, resulting in reduced simulated evapotranspiration and water stress (as indicated by the water stress coefficient threshold of 0.3 of maximum plant available water to reduce transpiration [26] during early growth). Again, the revised model will be validated against other data sets that have observed yield and yield components to further evaluate the effect of the revised calculation of individual leaf area.

4. CONCLUSION

Individual leaf development was generalized to depend only on total leaf number. This improved individual leaf area simulation, particularly for lower leaves and for leaf area index. Root mean square error and bias of individual leaf area were both reduced with the generalized approach. However, simulation of total plant leaf area produced over the whole season was not improved.

Modifications to the functions for leaf appearance and leaf expansion rate and duration improved the simulation accuracy of individual leaf areas, particularly the lower, smaller leaves which determine canopy cover early in the season. This is associated with a more accurate simulation of light interception, dry matter production, and tiller production. Thus, the changes in leaf area simulation reported here could greatly improve the capability of SORKAM to mimic the leaf development and response of grain sorghum. Further studies will compare the SORKAM and revised models with a larger data set containing observed yields and yield components (seed number, tiller number, seed weight, etc.).

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