

Evaluating the CROPGRO Soybean Model for Predicting Impacts of Insect Defoliation and Depodding

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ABSTRACT

Insect feeding on leaves, pods, and seeds causes significant yield loss in soybean [*Glycine max* (L.) Merr.]. Robust soybean growth models would be helpful to simulate the effect of defoliation or depodding on soybean growth and yield. The objective of this study was to evaluate the CROPGRO-Soybean model for its ability to predict the impacts of insect defoliation and depodding. Growth data were used to calibrate the model for two cultivars in Griffith, NSW, Australia. The model was evaluated against independent data from defoliation and depodding experiments at Griffith and at Gainesville, FL. The work tested the sensitivity of the model to defoliation and depodding at various growth stages, by comparison to data on manual defoliation of 30 and 60% in Australia and 30 and 70% in the USA, and depodding of 50 and 100% in Australia. The model predicted small yield reductions (4–11%) from 30% defoliation and greater reductions (17–49%) from 60 to 70% defoliation. The model illustrated well the pattern of sensitivity to defoliation: low during vegetative growth, increasing until beginning seed growth, and decreasing thereafter. The model overpredicted yield loss for severe defoliation but predictions improved after model modification to include photosynthetic contribution of green area of stems, petioles, and pods. Depodding predictions were generally accurate, but showed the need to evaluate model ability to add late pods after depodding. We conclude that the CROPGRO-Soybean model has adequate capabilities for use as a tool to predict the effects of timing and intensity of defoliation and depodding.

AN IMPORTANT ISSUE in soybean production worldwide is the loss in grain yield caused by insect defoliation and insect feeding on flowers, pods, and seeds. Therefore it is important to define and predict the maximum amount of insect-induced leaf, flower, and pod loss a soybean crop can sustain at various stages of development without suffering a significant reduction in seed yield. Defoliation and depodding at different stages may have different consequences on yield loss. Information aggregated in this manner may be useful in integrated pest management, particularly when assisted with crop model analyses of yield sensitivity to defoliation and depodding.

Defoliation studies on soybean in Alabama (Begun and Eden, 1965), South Carolina (Turnipseed, 1972), and Georgia (Todd and Morgan, 1972) showed that 33% defoliation during reproductive stages reduced yield by 3 to 28% on average, while 67% defoliation caused yield reductions from 21 to 53%. Hinson et al. (1978)

observed yield reductions of 8, 21, 31, and 30% with 67% defoliation at 3 (R2), 17 (R3), 31 (R5), and 42 (R5.5) d after flowering, respectively, while only 4% yield loss occurred with 33% defoliation regardless of the time of defoliation in Florida. Defoliation during the reproductive phase is more damaging than during the vegetative phase, although the effects may be variable. Thus, in Arkansas, Caviness and Thomas (1980) reported an average yield reduction of 11 to 17% for 50 to 100% defoliation at R4 to R5, but almost no yield loss even with 100% defoliation at V5 (Pickle and Caviness, 1984). Fehr et al. (1977, 1981) demonstrated that the stages most sensitive to defoliation were R5 or R5.5, with 80% yield loss from 100% defoliation. Board et al. (1994) showed that yield sensitivity to defoliation declines as seed filling progresses from R5 to R6 to R7. They found that 100% defoliation at R6.3 caused 40% yield loss, whereas 100% defoliation at R6.6 caused only 20% loss. Turnipseed and Kogan (1987) reported 20% yield loss for 70% defoliation at R6 in South Carolina.

In Queensland, Australia, Rowden et al. (1982) reported no yield loss for any level of defoliation at 22 d after emergence (DAE), but defoliation at end of flowering (70 DAE) resulted in severe yield loss. Depodding when a large proportion of seeds were fully formed also caused severe yield loss. Brier and Zalucki (1996), also in Queensland, reported that 'Davis' soybean compensated completely for total depodding during pod elongation and early pod fill by setting additional pods, which developed from new flowers or from fertilized flowers that had not yet developed pods.

A desirable objective in soybean management is to be able to predict the probable yield loss due to defoliation and depodding caused by different insects. The corn earworm, *Helicoverpa armigera* (Hubner), and native budworm, *H. punctigera* (Wallengren), are the major insect pests of irrigated soybean in southern New South Wales and northern Victoria in Australia (Colton et al., 1995; Colton and Rose, 2000). *Helicoverpa punctigera* tends to be the most abundant species during the early season, and *H. armigera* toward the end of the season, but oviposition by both species occurs throughout crop development. These insects remove leaf area and seeds, but consumptive removal of flowers, sometimes up to 65%, is also a major cause of yield loss due to *Helicoverpa* in Australia (Duffield and Chapple, 2001). In years of heavy infestation, yield losses to these species of >40% have been reported, with up to five insecticide sprays applied annually (D. McCaffery, unpublished

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Modeling

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Abbreviations: DAE, days after emergence; LAI, leaf area index; LFMAX, maximum leaf photosynthesis coefficient; MG, maturity group; SIZELF, maximum leaf size coefficient; SLA, specific leaf area; SLAVAR, specific leaf area coefficient.

data, 1999, as reported by Duffield and Jordan, 2000). In the southern USA, velvetbean caterpillar (*Anticarsia gemmatilis* Hubner), soybean looper (*Pseudoplusia includens* Walker), and corn earworm (*Heliothis zea* Boddie) rank highest to lowest in terms of damage to the soybean crop (Turnipseed and Kogan, 1987). Knowledge of the yield reductions from removal of leaves, seeds, or flowers is needed to devise spray thresholds in both countries.

Robust soybean models would be helpful to simulate growth and final yield response caused by defoliation, deflowering, or depodding at different stages of soybean growth. There is potential for using crop models to predict the consequences of insect damage from defoliation or depodding on seed growth and yield via two different modes of input into the model: (i) entering the defoliation or depodding percentage, and (ii) entering the number of insects of various instars and their feeding rate. The second mode requires knowledge from entomologists concerning the amount of leaf area, or the pod or flower number or mass consumed per larvae of a given instar. An early version of the CROPGRO-Soybean model named SOYGRO was used in both modes to predict yield losses from insect damage (Boote et al., 1993; Batchelor et al., 1989, 1993). Before attempting such applications, however, the model must be calibrated and validated for new climatic regions and cultivars for which use in decision making is intended. In addition, the model should be evaluated for accurate response to defoliation, depodding, and deflowering.

CROPGRO, a generic model, simulates a range of grain legumes in both dryland and irrigated environments across a range of latitudes in both northern and southern hemispheres. The history of CROPGRO dates back to the early 1980s when the original version of SOYGRO Version 4.2 for soybean was released (Wilkerson et al., 1983). Since then several improvements to the model have been made and several versions released. Boote et al. (1998a, 1998b) described the model processes of CROPGRO Version 3.5, which is very similar to the most recent version (Version 4.0) released in 2004 (Hoogenboom et al., 2004). CROPGRO has been evaluated across a wide range of experiments (Boote et al., 1997; Sau et al., 1999; Ruiz-Nogueira et al., 2001), including preliminary evaluation with 'Djakal' for southern New South Wales (Timsina et al., 2005). The ability to account for the effects of pest damage on yield is included in the model and has been evaluated against limited experimental data (Boote et al., 1993). The objective of this study was to evaluate the CROPGRO-Soybean Version 4.0 model for its ability to predict the impacts of insect defoliation and depodding on soybean yield using data sets from Griffith, in southern Australia, and Gainesville, FL, in the southern USA.

MATERIALS AND METHODS

Description of Field Experiments

Data for the evaluation of CROPGRO were obtained from a field experiment conducted in 1999–2000 on a Hanwood loam soil at CSIRO Land and Water, Griffith (34°19'S,

146°4'E), NSW, Australia (Marston, unpublished data, 2000) and a 1977 experiment at Gainesville (29.63° N and 82.37° W), FL (Hinson et al., 1978). Briefly stated, in Australia, two indeterminate soybean cultivars (Hooper and Stephens belonging to late maturity group [MG] 3 or early MG 4) were sown at 30 seeds m⁻² in 0.80-m row spacing, in 30- by 10-m plots, in four replicates on 15 November, 8 December, and 6 January. Three levels of defoliation (0, 30, and 60%) at V4, R1, R3, and R5 stages and three depodding levels (0, 50, and 100%) at R4 and R6 stages were applied for each sowing date (Table 1). For the 30% defoliation, a single side lobe was removed, while for 60% defoliation, both side lobes were removed. For 50% depodding, half of all pods >5 mm, and for 100% depodding, all pods >5 mm were removed. For time-course analysis of leaf area index (LAI), total crop weight, and component partitioning, three 1.0-m rows were sampled, while for defoliation and depodding, three 0.5-m rows were used each time.

The soil at Griffith was a Hanwood loam which was characterized for use by the DSSAT crop models, using the DSSAT pedotransfer functions (Hoogenboom et al., 2004): albedo (0.14); Stage 1 evaporation limit (8.0); mineralization factor (1.0); runoff curve number (76); daily drainage fraction (0.40); and default soil fertility factor (1.0). Tensiometers were installed in each plot at 30-, 60-, and 100-cm depths to monitor soil water potential, and irrigation was scheduled with a soil water balance approach to minimize crop water deficit.

In the USA, the model was tested against the defoliation experiment of Hinson et al. (1978) conducted at Gainesville, FL. Cultivar Bragg (MG 7) was sown on 16 June 1977 at high density in 0.90-m rows and thinned at 3 wk after sowing to 7.5-cm plant spacing (14.8 plants m⁻²). The soil was Arrendondo fine sand (loamy, siliceous, hyperthermic Grossarenic Paleudalf). The experiment was irrigated as needed to prevent water deficit. Two defoliation levels (30 and 70%) were applied on four dates (3, 17, 31, and 42 d after anthesis [DAA]), by removing either one lateral leaflet (30%) or one lateral and one terminal leaflet (70%), corresponding to R2, R3, R5, and R5.5 stages, respectively. Two multiple defoliation treatments were also created at 38 DAA, by redefoliating the 3 DAA defoliation treatment to 30 and 70% levels. There were four replicates of each treatment. Leaf area index in adjacent border rows was reduced by removing every third plant for 30%, or two of every three plants for 70% defoliation treatments.

Limited growth samples were collected during each defoliation event by collecting the removed leaf area and mass from a 1.1-m length of row. Samples were analyzed for leaf area, leaf mass, leaf N concentration, N mass, and specific leaf area. In addition, on two dates, 14 and 29 September, a 30-cm section of row (four plants) was harvested in each plot to de-

Table 1. Dates of defoliation and depodding for two cultivars at three sowing dates at Griffith, Australia (the four dates of defoliation correspond to V4, R1, R3, and R5 growth stages, and the two dates of depodding correspond to R4 and R6 stages).

Sowing dates	'Hooper'	'Stephens'
Dates of defoliation		
15 Nov.	10 Dec., 9 and 28 Jan., 9 Feb.	20 Dec., 5 and 20 Jan., 7 Feb.
8 Dec.	5 and 21 Jan., 16 and 21 Feb.	5 and 21 Jan., 9 and 16 Feb.
6 Jan.	2 and 11 Feb., 5 and 16 Mar.	28 Jan., 11 and 24 Feb., 16 Mar.
Dates of depodding		
15 Nov.	4 and 22 Feb.	1 and 22 Feb.
8 Dec.	19 Feb., 17 Mar.	13 Feb., 5 Mar.
6 Jan.	8 and 29 Mar.	5 and 29 Mar.

termine defoliation effects on LAI remaining, extent of new leaf area growth after defoliation, leaf mass, specific leaf area, N concentration, and seed size. Experimental details are reported in Hinson et al. (1978) and Nino (1978).

Procedure for Model Calibration and Validation

The two cultivars, Hooper and Stephens from Australia, correspond to late MG 3 or early MG 4; thus the default genetic coefficients for MG 4 available in DSSAT Version 4.0 (Hoogenboom et al., 2004) were chosen initially. The cultivar coefficients in Table 2 were modified slightly from the default MG 4 values by comparing the simulated phenology, time-series growth, final biomass, and yield with observed data for only the first sowing date (Table 3), following the procedures outlined by Boote (1999). The model's species and ecotype files were the standard default for Version 4.0. The extent of changes from model default coefficients was small and calibration was not the point of the study, but to give a more accurate prediction of LAI and timing of reproductive growth to allow evaluation of the effects of defoliation. Subsequently, the model was compared with all three sowing dates, but without calibrating the second and third sowing dates in any way, in an effort to maintain two-thirds of the data for independent validation. Model validation was illustrated in two ways: first by comparison of the model performance against data collected at final harvest for all six treatments from the second and third sowing dates (Table 3), and second, by comparison of time-course simulations of LAI and dry matter growth of those treatments (Fig. 1, 2, and 3) since no genetic coefficients were set based on those data.

Model evaluation for development, yield, and time-course of growth (LAI, leaf, stem, top weight, etc.) was performed using RMSE and index of agreement (D-index) (Table 4) as suggested by Willmott (1982) and Willmott et al. (1985). The RMSE summarizes the root mean sum of squares differences in the units of observed (O) and predicted (P) values, calculated as

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (P_i - O_i)^2}{n}}$$

Table 2. Genetic coefficients for the Hooper and Stephens cultivars grown at Griffith, Australia, compared with default DSSAT genetic coefficients for Maturity Group (MG) 3 and 4 soybean cultivars.

Genetic coefficients	Hooper	Stephens	MG 3	MG 4
Critical short day length, h	13.2	13.26	13.40	13.09
Slope of response to photoperiod, h ⁻¹	0.294	0.293	0.285	0.294
Time from emergence to R1, pd†	20.5	20.0	19.0	19.4
Time from R1 to R3, pd	6.5	6.5	6.0	7.0
Time from R1 to R5, pd	11	11	14.0	15.0
Time from R5 to R7, pd	30.2	30.6	33.2	34.0
Time from R1 to end leaf, pd	24	24	26	26
Maximum leaf photosynthesis, mg CO ₂ m ⁻² s ⁻¹	1.02	1.05	1.03	1.03
Specific leaf area, m ² kg ⁻¹	40	40	37.5	37.5
Maximum leaf size, cm ²	215	230	180	180
Maximum fraction of partitioning to seeds	1.0	1.0	1.0	1.0
Maximum weight per seed, g	0.175	0.185	0.190	0.190
Seed filling duration, pd	24.5	23.5	23.0	23.0
Seeds per pod, no. pod ⁻¹	2.2	2.2	2.2	2.2
Pod addition duration, pd	11.0	10	10.0	10.0
Shelling percentage, %	78.0	78.0	78.0	78.0

† Photothermal day.

Table 3. Simulated and observed number of days to phenological events, maximum leaf area index (LAI), and final grain and aboveground biomass yields for two cultivars at three sowing dates at Griffith, Australia.†

Attribute	Cultivar	Sowing date	Simulated	Observed
Days to first flower, d	Hooper	15 Nov.	60	60
		8 Dec.	53	56
		6 Jan.	42	41
	Stephens	15 Nov.	58	58
		8 Dec.	50	51
		6 Jan.	40	41
Days to first pod, d	Hooper	15 Nov.	73	71
		8 Dec.	63	70
		6 Jan.	50	58
	Stephens	15 Nov.	71	71
		8 Dec.	61	63
		6 Jan.	49	49
Days to physiological maturity, d	Hooper	15 Nov.	117	112
		8 Dec.	104	109
		6 Jan.	91	94
	Stephens	15 Nov.	115	112
		8 Dec.	102	109
		6 Jan.	89	94
Grain yield, t ha ⁻¹	Hooper	15 Nov.	4.10	3.28
		8 Dec.	3.54	3.96
		6 Jan.	2.64	3.47
	Stephens	15 Nov.	4.27	4.17
		8 Dec.	3.57	4.38
		6 Jan.	2.72	3.32
Biomass yield, t ha ⁻¹	Hooper	15 Nov.	7.81	7.57
		8 Dec.	6.10	6.73
		6 Jan.	4.15	5.69
	Stephens	15 Nov.	7.72	7.13
		8 Dec.	5.92	6.67
		6 Jan.	4.15	5.68
LAI maximum	Hooper	15 Nov.	6.3	5.6
		8 Dec.	5.1	4.7
		6 Jan.	3.4	4.3
	Stephens	15 Nov.	6.2	5.2
		8 Dec.	4.9	4.8
		6 Jan.	3.4	3.8

† RMSE for days to first flower (d), days to first pod (d), days to physiological maturity (d), grain yield (t ha⁻¹), biomass yield (t ha⁻¹), and LAI maximum was 1.4, 4.5, 4.9, 0.66, 1.10 and 0.64, and the index of agreement (D-index) for those traits was 0.99, 0.93, 0.93, 0.61, 0.80, and 0.86, respectively.

while the D-index is a descriptive index (both relative and bounded), that measures dispersion of the simulated and observed data, calculated as

$$\text{D-index} = 1 - \left[\frac{\sum_{i=1}^n (P_i - O_i)^2 / \sum_{i=1}^n (|P_i'| + |O_i'|)^2}{n} \right]$$

where n is the total number of observations, P_i is the predicted value for the i th measurement, O_i is the observed value for the i th measurement, and $P_i' = P_i - \bar{O}$ and $O_i' = O_i - \bar{O}$, where \bar{O} is

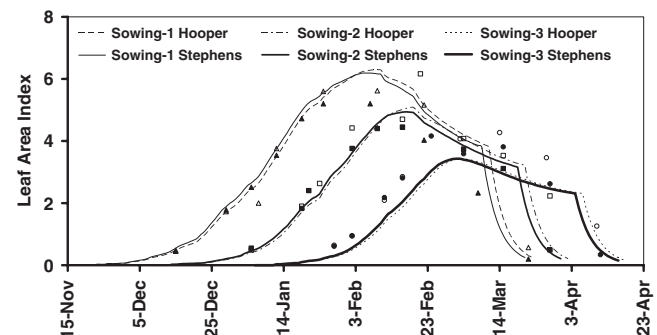


Fig. 1. Simulated and observed seasonal leaf area index for two cultivars and three sowing dates at Griffith, Australia (continuous lines represent simulations, symbols are observed data).

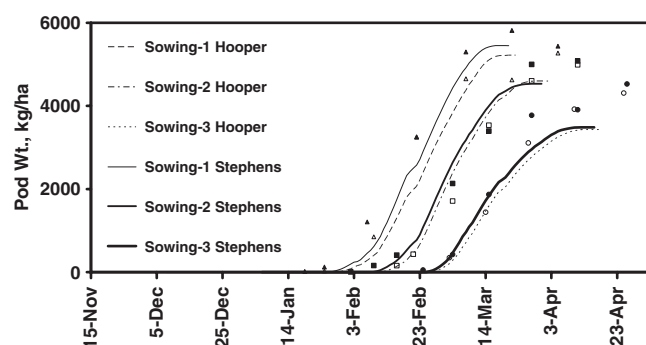


Fig. 2. Simulated and observed seasonal pod weight for two cultivars and three sowing dates at Griffith, Australia (continuous lines represent simulations, symbols are observed data).

the overall mean of the observed values. A model performs well when the RMSE approaches zero and the D-index is close to 1.0.

Procedure for Simulating Effects of Defoliation and Depodding

The effect of defoliation or depodding was simulated by entering the reported level of defoliation or depodding percentage for the corresponding day of year into the crop performance file (File T) of DSSAT, under the headers of PCLA (cumulative defoliation percentage) and PPDN (depodding percentage). The model code is designed to read this file and create leaf area loss (also leaf mass and N loss) and pod (and seed) loss on a given day of year (Batchelor et al., 1993, Boote et al., 1993, Hoogenboom et al., 2004). The model then runs the remainder of the season with the reduced LAI or pod numbers, resulting in reduced light interception, photosynthesis, and yield. The model's degree of leaf area regrowth after defoliation depends on the reproductive stage, assimilate supply, and the photothermal time left to grow leaves. The effect of depodding depends on where the modeled crop is in the pod-adding phase and the remaining time left to add pods. Statistical evaluation, using the RMSE and the D-index, was used to compare simulated with observed crop biomass and seed yield for defoliated and depodded treatments.

Model sensitivity to defoliation was evaluated by hypothetically creating 30 and 60% defoliation throughout the entire crop life cycle at 5-d intervals, using the same procedure as

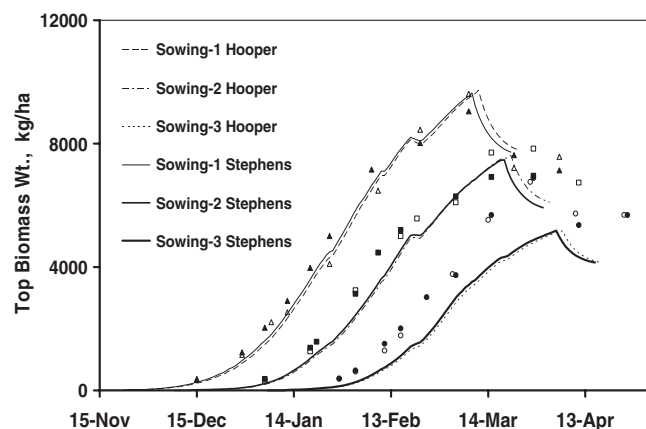


Fig. 3. Simulated and observed seasonal total top biomass weight for two cultivars and three sowing dates at Griffith, Australia (continuous lines represent simulations, symbols are observed data).

Table 4. Root mean square error and index of agreement (D-index) values for time course of leaf area index (LAI) and leaf, stem, pod, and total weight for two cultivars at three sowing dates at Griffith, Australia.

Attribute	Cultivar	Sowing date	RMSE	D-index
LAI	Hooper	15 Nov.	0.36	0.99
		8 Dec.	0.78	0.94
		6 Jan.	0.76	0.91
	Stephens	15 Nov.	0.70	0.96
		8 Dec.	0.23	0.99
		6 Jan.	0.61	0.94
Top weight, kg ha ⁻¹	Hooper	15 Nov.	368	1.00
		8 Dec.	709	0.98
		6 Jan.	1150	0.93
	Stephens	15 Nov.	386	1.00
		8 Dec.	590	0.99
		6 Jan.	1128	0.92
Leaf weight, kg ha ⁻¹	Hooper	15 Nov.	238	0.97
		8 Dec.	332	0.94
		6 Jan.	379	0.85
	Stephens	15 Nov.	233	0.97
		8 Dec.	121	0.99
		6 Jan.	306	0.89
Stem weight, kg ha ⁻¹	Hooper	15 Nov.	211	0.99
		8 Dec.	430	0.95
		6 Jan.	636	0.81
	Stephens	15 Nov.	277	0.99
		8 Dec.	403	0.95
		6 Jan.	662	0.77
Pod weight, kg ha ⁻¹	Hooper	15 Nov.	641	0.97
		8 Dec.	334	0.99
		6 Jan.	335	0.98
	Stephens	15 Nov.	486	0.98
		8 Dec.	379	0.99
		6 Jan.	413	0.98

above, and 50 and 100% depodding at 5-d intervals, beginning at the date of first pod appearance. In the USA, model sensitivity to 30 and 70% defoliation was evaluated at weekly intervals, and defoliated yields compared relative to the undefoliated check.

RESULTS AND DISCUSSION

Model Calibration for Southern Australia

Table 3 shows the simulated and observed number of days to first flower, first pod, and physiological maturity, and grain yield, total crop biomass, and LAI, together with RMSE and D-index values. Figures 1 to 3 show the simulated and observed seasonal time courses of LAI, pod and total top mass, along with statistics (Table 4).

For the first sowing date treatment, Hooper flowered in 60 d and Stephens in 58 d, while both reached physiological maturity in 112 d (Table 3). The simulated time to first flower was set to 60 (or 58) d by slightly increasing the default critical short day length (CSDL) coefficient of MG 3 cultivars from 13.09 to 13.20 h for Hooper, and to 13.26 h for Stephens, along with small increases in the coefficient for the time from emergence to R1 from 19.4 to 20.5 photothermal days (pd) for Hooper, and 20.0 pd for Stephens. These CSDL changes were consistent with somewhat earlier cultivars than MG 4. The higher CSDL, along with smaller values of the time from R1 to R5 (FL-SD) and time from R5 to R7 coefficients, was also needed for correct simulation of physiological maturity (Tables 2 and 3). Based on the projected end-of-season decline in observed LAI, leaf mass, and total crop biomass compared with simulations, the simulated physiological maturity was set at 117 and

115 d, respectively, for those cultivars, rather than the reported 112 d. Days to beginning pod addition was achieved by setting the coefficient for time from R1 to R3 (FL-SH) to 6.5 pd, halfway between the defaults for MG 3 and MG 4, and onset of pod-plus-seed mass was accelerated by decreasing the FL-SD from the default of 15 to 11 pd. Potential maximum weight per seed was set by decreasing the default of 0.19 to 0.175 and 0.185 g seed⁻¹ for Hooper and Stephens, respectively.

The time course of LAI was generally well simulated with RMSEs of 0.36 and 0.70, respectively (Fig. 1, Table 4) after minor calibration of three traits: first, the specific leaf area (SLAVAR) coefficient for both cultivars was increased from 37.5 to 40 m² kg⁻¹ because modeled specific leaf area (SLA) was less than the observed SLA. Second, the maximum leaf size (SIZELF) coefficient was increased from 180 to 215 and 230 cm² for the respective cultivars to increase LAI during early season development. This trait is like a vegetative vigor trait up through the first five leaves. Third, the time from R1 to end leaf coefficient was shortened from 26 to 24 pd for both cultivars to make the peak of LAI occur earlier and be somewhat lower. With these changes to set LAI, the leaf weight of both cultivars (not shown) was generally well predicted until the end of January, after which it was slightly overpredicted (RMSE of 238 and 233 kg ha⁻¹). Stem mass was well simulated until February, after which the model somewhat overpredicted the stem mass of both cultivars (data not shown). Creating earlier onset of pod and seed growth discussed above was needed to limit the overprediction of stem mass (or LAI and leaf mass).

Pod mass was somewhat underestimated especially early, despite using smaller coefficients (FL-SH and FL-SD) to create earlier pod and seed set (Fig. 2). The RMSE for pod mass was 641 and 486 kg ha⁻¹ for the two cultivars (Table 4). Total crop mass was simulated well throughout the season (Fig. 3) with low RMSE (368 and 386 kg ha⁻¹ for Hooper and Stephens, respectively; Table 4). Very little model modification was required to obtain this predictability other than changes to achieve the correct LAI prediction and timing of the life cycle and reproductive onset. This performance is with the default soil fertility value of 1.0 (assumes highly fertile soil) and minor change in the maximum leaf photosynthesis (LFMAX) from the default of 1.03 to 1.02 and 1.05 mg CO₂ m⁻² s⁻¹, respectively, to differentiate the cultivars, especially to increase growth and yield of Stephens relative to Hooper.

Model Validation for Southern Australia

The model substantially captured the earlier flowering and maturity aspects of later sowings, with D-index values >0.93 and RMSE of 1.4 d for flowering and 4.9 d for maturity (Table 3). Both predicted and observed biomass, grain yield, and LAI were progressively reduced from early to later sowings, with some model underprediction in growth and yield for the later sowings (Table 3). As a result, the RMSE across all six treatments was fairly high and the D-index only moderate.

The model accurately predicted LAI, leaf mass, and pod mass, and fairly accurately predicted total crop biomass with time for the second sowing (Fig. 1, 2, and 3), although for biomass, the underprediction was associated with underprediction of stem mass (not shown). The D-index for the time-series variables for the second sowing date ranged from 0.94 to 0.99, indicating good predictions (Table 4). For the third sowing date, however, the model underpredicted all time-series variables, with most pronounced underestimations for total crop mass (Fig. 3) and stem mass. For pod mass, the prediction was good initially, but was underestimated later in the season (Fig. 2). Except for pod mass, there were lower D-index and generally higher RMSE values for the third sowing date, associated with model underprediction (Table 4).

Closer examination of weather data revealed that the late-sown crop received lower radiation and lower maximum and minimum temperatures, especially during the reproductive phases, than the first two earlier sown crops. While no model modifications were made, these underpredictions for late sowing dates are consistent with prior observations on soybean grown in cool regions of Spain (Sau et al., 1999) and Argentina (A. Confalone, personal communication, 2005) showing that the photosynthesis functions of the CROPGRO-Soybean model are reduced too much at low temperatures.

Evaluating Model Sensitivity to Defoliation and Depodding in Southern Australia

Figure 4 illustrates simulated vs. observed grain yield across all defoliation treatments at Griffith. This constitutes a validation as well as a test of how well the model predicts defoliation effects, as the model was not previously calibrated with these data. The model slightly overestimated seed yield of defoliated treatments for the first sowing date, was fairly close for the second date, and underestimated for the third date (overall RMSE of 920 kg ha⁻¹ and D-index of 0.55). For top weight, it slightly overestimated the weight of the defoliated treatments for the first sowing date, while it underestimated for the second and third dates (overall RMSE of 1110 kg ha⁻¹ and D-index of 0.78; Fig. 4).

For the depodded treatments, the model predicted yields satisfactorily (Fig. 5), except for some individual cases (RMSE = 723 kg ha⁻¹, D-index = 0.93). For example, with 100% depodding at R6 for the first sowing date, there were yields of zero in simulations for both cultivars, but observed yields ranging from 200 to 800 kg ha⁻¹ means that the real crop had a somewhat extended ability to add pods after depodding. Critical inspection of the simulations and model-predicted growth stages revealed that depodding at R6 occurred after the "end pod" stage in the model, thus removing all pods resulted in zero yields as the model does not allow adding pods after the "end pod" stage. This observation suggests that a possible model improvement would be to create a later "end pod" stage and possibly a softer cutoff of pod addition. Also, there was one case (Stephens sown 6 January and 100% depodded at R4) where simulated

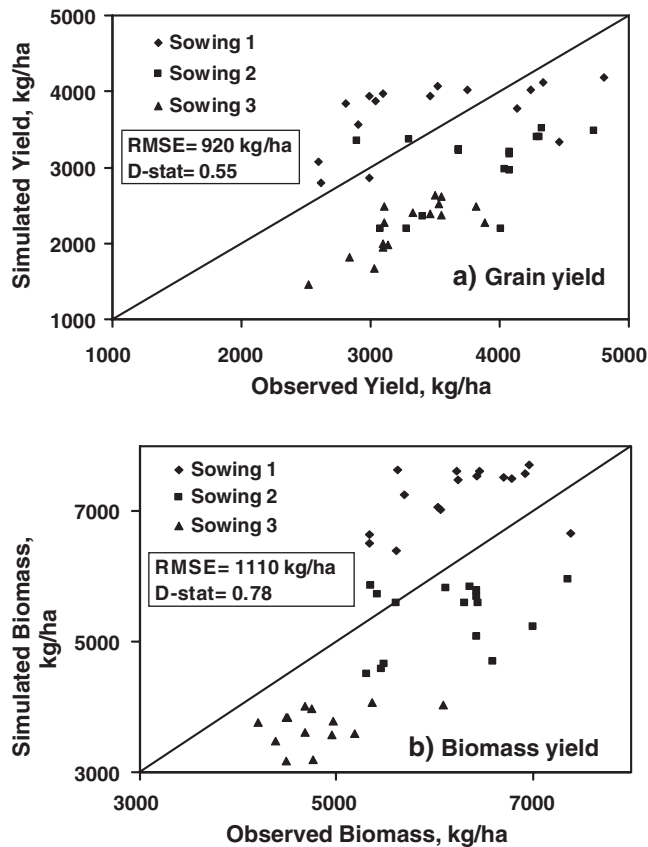


Fig. 4. Simulated and observed (a) grain yield and (b) aboveground biomass across defoliated treatments at Griffith, Australia.

yield was high (2355 kg ha^{-1}) despite quite low experimental yield (600 kg ha^{-1}). In this case, we suspect but cannot document experimental error. Generally, with some exceptions, the model predicted top weight satisfactorily ($\text{RMSE} = 1110 \text{ kg ha}^{-1}$, $\text{D-index} = 0.90$; Fig. 5).

Time sensitivity of yield to 30 and 60% defoliation at 5-d intervals showed that 30% defoliation for the 15 November sowing date caused maximum yield reductions of 4.2% for defoliation at 75 DAE. For 60% defoliation, simulated seed yields were reduced as much as 16.9%, with the largest reductions at 75 DAE. When sowing was delayed to 6 January, yield reductions were much greater, with up to 11.3% for 30% defoliation and up to 48.4% for 60% defoliation, with the largest reductions at 50 DAE (Fig. 6). For the first sowing, 75 DAE corresponded to 2 d after the R5 stage (beginning seed) and also the date of maximum LAI. For the third sowing, 50 DAE was the date of R5 and the date of maximum LAI. In this sense, it is logical that defoliation has its maximum effect on future seed growth when there is no opportunity for continued leaf growth.

Time sensitivity of yield to 50 and 100% depodding showed, for the 15 November sowing date, that seed yield reductions were up to 50% with 50% depodding at 30 d after R3 stage (first pod). For 100% depodding, seed yields were reduced up to 100% with complete reductions for depodding at 30 d after R3. There was little impact on yield if depodding soon after R3 (within the

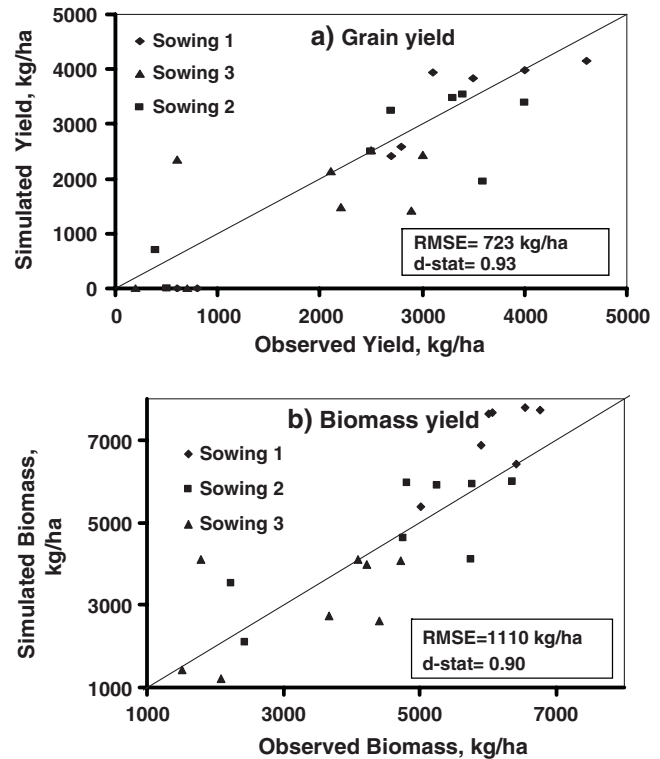


Fig. 5. Simulated and observed (a) grain yield and (b) aboveground biomass across depodded treatments at Griffith, Australia.

first 5 d), but the effect became more severe with later depodding dates. The transition to complete yield loss occurred sooner when sowing was delayed to 6 January, because the crop cycle was shorter (Fig. 7). With 50% depodding, yield reductions were up to 50%, with 36%

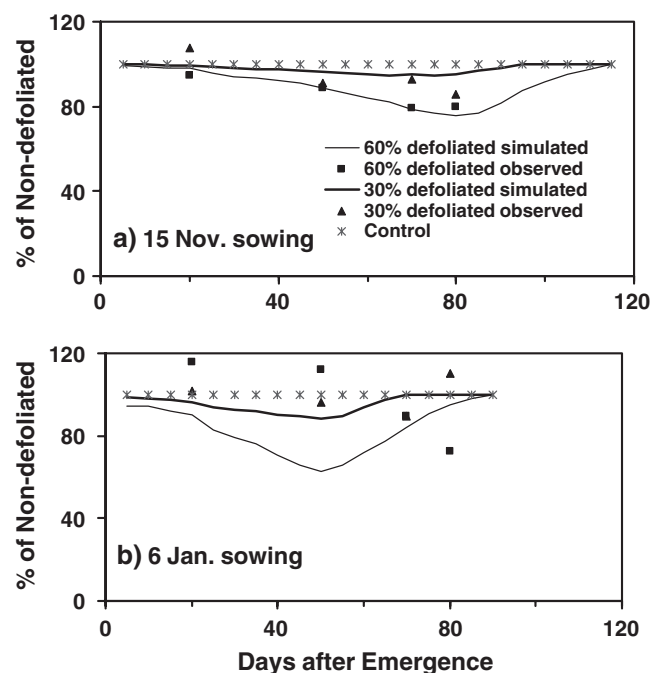


Fig. 6. Time sensitivity of 'Hopper' soybean yield to 30 and 60% defoliation for (a) 15 Nov. (early) and (b) 6 Jan. (late) sowings at Griffith, Australia.

reduction when depodded at 15 d after R3. With 100% depodding, yield reductions ranged from 18 to 100%, with complete reductions for depodding at 25 d after R3. The latest date of depodding where no yield was produced corresponded to about 5 d after the "end pod" stage, which marks the time in the model when pods can no longer be added.

Evaluating Model Sensitivity to Defoliation in the Southern USA

The CROPGRO-Soybean model with default coefficients accurately predicted the grain yield of the undefoliated check, with an overprediction by only 6%. The good performance was not unexpected because the model had earlier been intensively tested for the Bragg cultivar for the Gainesville location, but not for this year or experiment. Model simulations for the Gainesville experiment used the default traits for the Bragg cultivar, with no calibration. Automatic irrigation was used to run the model, as the field was irrigated but records were not available. Model predictions of grain yield across all 10 defoliation treatments plus the control showed reasonable predictability with an RMSE of 325 kg ha^{-1} and a D-index of 0.88 (Fig. 8), although the yield of the 70% defoliation treatments was underpredicted, and the regression slope was 1.54 and the intercept was less than zero.

We hypothesized possible reasons for the model's underestimation of yield for the high defoliation se-

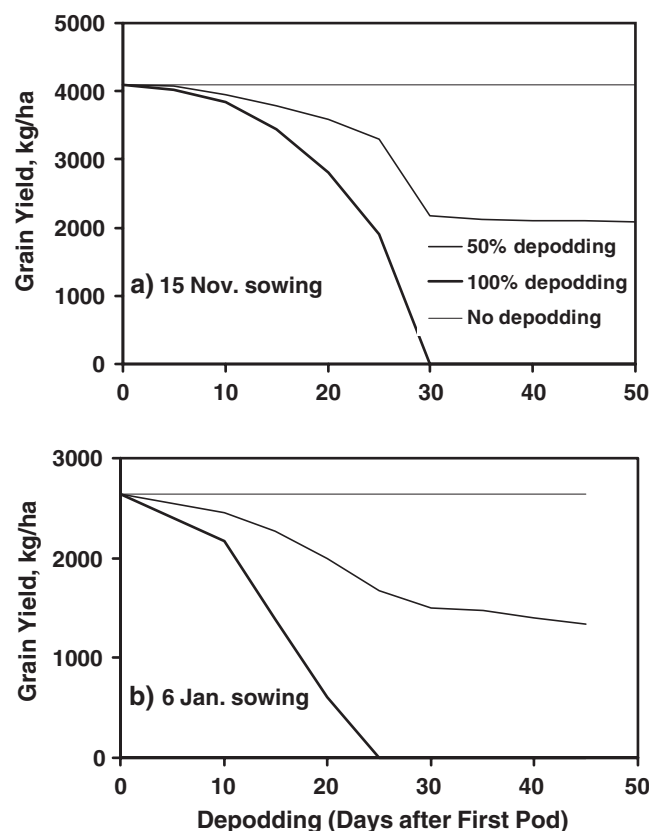


Fig. 7. Time sensitivity of 'Hopper' soybean yield to 50 and 100% depodding for (a) 15 Nov. (early) and (b) 6 Jan. (late) sowings at Griffith, Australia.

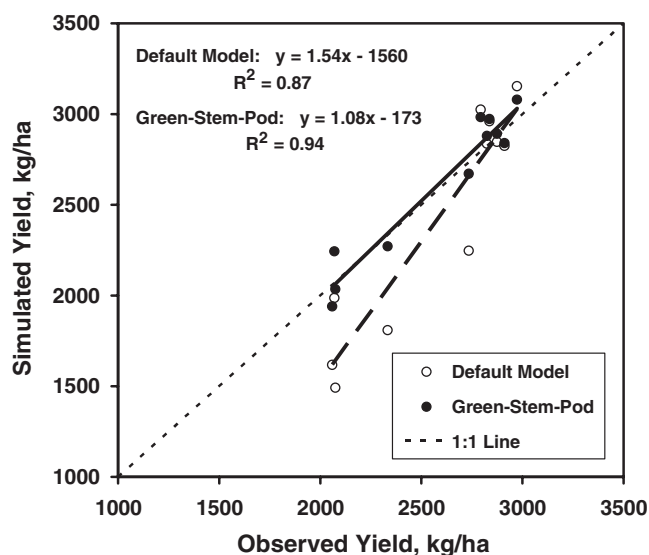


Fig. 8. Simulated and observed grain yields of 'Bragg' soybean across defoliated treatments at Gainesville, FL (Hinson et al., 1978) with the default model and with model adapted for green photosynthetic area of stem, petiole, and pod.

verity. One hypothesis was that underprediction of LAI associated with underprediction of SLA for this particular experiment may have led to underprediction of yield when defoliated. Thus, we recalibrated two parameters, SLAVAR from 355 to 430, and SIZELF from 170 to 230, to accurately predict observed SLA and LAI (after calibration, the observed and simulated LAI averaged 3.99 and 3.97, with an RMSE of 0.18 and a D-index of 0.98). Because the increased LAI caused increased light capture and photosynthesis even for the undefoliated plots, it was necessary to concurrently decrease LFMAX from 1.00 to $0.94 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. With these modifications to improve LAI prediction, model predictions of yield of defoliated treatments were improved somewhat, with an RMSE of 260 kg ha^{-1} and a D-index of 0.92 (data not shown). The slope of simulated vs. observed yield was slightly better (1.47) and the intercept somewhat closer to zero, thus we concluded that accurate prediction of LAI is important for accurate prediction of defoliation effects on grain yield. These changes, however, still left the model with serious underprediction of yield for severely defoliated treatments and a slope (1.47) much greater than 1.00.

We next hypothesized that the CROPGRO-Soybean model probably should also account for photosynthetic input by green area associated with stems, petioles, and pods. Rowden et al. (1982) reported a significant and important contribution of stems and petioles to photosynthesis of defoliated soybean. Such a feature, if included in the model, would be expected to increase yield for the defoliated treatments and improve the slope of observed to simulated yield.

Model Modification to Include Photosynthesis of Nonleaf Green Tissue

We added a subroutine to the CROPGRO code to compute green photosynthetic area associated with

stems, petioles, and pods, and simply added that increment to the LAI used for photosynthesis, assuming these structures had equal photosynthetic capacity as simulated leaf area, and equal allocation to sunlit and shaded leaf classes in the model. In reality, those structures probably have lower photosynthetic capacity and they would normally be shaded by upper leaves until defoliation exposed them to high light. Green stem area was calculated as a function of plant population, plant height, and stem diameter (d), while the green petiole area was a function of plant population, V stage (to give petiole number, limited to a maximum of $V = 15$), petiole length (l), and petiole diameter. From the default CROPGRO model, the plant population, plant height, V stage, and pod number are available and were used in simulating green area of stems, petioles, and pods using the relationships described below.

To obtain information and necessary relationships, we measured dimensions (length and diameter) and areas of individual petioles, stems, and pods of four 'Clark' (MG 4) plants at R5.5 stage at the V stage of 16 to 19 fully expanded leaves. The areas were measured using a LI-3100 leaf area meter (LI-COR, Lincoln, NE). Petiole dimensions and areas were evaluated as a function of node position (V stage). Stems and petioles were modeled to have one-sided green area like projected cylinders ($A = ld$). Stem diameter (d), in centimeters, was computed as: $0.10 + 0.04(V \text{ stage})$, up to $V = 15$. Petiole diameter was computed as: $0.09 + 0.02(V \text{ stage})$, up to $V = 10$. Petiole length (l) was computed as $3.3 + 2.5(V \text{ stage})$, up to $V = 12$. To account for petioles on up to two branches, a repeating function of V stage was added, initiated at $V = 5$ with a multiplier of 0.4, and at $V = 8$ with a multiplier of 0.2, where petiole number on each branch was limited to 10. Pod green area was model-predicted pod number multiplied by pod length and width multiplied by 0.866, with the assumption of 4.0-cm length and 0.9-cm width per pod. The 0.866 constant was derived from measurements and apparently reflects that the pod is not exactly a rectangle. Simulated area of all these tissues was converted to LAI ($\text{m}^2 \text{m}^{-2}$) before computing photosynthesis. In the model simulations, the computed nonleaf green tissue area index was 0.38 (from stems and petioles) by the beginning of pod addition (R3), and 0.68 by the end of pod addition (pod area index was 0.30). The pods, when present, contributed up to 45% of this nonleaf green area. The simulated nonleaf green area index amounted to 15.5% of the simulated LAI. For the experimental Clark plants, nonleaf green area index was 15.7% of the actual LAI.

With this modified model, the additional green area caused greater growth, thus we had to calibrate leaf photosynthesis to a lower value (LFMAX from 1.00 to $0.80 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to normalize to the same final yield. The modified model had a much better (less sensitive) response to defoliation (Fig. 8), because the green area of stem, petiole, and pods remained after defoliation. Yield of 70% defoliation treatments was increased considerably, without affecting the yield of undefoliated plots. The slope of simulated vs. observed yield was much closer to unity (1.08), the RMSE was

lower (108 kg ha^{-1}), and the D-index was higher (0.98). Statistics for predicted seed number and seed size were also improved considerably.

We conducted model sensitivity analyses for 30 and 70% defoliation at the Gainesville location, and compared yields as a percentage of the undefoliated check (Fig. 9). Both the simulated and observed yields for the defoliated treatments were normalized as a percentage of the appropriate undefoliated check to highlight where the simulated defoliation effects differed from the observed. Figure 9 shows that the default model correctly predicted the timing of maximum defoliation effects relative to time of defoliation, but the magnitude of reduction was too much. The maximum yield loss from 30% defoliation was 11 and 6% for the simulated and observed, respectively, while the maximum yield loss for 70% defoliation was 49% for simulated and 31% for observed, showing the default unmodified model to be too sensitive. The peak sensitivity to defoliation was at 73 d after emergence, which corresponded to 4 d after beginning seed (R5) stage, and about 6 d after the time of peak LAI. Thus, defoliation at this stage had its maximum effect on seed set and seed growth, when there was no opportunity for regrowth of LAI. The model prediction of peak sensitivity to defoliation (4 d after R5) agrees well with the literature that peak sensitivity is at R5 to R5.5 (Fehr et al., 1977, 1981), that sensitivity is less during vegetative phases (Caviness and Thomas, 1980; Pickle and Caviness, 1984), and that sensitivity declines progressively during seed fill (Board et al., 1994). Despite the good qualitative performance, the default model underestimated yield at high (70%) defoliation levels (predicting too much effect of defoliation), especially in the earlier two-thirds of the season. Predictions using the default model with modified values of SLAVAR and SIZELF gave accurate predictions of SLA and LAI, but this only marginally improved the early season predictions (Fig. 9). More importantly, when the model was modified for green area, predic-

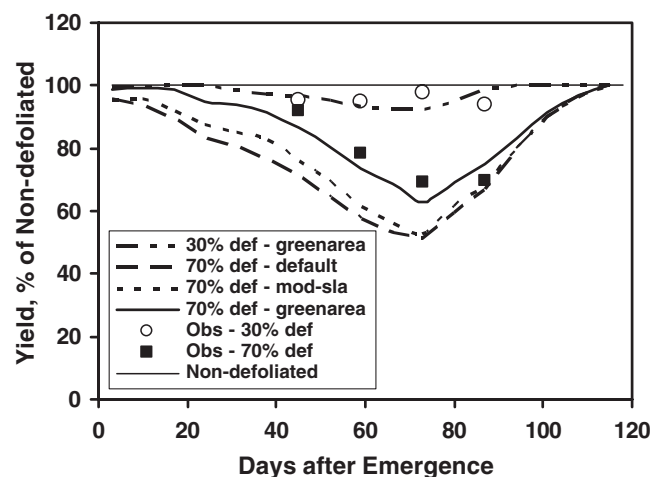


Fig. 9. Time sensitivity of 'Bragg' soybean yield to 30 and 70% defoliation (def) at Gainesville, FL (Hinson et al., 1978) for the default model (default), modified specific leaf area with the default model (mod-sla), and model adapted for green photosynthetic area of stem, petiole, and pod (greenarea).

tions were much closer to observed, with smaller yield loss (maximum loss of 37% for 70% defoliation) with less reduction, especially earlier in the season. This evidence (along with the slope closer to 1:1) suggests that the model should account for green photosynthetic area of stems, petioles, and pods throughout the season. It is very important to note that stems, petioles, and pods are mostly shaded before defoliation, and that they would become significant contributors to photosynthesis only after defoliation. The feature is an attractive one that should be further evaluated for permanent inclusion in the CROPGRO model, and the green surface area algorithm should be tested against additional data (inputs and measurements). It is logical that these tissues have some degree of photosynthetic surface area. The problem is to consistently predict the photosynthetic effectiveness or capacity of such tissues and the positional location of those tissues relative to upper leaves. Rowden et al. (1982) concluded that the photosynthetic efficiency (based on radiation use efficiency) of these nonleaf tissues was about 50 to 60% that of soybean leaf blades.

There was another possible cause for the severe modeled effects of the 70% defoliation treatments that was evident from the time course of LAI after defoliation. The real crop appeared to increase its LAI to a greater extent after the defoliations than did the simulated crop, especially for the earlier defoliation dates, despite no further increase in LAI for the undefoliated control (Fig. 10). This was attributed to more than just additional leaf area growth, as our 1977 field observations did not show differential growth of new leaves after defoliation compared with the control (Hinson et al., 1978). Rather, we suspect that the defoliated crop, once its leaves were in a higher light environment, had slower leaf senescence, thus maintaining leaf area better, whereas the undefoliated crop continued abscising leaves even while growing new leaves. The failure of the model to account for this phenomenon could account for part of the excessive yield loss for highly defoliated

treatments. Both green tissue area and reduced leaf senescence rates were probable contributors.

The model modified for nonleaf green photosynthetic area was reevaluated with the Australian data and found to improve the predictions of seed yield and total biomass for the defoliation treatments, but had no meaningful change in the prediction of depodding effects. With the modification, the RMSE value for yield of the defoliated treatments shown in Fig. 4 was reduced from 920 to 690 kg ha⁻¹ and the D-index improved from 0.55 to 0.61 (data not shown). Corresponding RMSE for biomass of defoliated treatments was reduced from 1110 to 989 kg ha⁻¹, while the D-index improved from 0.78 to 0.80 (data not shown). While much of the improvement was attributed to the nonleaf green area photosynthesis after defoliation, there was also improvement in prediction for the later sowing dates for both defoliated and undefoliated treatments. Yield of undefoliated treatments for the third sowing increased 190 to 280 kg ha⁻¹ and biomass by 150 to 250 kg ha⁻¹, relative to no change for the first sowing. Yield of undefoliated second sowing treatments was increased 30 to 190 kg ha⁻¹ and biomass by 80 to 120 kg ha⁻¹. With the lower LAI of the later sowing dates, there was a greater effect from the nonleaf photosynthetic area modification. For the six undefoliated treatments, the modification reduced the RMSE of yield from 656 to 545 kg ha⁻¹ and increased the D-index from 0.61 to 0.65, and reduced the RMSE of biomass from 1008 to 864 kg ha⁻¹ and increased the D-index from 0.80 to 0.84 (data not shown). To make these comparisons, we recalibrated the yield and biomass values only for the first sowing treatments, looking also at the time series of pod mass and biomass, concurrently adjusting LFMAX, SLAVAR, and SIZELF. This required a reduction in LFMAX (from 1.02 to 0.88 mg CO₂ m⁻² s⁻¹ for Hooper and 1.05 to 0.91 mg CO₂ m⁻² s⁻¹ for Stephens), a similar reduction as for Bragg in the Florida case. Concurrently, the SIZELF parameter was increased to 240 cm² for both cultivars and SLAVAR was reduced to 39 m² kg.

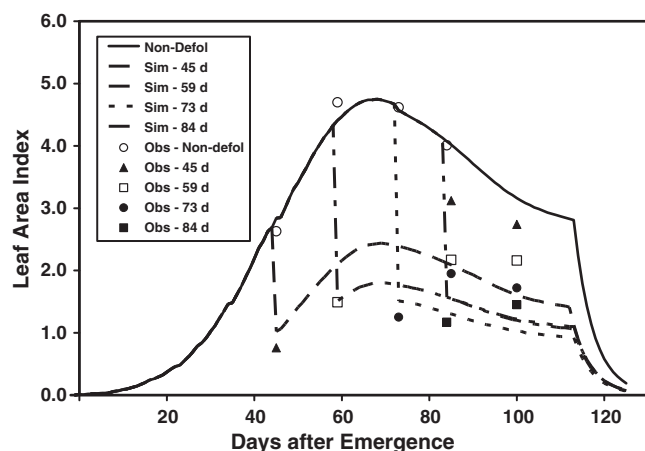


Fig. 10. Time sensitivity of leaf area index of 'Bragg' soybean to 70% defoliation at different times after emergence at Gainesville, FL (Hinson et al., 1978) using the default model with modified specific leaf area. First flower, first pod, first seed, and end of leaf expansion were simulated at 42, 61, 69, and 75 d after emergence.

CONCLUSIONS

We conclude that the default model (Version 4.0) has adequate capabilities to predict the effects of timing and intensity of defoliation and depodding. The model illustrated well the pattern of sensitivity to defoliation: low during vegetative growth, increasing until the period when maximum LAI is achieved and seed growth begins, and decreasing thereafter. The model, while qualitatively performing well, predicted too much yield loss for the 70% defoliated treatments. We recommend that the next version of the CROPGRO model be modified to account for green surface area associated with stems, petioles, and pods, because such modification provided less yield loss for severely defoliated plots. This modification improved model performance for defoliation and late sowing in terms of 1:1 comparisons (slope closer to unity, intercept closer to zero, lower RMSE, and higher D-index). The amount, photosynthetic effectiveness, and vertical placement in canopy layers of this nonleaf green

tissue needs further investigation. Indeed, this feature should be generalized for models of other crops and grain legumes, as many crops have significant nonleaf green tissue area. Depodding predictions, while generally accurate, showed the need to evaluate the model's ability to add late pods after depodding. While there is a need for improvement, we conclude that the current model release has adequate capabilities to be used as a tool to predict the effects of timing and intensity of defoliation and depodding.

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