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COUPLING SOYBEAN CYST NEMATODE DAMAGE TO CROPGRO–SOYBEAN

J. B. Fallick, W. D. Batchelor, G. L. Tylka, T. L. Niblack, J. O. Paz

ABSTRACT. The soybean cyst nematode (SCN) *Heterodera glycines* Ichinohe is responsible for substantial economic losses in soybean (*Glycine max* L. Merr.) production throughout the U.S. Results from past efforts to quantify the severity of crop damage resulting from SCN are often subject to variable experimental conditions resulting from differences in weather, soil type, and cultivar. Because of the difficulty in accounting for these variables, a process-oriented crop growth simulation model was chosen as a platform for studying the dynamics of SCN damage and for transferring knowledge between crop production scenarios. The objective of this study was to develop and evaluate hypotheses for coupling SCN damage to the process-oriented crop growth model CROPGRO–Soybean. A monomolecular function was used to relate daily SCN damage to initial population density of SCN eggs. The equation was incorporated into the crop model in order to test two hypotheses of how SCN damage occurs. The first hypothesis was that SCN reduce daily photosynthesis (Pg), while the second hypothesis was that SCN reduce daily potential root water uptake (RWU).

Canopy biomass data collected in 1997 and 1998 from a site in Iowa were used to estimate damage function parameters for two distinct coupling points, one applied to reduce daily photosynthesis (Pg) and the other applied to reduce daily potential root water uptake (RWU). Function parameters were estimated by minimizing the log transformation of root mean square error (RMSE) between predicted and measured canopy biomass collected every 2 weeks during the season in Iowa. Biomass data collected in 1997 and 1998 from an independent site in Missouri were used to validate the SCN damage models. The minimum root mean squared errors (RMSE) of canopy and grain biomass were 0.245 and 0.198 $\log_{10}(\text{kg ha}^{-1})$, respectively, for the RWU coupling point, and 0.238 and 0.193 $\log_{10}(\text{kg ha}^{-1})$, respectively, for the Pg coupling point at the independent site in Missouri. The damage functions transferred very well to the independent site. Validation showed that the Pg coupling point represented the variability of both canopy and final yield data slightly better than the RWU coupling point.

Keywords. Crop modeling, Soybeans, Soybean cyst nematodes.

The soybean cyst nematode (SCN) *Heterodera glycines* Ichinohe is a plant-parasitic roundworm that attacks the roots of soybean, *Glycine max* (L.) Merr. SCN is responsible for substantial economic losses in soybean production systems throughout the world. Estimated yield losses attributed to SCN damage for the year 1994 in the ten leading soybean-producing nations totaled 3.0×10^6 Mg (Wrather et al., 1994). The estimated yield losses attributed to SCN in the U.S. for 1994 totaled 2.0×10^6 Mg, greater than the combined yield losses attributed to the

five next most damaging plant diseases (Wrather et al., 1994).

Above-ground symptoms of SCN damage range from reduced yield, stunted growth, reduced number of vegetative nodes, chlorosis, necrosis, and drought susceptibility to no detectable symptoms. Crop damage is not consistently observed in infested fields from one year to another (Niblack et al., 1992). Young (1996) observed yield losses ranging from 14% to 24% in fields that showed no visible symptoms of infestation. Crop damage and yield reduction results from a combination of cellular responses to esophageal gland secretions from the nematode and changes in plant growth processes (Hussey, 1989). Understanding the physiological basis of SCN damage is necessary to predict the crop response to SCN. Growth processes affected by SCN examined in the literature include: inhibiting nodulation and nitrogen fixation (Ko et al., 1991), decreasing stomatal conductance to CO_2 (Koenning and Barker, 1995), and changing translocation of nutrients from the roots to the shoots (Price et al., 1995).

CROPGRO–Soybean (Boote et al., 1998; Hoogenboom et al., 1994) is a FORTRAN program that simulates daily growth and development of leaves, stems (including petioles), roots, shells, and grain. The model requires inputs such as management practices (variety, row spacing, plant population, and fertilizer and irrigation application dates and amounts) and environmental conditions (soil type, daily maximum and minimum temperature, rainfall, and solar

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radiation). Photosynthesis, respiration, development, nitrogen fixation, pest damage, water stress, and nitrogen stress are calculated daily. These processes affect the amount of available photoassimilate (photosynthesis, respiration, water stress, and nitrogen stress), the partitioning of carbon, senescence of tissue, and pest damage.

In this study, CROPGRO was chosen as a platform for modeling SCN damage because of the model's orientation towards simulating crop growth processes, and its ability to simulate crop stress dynamics throughout a season and over multiple seasons. The objective of this study was to develop and evaluate hypotheses for coupling SCN damage to the process-oriented crop growth model CROPGRO-Soybean.

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

Field plots were located in SCN-infested fields at the Woodruff farm near Ames, Iowa, on a Nicollet soil (fine-loamy, mixed, mesic Aquic Hapludolls) and at the Marcus Reinkie farm near Concordia, Missouri, on Higginsville soil (fine-silty, mixed, mesic Aquic Arguidolls). At each location, two experiments were established with adapted, high-yielding SCN-resistant and SCN-susceptible cultivars. At the Iowa location, Kenwood 94 (relative maturity 2.6, susceptible) and Jack (relative maturity 2.9, resistant to SCN races 3 and 4) were planted in 76-cm rows on 22 May 1997. The following year in Iowa, Mohegan II (Merschman Seeds, maturity group 2, susceptible) and Osage III (Merschman Seeds, maturity group 2, resistant to SCN race 3) were planted in 76-cm rows on 13 May 1998. At the Missouri location, Pioneer 9381 (relative maturity 3.8, susceptible) and Pioneer 9362 (relative maturity 3.6, resistant to SCN races 3 and 14) were planted in 76-cm rows on 21 May 1997 and 28 May 1998.

The resistant and susceptible cultivars were planted in alternating four-row transects, with four border rows between transects. Six hundred 4-row by 3-m field plots per location were established before planting, allowing for two experiments containing five treatment levels, with allowance for 15 sampling dates and four replications per sampling date. Five treatments were established for each experiment based on the initial population density (P_i) of SCN eggs within the field plots (table 1). Multiple soil cores to a depth of 15 cm were collected within a single field plot and mixed thoroughly to obtain a representative SCN count. A subsample was removed from the soil and kept under cool storage until processing. SCN population densities were determined from cysts extracted from soil with a semi-automatic elutriator (Byrd et al., 1976) and crushed with a motorized stainless steel pestle (Niblack et al., 1993). Eggs were counted and recorded as number of eggs per 100 cm³ soil.

BIOMASS SAMPLING

Biomass samples were collected on a 14-day interval. Samples covering 1.524 m² land area were collected in Iowa starting between the V1 and V2 stages of development (Fehr and Caviness, 1979). Samples covering 0.762 m² land area were collected in Missouri starting between the V1 and V2 stages of development. During sample collection, a three-plant subsample was arbitrarily removed from the sample and separated into leaf, stem, pod, and seed components (petioles were included in the stem fraction). Samples were dried at 60°C and weighed to determine the total canopy dry weight. Leaf, pod, seed, and stem weight per m² were calculated as the product of the total canopy dry weight and the fraction of the respective plant component in the subsample.

Table 1. Minimum, mean, and maximum SCN initial population (P_i) (eggs per 100 cm³ soil) for the treatments in the Iowa and Missouri field studies.

Treatment ^[a]	Iowa Experiments				Missouri Experiments			
	1997		1998		1997		1998	
	S	R	S	R	S	R	S	R
1	3,900 ^[b]	2,700	500	0	40	160	0	0
	6,647 ^[c]	5,561	1,460	1,113	500	754	43	117
	8,300 ^[d]	6,800	2,200	1,800	864	1,320	112	392
2	8,400	7,100	2,300	1,900	960	1,320	112	240
	9,542	8,478	2,863	2,678	1,580	1,865	139	529
	10,500	10,000	3,600	3,500	2,304	2,400	168	784
3	10,600	10,200	3,600	3,500	2,320	2,440	200	952
	11,586	11,367	4,616	4,513	3,017	3,225	261	1,568
	12,900	12,600	5,200	5,400	3,840	4,240	336	2,240
4	12,900	12,700	5,200	5,500	3,840	4,240	336	2,352
	14,572	14,619	6,306	6,409	4,881	5,144	484	3,562
	16,400	16,200	7,400	7,500	6,840	6,840	616	5,040
5	16,500	16,400	7,500	7,600	7,104	7,008	616	5,120
	18,875	18,542	9,288	9,653	12,604	12,411	1,584	7,627
	26,400	26,600	12,900	15,100	33,712	28,480	5,376	12,656

^[a] The five treatment levels were based on pre-season SCN egg population densities (P_i). S designates the susceptible cultivar experiment, and R designates the resistant cultivar experiment.

^[b] The top number is the minimum P_i in the treatment level.

^[c] The middle number is the mean P_i in the treatment level.

^[d] The bottom number is the maximum P_i in the treatment level.

ESTIMATING SOIL PARAMETERS

Soil properties required to run the crop model include lower limit (LL, $\text{cm}^3 \text{cm}^{-3}$), drained upper limit (DUL, $\text{cm}^3 \text{cm}^{-3}$), saturated water content (SAT, $\text{cm}^3 \text{cm}^{-3}$), saturated hydraulic conductivity (KSAT, cm hr^{-1}) and soil hospitality factor (0 to 1) in each soil layer, as well as maximum rooting depth (cm). Water holding characteristics for each site were estimated based on county soil survey reports for Story County, Iowa (USDA-SCS, 1984), and Lafayette County, Missouri (USDA-SCS, 1975). Values for lower limit and drained upper limit were based on the mean reported soil texture of the Nicollet and the Higginsville soil series, and on field values reported by Ratliff et al. (1983). The soil horizons of the top 15 cm and the bottom 75 to 210 cm of the Nicollet soil series is loam (DUL = 0.250, LL = $0.114 \text{ cm}^3 \text{cm}^{-3}$), and the soil horizons between 30 cm and 75 cm are clay loam (DUL = 0.338, LL = $0.208 \text{ cm}^3 \text{cm}^{-3}$). The soil horizons of the top 30 cm of the Higginsville soil series are silt loam (DUL = 0.290, LL = $0.147 \text{ cm}^3 \text{cm}^{-3}$), and the soil horizons between 30 cm and 210 cm are clay loam (DUL = 0.338, LL = $0.208 \text{ cm}^3 \text{cm}^{-3}$).

Paz et al. (1998) attributed seasonal yield variability of soybeans grown in Iowa to early season perched water tables, leading to shallow root systems and late season drought stress. Following his approach, we adjusted the saturated hydraulic conductivity of the impermeable layer (at 2 m depth) and the effective tile drain spacing (FLDS, at 1 m depth) at the Iowa site to minimize error between predicted and measured canopy weight and yield for the susceptible cultivar.

Maximum rooting depth and root growth is restricted by hardpan soils in Missouri. Because soil drainage is not an issue in Missouri, a specified hard pan depth and a series of soil hospitality factors (RHRF) were used to limit maximum rooting depth and root growth for the Missouri experiments in this study. The soil hospitality factor is a unitless 0-to-1 soil parameter that controls the ability of roots to penetrate and explore a soil layer. The maximum potential rooting depth of the soil was limited by setting the soil hospitality factor close to zero in the C soil horizon (105 cm to 225 cm). A hard pan was placed beneath the plow layer (30 cm) to delay the downward growth of the root. These factors were adjusted to minimize error between predicted and measured canopy weight and yield for the resistant cultivar.

The SCN-susceptible and SNC-resistant cultivars used at each location were assumed to be isogenic, and therefore one set of genetic coefficients was used at each location. The cultivar coefficients distributed with the CROPGRO model (Version 3.1, Release 1996) for late maturity group 3 were used for Pioneer 9381 and Pioneer 9362. The generic cultivar coefficients for maturity group 2 were used for Kenwood 94, Mohegan II, Jack, and Osage III. This process provided a unique set of soil properties for each site that gave good predictions of growth, development, and yield for the SCN-resistant cultivars, where the SCN-susceptible cultivar was used as a control treatment.

MODELING SCN DAMAGE

Crops are in constant competition for water, nutrients, and energy. The approach used in CROPGRO to simulate the interaction between plant competition and environmental stressors is to first calculate the potential rate of resource accumulation, and then calculate the actual rate by multiply-

ing the potential by a series of dimensionless 0-to-1 stress factors. Resource accumulation rates are calculated daily, and state variables are updated following an energy and mass balance. In this study, nematode damage was coupled to photosynthesis and potential root water uptake through a 0-to-1 damage factor. A monomolecular function (eq. 1) was used to model SCN damage as a function of initial population density (P_i , eggs per 100 cm^3 soil):

$$D = (1 - e^{-\mu P_i}) D_{\max} \quad (1)$$

where

D = SCN damage factor (0 to 1)

μ = slope constant

D_{\max} = constant defining the maximum damage threshold.

Wilting may be encountered in areas of the field with known SCN problems. A number of possible connections between soil water potential and SCN have been suggested. One possibility is that SCN limits photosynthesis by decreasing the conductance of stomata to CO_2 (Wallace, 1987). Poskuta et al. (1986) tested this hypothesis in a growth chamber that measured CO_2 exchange of the shoots and roots. Seedlings were grown in SCN-infested soil and after 28 days were transferred to a hydroponic culture in a test chamber. After an acclimation period of two days, CO_2 exchange was measured. The gross photosynthesis of infected susceptible plants was 30% lower than that of uninfected susceptible plants. The gross photosynthesis of infected resistant plants was 10% lower than that of uninfected resistant plants. Root respiration was 50% higher in the infected susceptible treatment and 35% higher in the infected resistant treatment than in the uninfected susceptible and resistant control plants. In a field experiment, Koening and Barker (1995) measured photosynthetic rates of susceptible varieties over different soil type treatments and water stress treatments. Photosynthetic rate was better correlated to the initial SCN population density (P_i) in coarse-textured soils than fine-textured soils.

Because of the dramatic effect that SCN has on stomatal conductance and photosynthesis, the hypothesis that SCN directly inhibit photosynthesis and the hypothesis that SCN indirectly inhibit photosynthesis by disrupting root water uptake were tested to determine the best method to couple SCN damage to the CROPGRO model.

PHOTOSYNTHESIS

Photosynthesis is dependent on light interception, leaf age, temperature, CO_2 concentration, water stress, and leaf chlorophyll concentration (Boote and Pickering, 1994). CROPGRO calculates daily potential photosynthesis as a function of photosynthetically active radiation (PAR , MJ m^{-2}) by:

$$PTS_{\max} = PHT_{\max} \left[1.0 - e^{-\left(\frac{PAR}{PAR_{\max}} \right)} \right] \quad (2)$$

where

PTS_{\max} = daily potential photosynthetic rate ($\text{g CH}_2\text{O m}^{-2} \text{d}^{-1}$)

PHT_{\max} = constant defining the maximum possible photosynthetic rate

PAR_{max} = light saturation constant.

Gross photosynthesis (P_g , g CH_2O $m^{-2} d^{-1}$) is a function of the photosynthetic potential:

$$P_g = PTS_{max} \cdot (1-D) \cdot SWFAC \cdot \prod_{i=1}^N RFAC_i \quad (3)$$

where

- D = SCN damage factor defined in equation 1
- $SWFAC$ = photosynthetic water stress factor (0 to 1)
- $RFAC_i$ = series of 0-to-1 reduction factors (e.g., leaf N factor, canopy factor, leaf age factor, atmospheric CO_2 concentration factor, etc.).

POTENTIAL ROOT WATER UPTAKE

In the crop model, daily potential root water uptake is summed across each soil layer (L) in the soil profile by:

$$RWU = (1-D) \cdot \sum_{L=1}^N \left[(SW_L - LL_L) \cdot DLAYR_L \cdot RUCO_L \cdot \left(1 - e^{-8.0 \cdot RLV_L} \right) \cdot (1 - RWUF_L) \right] \quad (4)$$

where

- RWU = potential daily root water uptake ($cm d^{-1}$)
- D = SCN damage factor defined in equation 1 (0 to 1)
- N = number of layers in the soil profile
- SW = soil water content ($cm^3 cm^{-3}$)
- LL = lower limit or wilting point of the soil ($cm^3 cm^{-3}$)
- $DLAYR$ = depth of the soil layer (cm)
- $RUCO$ = root water uptake coefficient (0 to 1)
- RLV = root length density ($cm cm^{-3}$)
- $RWUF$ = water logging factor (0 to 1).

Potential root water uptake affects photosynthesis through a water stress factor computed by:

$$SWFAC = \frac{RWU}{EP} \quad (5)$$

where

- $SWFAC$ = photosynthetic water stress factor defined in equation 3
- RWU = potential root water uptake ($cm day^{-1}$)
- EP = evapotranspiration ($cm day^{-1}$).

A reduction of potential root water uptake will lead to decreased photosynthesis when water demanded by evapotranspiration is greater than water supplied by root water uptake (eqs. 3 and 5). If the potential root water uptake is greater than the demand, then actual root water uptake is calculated so that supply equals demand. On days when this occurs, SCN does not reduce photosynthesis.

CALIBRATION AND TESTING SCN DAMAGE FUNCTION PARAMETERS

Canopy biomass data collected in 1997 and 1998 at Iowa for the susceptible cultivar experiments were used to estimate the SCN damage function parameters μ and D_{max} (eq. 1). Nonlinear least-squares analysis was performed using the downhill simplex method (Nelder and Mead, 1965) available in the ISML FORTRAN Numeric Libraries Version 3.0

(Visual Numerics, Inc). The objective function for the optimization was:

$$\text{Min: SSE} = \sum_{i=1}^n (\log_{10}(Y) - \log_{10}(\hat{Y}))^2 \quad (6)$$

where SSE is \log_{10} of the sum of squared errors between Y (observed canopy biomass, $kg ha^{-1}$) and \hat{Y} (predicted canopy biomass, $kg ha^{-1}$). The squared error was calculated using the observed and predicted canopy biomasses for each of the 338 plots sampled in 1997 and 1998 at Iowa. Because the variance of the biomass data increased with the magnitude of the data, a log transformation was used to calculate both the SSE and the root mean squared error (RMSE).

The SCN damage parameters calibrated for the 1997 and 1998 Iowa sites were tested for the SCN-susceptible cultivars at the 1997 and 1998 Missouri sites to determine if the SCN relationship could be transferred to a different location. The model was run for the five measured SCN levels. The predicted and measured yields were compared using SSE and RMSE values.

RESULTS AND DISCUSSION

MODEL PREDICTIONS WITH ESTIMATED SOIL PARAMETERS

Soil parameters were estimated using the SCN-resistant cultivar experiments as a control. In Iowa, a perched water table was created to limit maximum rooting depth. In 1997, downward root progression was inhibited by the water table beginning 41 days after planting (DAP), at 105 cm below the soil surface, resulting in a maximum rooting depth of 143 cm. The 1998 season received higher than normal rainfall amounts (536 mm compared to 382 mm in 1997 during the growing season, fig. 1), resulting in a simulated water table at 75 cm below the soil surface beginning 32 DAP and remaining for a 6-day period. The maximum rooting depth in 1998 was 141 cm. In Missouri, a hard pan was created to impede the rate of root depth, root distribution below the hardpan, and ultimately limit maximum rooting depth. The hard pan required approximately 8 days for roots to penetrate in 1997 and 11 days in 1998. Roots reached a maximum depth of 182 cm in 1997 and 194 cm in 1998; however, the simulated root length volume below the hard pan was reduced due to the hardpan effect.

The simulated root depth and distribution coupled with rainfall and other soil properties led to simulated differences in biomass between the Iowa and Illinois sites. Figure 2 shows simulated and measured canopy and grain growth for the SCN-resistant cultivar using the calibrated soil parameters. The 1997 season was drier than the 1998 season at both locations (fig. 1). This led to differences in maximum measured canopy and final grain weight at the Missouri site (figs. 2c and d). The measured canopy biomass was similar in both years at the Iowa site (figs. 2a and b). However, final grain yield was higher in 1998 (the wet year) in Iowa. At the Missouri site, the model simulated the measured canopy and grain biomass very well in both 1997 and 1998, indicating that the model adequately represented the plant-soil-water relationships for this soil type.

The model simulated the measured grain biomass very well in both years at the Iowa site. However, the canopy biomass was systematically overpredicted in 1998 (fig. 2b).

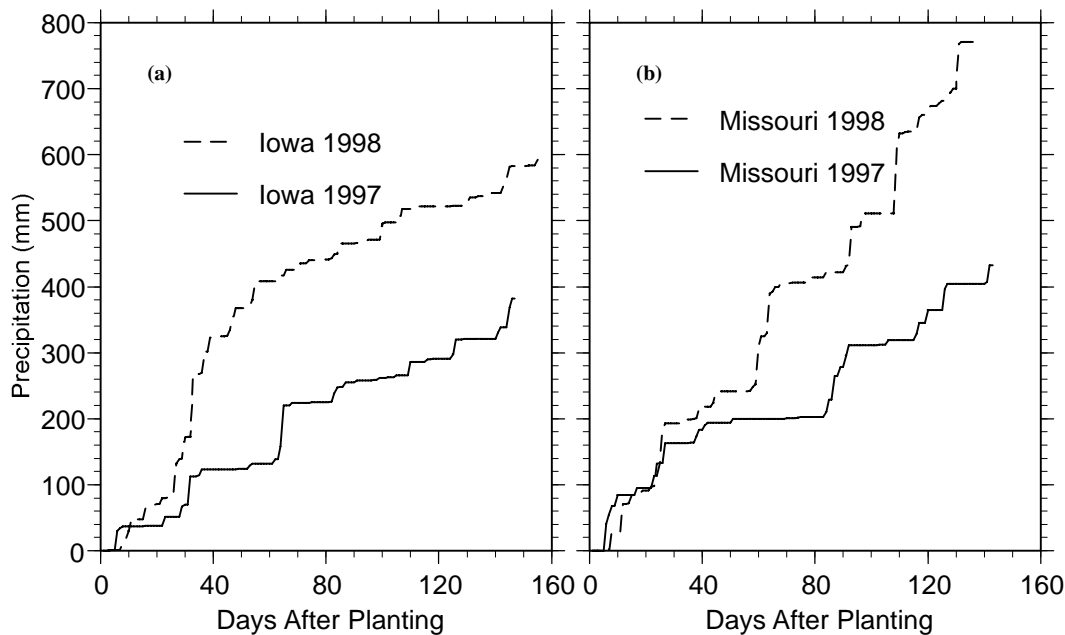


Figure 1. Cumulative precipitation recorded over the growing season in (a) Iowa and (b) Missouri.

The total RMSE of canopy biomass for Iowa in 1998 was greater than the total RMSE of canopy biomass in 1997 (table 2). Initial attempts to adjust initial soil water content and effective tile drain spacing decreased the prediction error for the canopy biomass in 1998 but increased the error for grain biomass. This leads us to believe that other processes contributed to this problem. Upon closer examination, the systematic error resulted primarily because the model predicted more rapid early season vegetative growth than what was measured in the field. This led to faster simulated growth rates during the mid-vegetative stages as well.

Several factors likely contributed to this problem. First, the 1998 season had tremendous rainfall from emergence through the end of June, coupled with cool temperatures. This caused excessive surface water ponding and stunting due to water logging and cool soil temperatures during early vegetative growth. These factors contributed to slow plant growth rates during the early part of the season (prior to the end of June). The crop model does not account for surface water ponding, and has a very limited (and untested) capability to represent waterlogging effects. Furthermore, Andales et al. (2000) showed that the crop model tended to overpredict early season growth and development under cool wet conditions because it inadequately computes the effect of soil water content on shallow soil temperature, which affects the rate of emergence. Inadequate representation of these factors likely contributed to the overprediction of early season canopy biomass and subsequent systematic overprediction of canopy biomass later in the season for the 1998 Iowa experiment.

CALIBRATING THE SCN DAMAGE FUNCTIONS

Figures 3 and 4 show the trends in measured canopy and grain weight for the four SCN levels (P_i) in the 1997 and 1998 Iowa SCN-susceptible cultivar treatments. In 1997, the maximum observed canopy biomass decreased with increasing SCN populations (figs. 3a–3d). However, while the final grain yield was not much affected by differences in SCN

populations, ranging from 900 to 1,100 kg ha⁻¹, the grain yields were approximately 40% of the yields measured in the SCN-resistant experiments for the same year (approximately 2,500 kg ha⁻¹, fig. 2). This indicates that SCN caused a yield loss of nearly 60%. This is consistent with field observations that most of the yield loss due to SCN occurs when pre-season populations are between 500 and 2,000 eggs 100 cm⁻³ soil.

Since the lowest SCN population in 1997 was 6,647 eggs 100 cm⁻³ soil in the SCN-susceptible treatments, these relationships were consistent with other field observations. In 1998, the maximum canopy biomass for the two lowest SCN populations was approximately 7,000 kg ha⁻¹ (figs. 4a and 4b), while the two highest populations had maximum canopy biomass of approximately 5,000 kg ha⁻¹ (figs. 4c and 4d). Thus, high levels of SCN appeared to impede canopy development. The final grain biomass was in the range of 2,900 to 3,100 kg ha⁻¹ across all SCN population levels, compared to yields of approximately 3,100 kg ha⁻¹ in for the SCN-resistant cultivar (fig. 2). It appears that in 1998, SCN inhibited canopy growth in the SCN-susceptible cultivar but had little impact on final yield compared to the SCN-resistant cultivar.

Canopy biomass data collected in 1997 and 1998 for the Iowa SCN-susceptible cultivar treatments were used to estimate parameters μ and D_{max} for the SCN damage function (eq. 1). The model was run for each year and SCN treatment combination using the soil parameters calibrated for the SCN-resistant cultivar at the Iowa site. An optimization technique was used to estimate the parameter values that minimized the SSE between predicted and measured canopy biomass during the season. Because the variance of the biomass data increased with the magnitude of the data, a log transformation (\log_{10}) was used to calculate both the SSE and the RMSE.

This calibration was performed separately for each SCN damage hypothesis. The first hypothesis was that SCN directly reduce daily photosynthesis rate (P_g hypothesis). For this hypothesis, the optimum values for the damage threshold

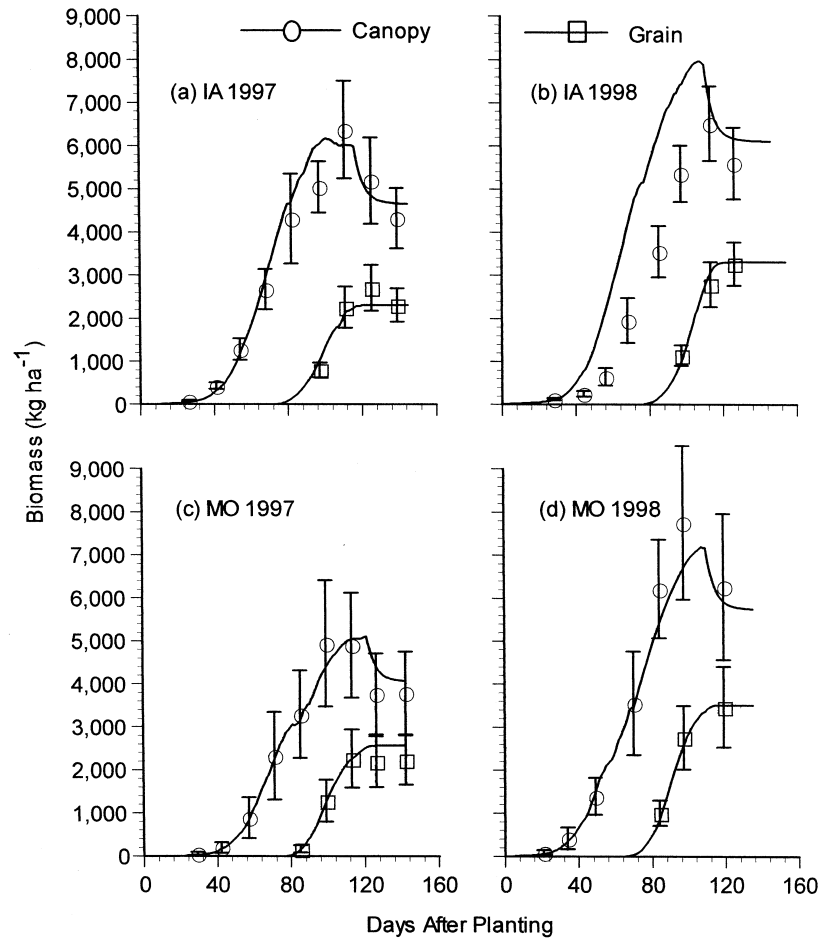


Figure 2. Simulated and observed canopy and grain biomass for the calibrated soil properties for (a and b) Iowa and (c and d) Missouri using the SCN-resistant cultivar. Error bars represent one standard deviation, and points represent the mean ($n = 20$) of measured data.

Table 2. Results of simulated and observed biomass for the Iowa (IA) and Missouri (MO) SCN-resistant cultivar experiments. Soil parameters were calibrated to fit observed canopy and grain biomass at each site. SSE units are $\log_{10}(\text{kg ha}^{-1})$ and RMSE units are $\log_{10}(\text{kg}^2 \text{ha}^{-2})$ due to log transformation of the data.

Experiment	Canopy Biomass			Grain Biomass		
	N	SSE	RMSE	N	SSE	RMSE
IA 1997	180	2.713	0.123	80	0.897	0.107
IA 1998	160	7.258	0.214	60	0.543	0.097
Total	340	9.971	0.172	140	1.440	0.102
MO 1997	177	11.272	0.254	97	4.283	0.212
MO 1998	140	5.129	0.193	58	0.893	0.126
Total	317	16.401	0.228	155	5.176	0.184

parameter (D_{\max}) and slope constant (μ) were 0.289 and 0.000296, respectively (eq. 1). The second hypothesis was that SCN impede root water uptake, which causes water stress and reduces photosynthetic rates, especially during dry seasons (*RWU* hypothesis). The estimated damage threshold (D_{\max}) for this hypothesis was 0.646, and the slope constant (μ) was 0.000737.

The *RWU* hypothesis gave lower overall SSE (13.38 vs. 15.25 $\log_{10}[\text{kg}^2 \text{ha}^{-2}]$) and RMSE (0.2 vs. 0.213 $\log_{10}[\text{kg ha}^{-1}]$) values for canopy biomass compared to the *Pg*

hypothesis over both seasons (table 3). However, the *Pg* hypothesis gave lower overall SSE (9.05 vs. 10.12 $\log_{10}[\text{kg}^2 \text{ha}^{-2}]$) and RMSE (0.257 vs. 0.272 $\log_{10}[\text{kg ha}^{-1}]$) values for grain biomass compared to the *RWU* hypothesis over both seasons (table 3).

Figures 3 and 4 show the trends in predicted and measured canopy and grain weight for the four SCN levels (P_i) in the 1997 and 1998 Iowa SCN-susceptible cultivar treatments. The model tended to underpredict canopy biomass in the lowest two SCN populations in 1997 (figs. 3a and 3b). The *Pg* hypothesis appeared to fit the observed canopy biomass levels better than the *RWU* hypothesis. Both models gave similar predictions of grain biomass across all SCN levels in 1997, with a tendency to overpredict final grain biomass. In 1998, both models were able to simulate the differences in maximum canopy weight between the first two (figs. 4a and 4b) and second two (figs. 4c and 4d) SCN levels. Both models underpredicted the final grain weight across all SCN levels. The model typically gave simulated values that were within one standard deviation of the measured mean for both canopy and grain biomass. Because of the dramatic differences in rainfall and subsequent water stress patterns between the two years, the problems in predicting yield may be related to additional complex interactions between SCN and water stress that these simple models do not account for.

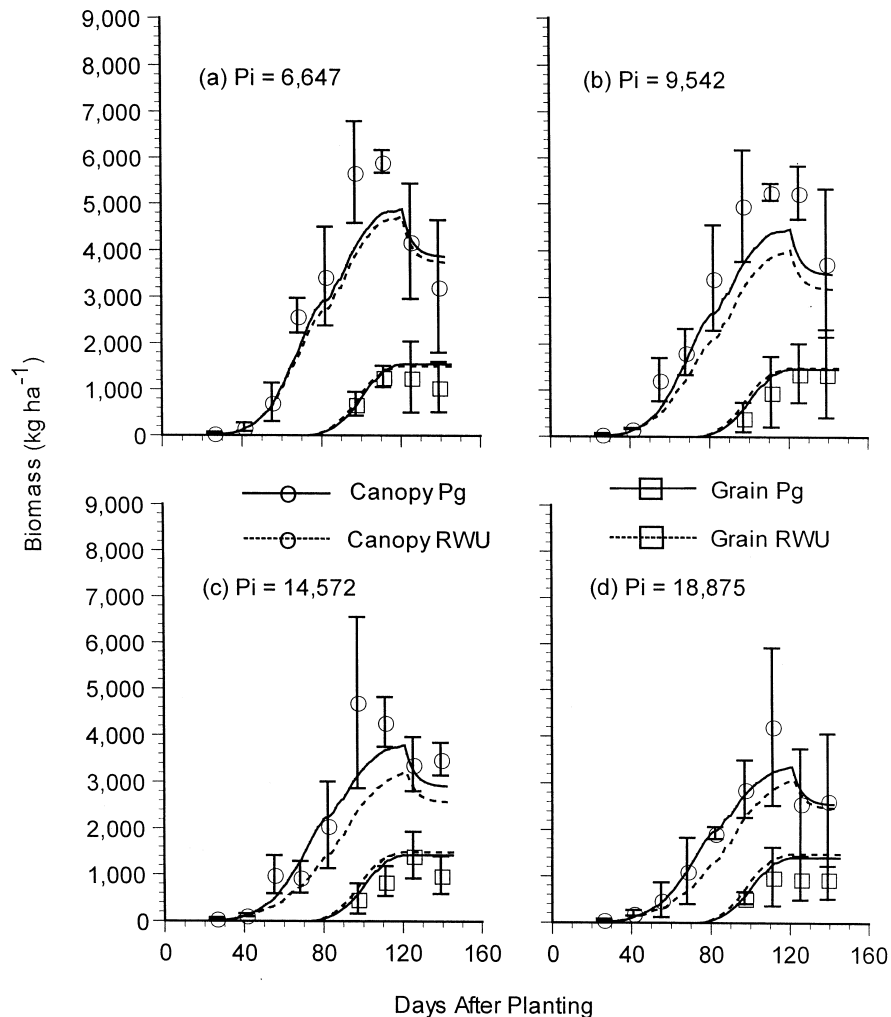


Figure 3. Simulated SCN damage for (a) treatment 1, (b) treatment 2, (c) treatment 4, and (d) treatment 5 of the 1997 Iowa SCN-susceptible experiments. Parameters for the photosynthesis (P_g) and potential root water uptake (RWU) SCN damage models were estimated using the 1997 and 1998 Iowa SCN-susceptible experiments. Error bars represent one standard deviation, and points represent the mean ($n = 4$) of measured data.

TESTING THE SCN DAMAGE FUNCTIONS

The 1997 and 1998 Missouri SCN-susceptible treatments were used as an independent test of the damage functions. The parameters estimated for the 1997 and 1998 Iowa site were used to predict yield at four SCN populations in Missouri. Figure 5 shows simulated and measured final grain biomass for each hypothesis (RWU and P_g) for the five SCN levels each year. The model gave reasonable predictions of the trend for decreasing yield as a function of increasing SCN population. The model was also able to simulate the large differences in yield between the two years. Both the P_g and RWU models gave similar results for both years. The RWU hypothesis resulted in a larger tolerance to P_i before yield was significantly reduced than did the P_g hypothesis. Once this threshold was surpassed, the severity of expected yield reduction in 1998 was greater for RWU than for P_g . Yield response to SCN in 1997 was similar for both hypotheses. The RMSE of canopy and grain biomass over both years was 0.245 and 0.198 $\log_{10}(\text{kg ha}^{-1})$, respectively, for the RWU coupling point and 0.238 and 0.193 $\log_{10}(\text{kg ha}^{-1})$, respectively, for the P_g coupling point (table 4). Thus, both models performed in a similar manner.

CONCLUSIONS

CROPGRO was used as a platform for predicting SCN damage based on the initial population density of eggs in the soil. A monomolecular function was selected as an SCN damage function. Two hypotheses to represent SCN damage were tested. The first hypothesis was that SCN reduce daily photosynthesis rate, thereby reducing crop growth and yield. The second hypothesis was that SCN reduce root water uptake, causing water stress and reduced photosynthesis and crop growth rate. Soil properties required by the crop model were calibrated for sites in Iowa and Missouri using seasonal measurements of canopy and grain biomass for 1997 and 1998. Both SCN damage hypotheses were calibrated for the Iowa site using these soil properties and seasonal canopy and grain biomass data collected under four different SCN population levels for an SCN-susceptible cultivar in 1997 and 1998. The model gave reasonable predictions of canopy weight but tended to underpredict yield in the wetter year and overpredict yield in the drier year. The calibrated SCN damage function was then used to predict the yield response of an SCN-resistant variety for five SCN populations at the Missouri site in 1997 and 1998. Both hypotheses gave good simulations of final grain weight across all SCN populations.

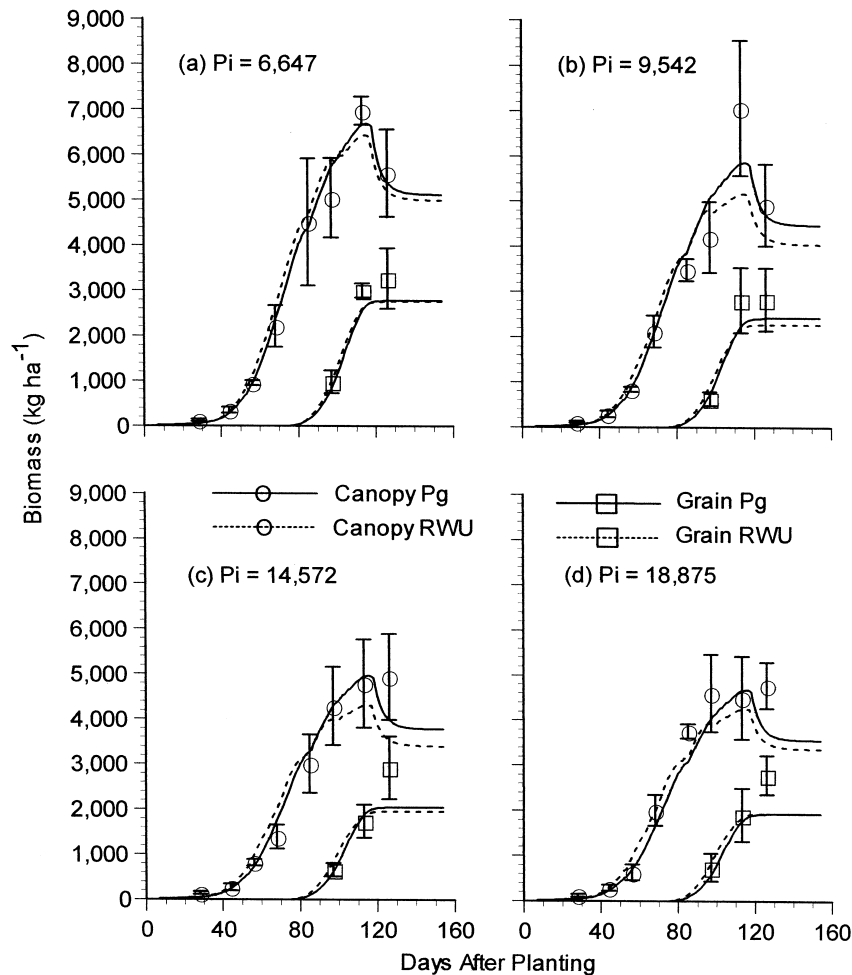


Figure 4. Simulated and measured SCN damage for (a) treatment 1, (b) treatment 2, (c) treatment 3, and (d) treatment 5 of the 1998 Iowa SCN-susceptible experiment. Parameters for the photosynthesis (P_g) and potential root water uptake (RWU) SCN damage models were estimated using the 1997 and 1998 Iowa SCN-susceptible experiments. Error bars represent one standard deviation, and points represent the mean ($n = 4$) of measured data.

Table 3. Results of simulated and observed biomass for the 1997 and 1998 Iowa SCN-susceptible cultivar experiments. SCN damage was coupled to potential root water uptake (RWU) and photosynthesis (P_g). SSE units are $\log_{10}(\text{kg ha}^{-1})$ and RMSE units are $\log_{10}(\text{kg}^2 \text{ha}^{-2})$ due to log transformation of the data.

	Canopy Biomass			Grain Biomass		
	N	SSE	RMSE	N	SSE	RMSE
<i>RWU</i>						
IA 1997	179	7.90	0.211	79	8.91	0.340
IA 1998	159	5.48	0.187	60	1.21	0.145
Total	338	13.38	0.200	139	10.12	0.272
<i>P_g</i>						
IA 1997	179	9.89	0.236	79	8.00	0.322
IA 1998	159	5.36	0.185	60	1.05	0.135
Total	338	15.25	0.213	139	9.05	0.257

Based on the results of this work, it is difficult to determine which approach is best. However, it is clear that the SCN models proposed in this research provide a simple way to approximate the effect of SCN in the CROPGRO model. Future work should focus on developing more mechanistic methods to simulate within-season SCN population dynamics and subsequent effect on soybean growth.

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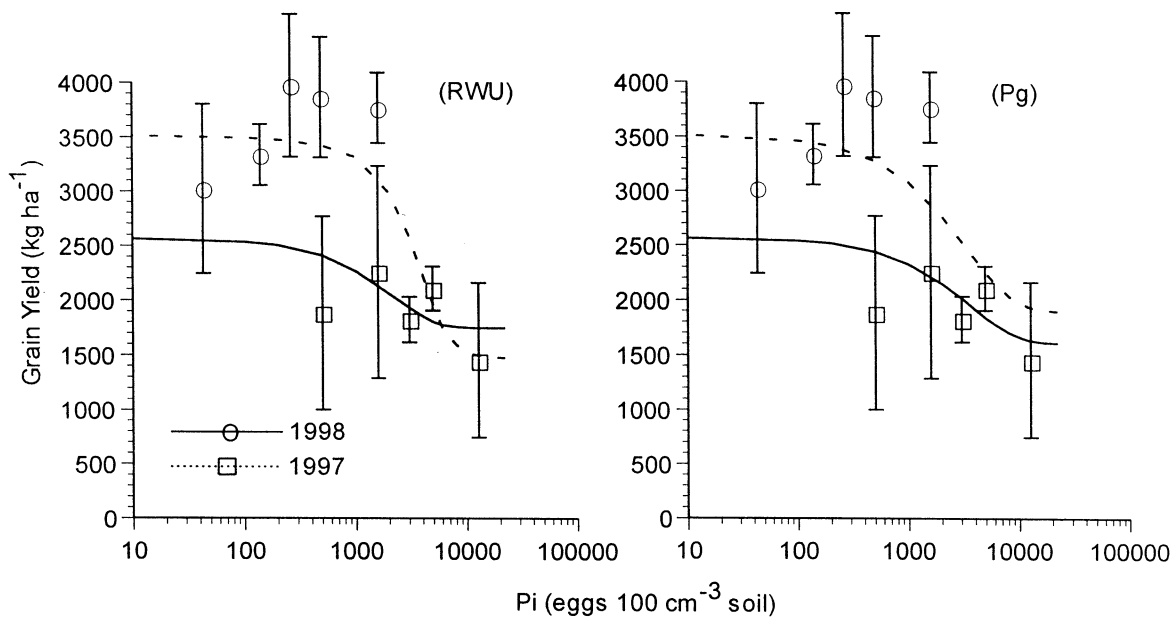


Figure 5. Simulated and measured final grain biomass for the 1997 and 1998 Missouri SCN-susceptible experiments. SCN damage was applied using both the photosynthesis (P_g) and potential root water uptake (RWU) SCN damage models. Error bars represent one standard deviation, and points represent the mean ($n = 4$) of measured data.

Table 4. Results of the simulated and measured biomass for the 1997 and 1998 Missouri SCN-susceptible cultivar experiment. Damage coefficients from Iowa were used at this independent site. SCN damage was coupled to potential root water uptake (RWU) and photosynthesis (P_g). SCN damage function coefficients derived from Iowa were used for this site. SSE units are $\log_{10}(\text{kg ha}^{-1})$ and RMSE units are $\log_{10}(\text{kg}^2 \text{ha}^{-2})$ due to log transformation of the data.

	Canopy Biomass			Grain Biomass		
	N	SSE	RMSE	N	SSE	RMSE
<i>RWU</i>						
MO 1997	176	12.41	0.267	97	4.79	0.224
MO 1998	140	6.50	0.217	60	1.29	0.149
Total	316	18.91	0.245	157	6.08	0.198
<i>Pg</i>						
MO 1997	176	11.19	0.254	97	4.40	0.215
MO 1998	140	6.55	0.218	60	1.36	0.153
Total	316	17.74	0.238	157	5.77	0.193

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