

Modeling nitrogen accumulation and use by soybean[☆]

T.R. Sinclair^{a,*}, J.R. Farias^b, N. Neumaier^b, A.L. Nepomuceno^b

^aUSDA-ARS, Agronomy Physiology and Genetics Laboratory, University of Florida,
P.O. Box 110965, Gainesville, FL 32611-0965, USA

^bEmbrapa Soja, Cx. Postal 231-CEP, 86001-970 Londrina, PR, Brazil

Received 4 September 2002; received in revised form 4 November 2002; accepted 4 November 2002

Abstract

Simulation of soybean growth and yield requires an accurate representation of nitrogen accumulation and distribution in the developing crop. Approaches to simulate nitrogen accumulation by soybean have been complicated by the need to account for both soil nitrate uptake and symbiotic nitrogen fixation. Past approaches to simulating soybean have generally been empirical requiring ‘calibration’ for each new environment. Recently, Jamieson and Semonov [Field Crops Res. 68 (2000) 21] proposed a relatively simple approach for simulating nitrogen accumulation by wheat based on the nitrogen demand imposed separately by the development of leaf area and the growth of stems. This paper assesses this approach for soybean. This approach was further simplified by assuming that nitrogen availability to the plant was limited only by soil moisture conditions and a maximum uptake rate and that it was not necessary to distinguish between nitrate uptake and symbiotic nitrogen fixation. The simplified model generally resulted in simulations that corresponded to experimental observations on nitrogen and mass accumulation through the growing season, and on yield over a number of years. Sensitivity analysis of the model indicated that storage of nitrogen in the stem might be a key trait in increasing soybean yield potential.

© 2002 Elsevier Science B.V. All rights reserved.

Keywords: Nitrogen accumulation; Soybean; N₂ fixation; Crop modelling

1. Introduction

A relatively simple model simulating the development and growth of soybean [*Glycine max* (L.) Merr.] has been available for several years (Sinclair, 1986). This model grows leaves as a function of temperature, increases crop mass as a function of intercepted solar radiation, and grows seed mass based on a linear

increase in harvest index. The model also calculates soil water balance on a daily basis and, when the soil becomes sufficiently dry there is inhibition of leaf development, mass accumulation and symbiotic N₂ fixation. Symbiotic N₂ fixation activity in soybean is especially sensitive to soil drying (Serraj et al., 1999), which can result in a substantial influence on simulation results because insufficient N levels cause inhibited leaf area development and decreased persistence, decreased mass accumulation and early maturity.

While the earlier model has been used effectively to analyze soybean yield (Muchow and Sinclair, 1986; Spaeth et al., 1987; Sinclair et al., 1987, 1992), the N accumulation functions were empirical, and the model had to be ‘calibrated’ for each new situation. The

[☆]Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the US Department of Agriculture and does not imply approval or the exclusion of other products that may also be suitable.

* Corresponding author. Tel.: +1-352-392-6180;

fax: +1-352-392-6139.

E-mail address: trsinc1@mail.ifas.ufl.edu (T.R. Sinclair).

amount of soil N available to the crop was an input to the model and had to be derived by model calibration for each particular soil. The daily rate of symbiotic N_2 fixation was calculated as a linear function of vegetative mass based on experimental observations. The difficulty is that the coefficient defining this relationship is empirical and is sensitive to environment, and possibly cultivar (Muchow and Sinclair, 1986). Quantification of these two variables introduced ambiguity into the calculation of N accumulation by the soybean crop and made the use of the model in other environments difficult and uncertain.

Complex models of soybean growth have calculated N uptake and use based on a series of assumed controls and interactions. For example, the simulation of soybean by CROPGRO (Boote et al., 1998) calculates plant N accumulation based on root characteristics, nodule mass and specific activity, and a N demand calculated from varying limits for tissue N concentration. Mobilization of N occurs both during vegetative growth and seed growth by an additional set of assumed relationships. The empiricism of the two coefficients in the simple model of Sinclair (1986) is replaced in the complex model with a large set of coefficients, which are generally empirical and require model 'calibration'.

An alternative to these models was an innovative, but simple, approach to calculating N accumulation by wheat suggested by Jamieson and Semonov (2000). In their approach, daily vegetative growth of leaves and stems was calculated and this growth was simply balanced with sufficient N to obtain specified N concentrations of leaves, roots, and eventually seeds. It was assumed that under conditions not limited by soil N availability, daily crop N uptake rate was sufficient for wheat leaves to maintain 1.5 g N m^{-2} (approximately 35 mg N g^{-1}) and stems at 15 mg N g^{-1} . If the soil was unable to provide sufficient N, stem N concentration was allowed to decrease to a minimum of 5 mg N g^{-1} . Once the stem N concentration had decreased to 5 mg N g^{-1} , then insufficient soil N resulted in inhibited leaf area development, and ultimately, the transfer of leaf N to the stem. Consequently, one of the major impacts of inadequate soil N was an inhibition of leaf area development.

An attractive feature of the approach of Jamieson and Semonov (2000) is that it is consistent with observations showing N concentration of the entire

shoot of a wheat crop to decrease as a well-defined function of total shoot mass (Justes et al., 1997). This dilution curve is reproduced by the Jamieson and Semonov (2000) approach because the shoot N concentration is initially high reflecting the fact that the shoot is composed virtually only of leaves, and then the shoot concentration decreases with the addition of stems at a low N concentration. Similar dilution curves have been identified for a wide range of crops, including soybean (Harper, 1971; Ney et al., 1997).

During grain fill of wheat, the approach of Jamieson and Semonov (2000) also allows the possibility of limited soil N uptake. The amount of N released from the leaves and stems for transfer to the grain was calculated on a daily basis, and if this was insufficient to meet the needs of the developing grains then soil N uptake was allowed when N was available in the soil. Consequently, a soil that provided N during grain fill resulted in an increased N for the grain.

The input variables needed to define N accumulation using the approach of Jamieson and Semonov (2000) are limited to a few relatively conservative parameters: leaf and stem N concentration during growth and at senescence, and the target grain N concentration used to trigger additional plant N accumulation. These parameters can be readily measured on tissue samples and require no model calibration.

The simplicity of the Jamieson and Semonov (2000) approach led us to consider the application of these concepts to modeling soybean N accumulation. Adaptation of this approach, however, requires consideration of N_2 fixation as a possible source of N. The fact that soybean has N_2 fixation as a ready source of N to compensate for inadequate soil N may minimize or eliminate the need to simulate the soil N budget. The objective of this investigation was to apply the approach presented by Jamieson and Semonov (2000) to soybean and test the simulation results of N and growth obtained in experiments at Londrina, Brazil. The modified model is intended to evaluate the potential influence of key plant and environmental variables on N accumulation by soybean and to examine the potential impact on yield. A model that includes a readily implemented N component may ultimately prove useful to simulate soybean growth and yield across a range of environments.

2. N accumulation model

2.1. Vegetative development

The Jamieson and Semonov (2000) approach to calculating daily N accumulation by wheat was based on nitrogen requirements to develop new leaf area and to grow new stem mass. Their concept can be applied directly to soybean. During vegetative development, soybean leaves commonly have leaf N contents of approximately 2.5 g N m^{-2} (Hanway and Weber, 1971; Lugg and Sinclair, 1981), and this value was assumed to be constant in the calculation of leaf N requirements. Soybean stem N concentration during vegetative growth has a maximum of approximately 20 mg N g^{-1} (Hanway and Weber, 1971; Hanway et al., 1984). This value was assumed to be the target stem N concentration when N is not limiting. Therefore, daily demand for N accumulation was calculated from the leaf area increase, which was calculated mainly as a function of temperature, and stem increase calculated from daily carbon accumulation.

Unlike the case for wheat where N accumulation was limited by N availability in the soil, soybean has the ability to obtain N both from the soil and from symbiotic N_2 fixation. In the model, the simplest assumption was that N demand could be met by one or both of these N sources so that it was not necessary to track the soil N budget. That is, soil N is preferentially recovered by soybean, but N_2 fixation is initiated once the soil N reaches low levels in order to meet plant N requirements (Sinclair, 2003). Since N accumulation rates are not unbounded, a maximum rate was imposed in the model. In an experiment using a field hydroponic gravel culture and various levels of N supply, Harper (1971) found that the maximum rate of N accumulation by soybean plants was about 0.6 g m^{-2} per day. This value was used in the model as the maximum N accumulation rate on the few occasions when the demand for exceedingly high rates of N were calculated.

In addition, N accumulation was made sensitive to soil water deficit. Nitrogen fixation in soybean has been found to be highly sensitive to soil drying and decreased rates are initiated earlier in the drying cycle than virtually all other physiological processes (Serraj et al., 1999). This sensitivity to soil drying was incorporated in the model of Sinclair (1986) and

retained as a constraining factor on N accumulation. An additional response to soil water was incorporated into the current model by setting N accumulation rate equal to zero whenever the soil was water saturated. Consequently, the maximum limit on N accumulation rate and the sensitivity to soil moisture meant that N accumulation could be calculated in the model to be less than the amount required to support fully the N requirements for new leaf area development and new stem growth.

At times when N accumulation rate does not fully meet demand, adjustments are required in the N distribution within the crop. As suggested by Jamieson and Semonov (2000), the first response to inadequate N supply during vegetative development is simulated as a decrease in stem N concentration. The decrease in stem N concentration during vegetative growth is allowed until the stem reaches 8 mg N g^{-1} (Hanway and Weber, 1971; Hanway et al., 1984). Once this minimum stem N concentration is reached, 8 mg N g^{-1} is maintained in additional stem growth by inhibiting new leaf area development, and hence, lessening the overall plant N requirements. In the more extreme cases where setting new leaf area development to zero still did not provide sufficient N for stem growth, leaves were senesced as sources of translocated N. The N content of the senesced leaves was assumed to be 0.8 g N m^{-2} (Hanway and Weber, 1971), and therefore, the recovery of N from the senesced leaves was 1.7 g N m^{-2} ($2.5 - 0.8$).

2.2. Reproductive development

During seed fill, the requirements for N by the seed alters the entire N balance of the plant. The highest priority for N in the crop becomes the seeds as they begin to grow. The mass increase in the seeds in the model is calculated based on a linear increase of 0.011 g g^{-1} per day in harvest index (Spaeth and Sinclair, 1985; Bindi et al., 1999), and the seeds are assumed to have a constant N concentration of 65 mg N g^{-1} ($406 \text{ mg protein g}^{-1}$). Therefore, total daily N demand by the seeds is calculated by multiplying the seed N concentration by seed growth.

The first option in the model to provide N for seeds is the accumulation of additional N by the crop. It is assumed, however, that this option could be exercised only if daily accumulation of photosynthate was in excess of the amount required to satisfy the carbon

requirements for seed mass growth. That is, additional N accumulation during seed fill was assumed to depend on availability of excess current photosynthate, which generally existed only during early phases of seed growth when seed growth rates are relatively low and photosynthetic rates are high. In cases where photosynthate is available for additional N accumulation, the daily amount of N accumulation rate is calculated similar to Sinclair (1986) based on the observation that N_2 fixation rate is closely correlated with vegetative mass (Denison et al., 1985). Basically, it is assumed that the capacity for N accumulation during the final stage of vegetative growth carries over to the early stages of seed growth if sufficient photosynthate is available. The N_2 fixation coefficient to do this calculation in the current model is determined within the model by calculating the ratio of N accumulation rate and vegetative mass for the days immediately preceding seed growth. This calculated coefficient multiplied by the vegetative mass during seed fill is used to calculate potential accumulation of N during seed fill. If the accumulation of N during seed fill is calculated to be in excess of that required by the growing seeds, the excess N is partitioned to the stems.

When plant accumulation of additional N is zero or inadequate to meet the full requirements of the growing seeds, N is translocated from the leaves and stems to the seeds. The fraction of the N translocated from leaves and stems is based on the relative amount of translocatable N in each tissue. The minimum N in senesced tissue is the same as above, that is, 0.8 g N m^{-2} for leaves and 8 mg N g^{-1} for stems. The translocation of N from the leaves results in loss of leaf area, which consequently, decreases radiation interception and daily mass accumulation. This logic results in the self-destruction of the crop as proposed by Sinclair and deWit (1976). When leaf area index (LAI) decreases to a value of 0.1, the crop is assumed to have reached maturity and the model is stopped (Sinclair, 1986).

3. Methods and materials

3.1. Simulation studies

Weather data and phenology data were obtained from experiments done with soybean at Londrina, Brazil (described below). The first evaluation of the

model was done with experimental data from a tillage experiment performed in 1998/1999 (Zotarelli, 2000). This experiment included observations on changes through the season in crop mass, and N accumulation, as well as seed yield. Simulation results were compared against experimental observations through the season to assess the capability of the model in simulating crop performance and to determine if adjustments in input variables or concepts were needed in the model.

Data for yield under both rainfed and well-watered conditions for nine growing seasons at Londrina, Brazil, were also available for testing. Each of these seasons was simulated and an overall comparison of simulated yield and observed yield was made for this range of environments. Since the model does not account for any yield losses other than that from inadequate water and N, simulated yields were compared to the highest yielding cultivar in each season. The development stages of the highest yielding cultivar in each season were used in defining these stages in the model.

The N budget of the soybean crop in the Jamieson and Semonov (2000) approach is dependent on the nitrogen concentration of the growing and senescent leaves and stem. Sensitivity of yield to each of these four variables was tested over a range of possibilities in simulations of the 1998/1999 tillage experiment. Stem nitrogen concentration for the growing stem was varied among 16, 18, 20, and 22 mg N g^{-1} and for the senesced stems it was tested for 5 and 8 mg N g^{-1} . Leaf nitrogen for the growing leaves was varied among 0.9, 2.2, 2.5 and 2.8 g N m^{-2} and for the senesced leaves it was varied among 0.5, 0.8 and 1.1 g N m^{-2} .

3.2. Experimental studies

Growth and yield data were obtained from a series of experiments performed at Londrina, PR, Brazil ($23^{\circ}11'37''\text{S}$, $51^{\circ}11'03''\text{W}$, elevation 620 m). The soil at this location is classified as kaolinitic, clayey (very fine) thermic typic Haplorthox. The volumetric water content for total transpirable soil water storage of this soil was $0.15 \text{ m}^3 \text{ H}_2\text{O m}^{-3}$ and the depth of extraction was set equal to 0.6 m.

3.2.1. 1998/1999 tillage experiment

Data obtained in an experiment performed during the 1998/1999 growing season were of particular

interest. The crop N balance was monitored through the growing season for the cultivar Embrapa 48 in response to conventional tillage and no-tillage treatments. The experiment was sown on 12 November 1998 into four replicated plots. The plots were 5.5 m × 12 m consisting of 12 rows spaced 0.45 m apart with 18 plants m⁻¹ row. The average soil N at the beginning of the experiment was only 1.2 mg N g⁻¹ soil in the conventional tillage plots and 1.5 mg N g⁻¹ soil in the no-tillage plots. No N fertilizer was added but 25 g m⁻² of P and K were applied before sowing, and the seeds were inoculated with *Bradyrhizobium japonicum*. The plots were not irrigated and maintained by rainfall only.

The plots were harvested periodically through the growing season to determine crop mass and N accumulation. At each harvest, plants in 1 m of row were harvested. All the harvested plant material was dried in a 60 °C oven for at least 48 h to determine dry weight. The entire sample was ground and a 200 mg subsample collected for determination of N content. Nitrogen concentration was measured by Kjeldahl analysis (Alves et al., 1994). The dry weight and N amount per unit of land area was calculated for all samples.

3.2.2. 1991/1992 to 1999/2000 irrigation experiments

Experiments were conducted for nine growing seasons from 1991/1992 to 1999/2000 to evaluate the differences between rainfed and irrigated treatments on the growth and yield of soybean cultivars. In each growing season, the same five cultivars (Bragg, BR 4, BR 16, Embrapa 48, and Ocepar 4) were sown in mid-November in each year. There were four replicates of each cultivar that consisted of eight rows spaced 0.5 m apart and 4 m long. There were approximately 20 plants m⁻¹ of row, giving a population of 40 plants m⁻².

Standard cultural practices were employed including soil fertilization with P and K as recommended from soil tests and inoculation of the seed with *B. japonicum* at sowing. If needed, sprinkler irrigation was applied to both treatments during approximately the first 20 days following sowing to achieve uniform plant establishment. Herbicides were used to control weeds. Irrigation was applied to the irrigated treatment when soil water potential, as measured with tensiometers, decreased to -0.05 MPa at a depth of 0.30 m.

No water was applied to the non-irrigated plots following plant establishment.

During the growing season, 10-plant samples were periodically harvested from each replicate to determine leaf area development and plant dry weight. The leaves were detached from all plants and their area was measured using a leaf area meter (LI-3100, Li-Cor, Lincoln, NE). These data were expressed as LAI for the crop. All plant materials were then dried in an oven at 60 °C for at least 48 h. The dried samples were weighed and plant weight per unit land area calculated. At maturity, all plants in a 1 m × 2 m section of each plot were harvested by hand and machine threshed. The seed yield was expressed on the basis of 130 g moisture kg⁻¹.

In each growing season, weather data were recorded adjacent to the experimental site, and included air temperature, precipitation, and solar radiation. The highest yield obtained among the five cultivars in each year was selected for comparison with the yield simulated by the model. As inputs for the model, observed flowering data for the highest yielding cultivar in each season was used to estimate the date of termination of leaf development (10 days after stage R1) and the date of the beginning of seed growth (30 days after stage R1).

4. Results

Simulation of leaf area development for the Brazilian cultivars was initially examined. The appearance rate of the leaves (L_R) in the model of Sinclair (1986) was calculated based on a linear increase as a function of daily mean temperature (T) (Sinclair, 1984):

$$L_R = 0.018 \times (T - 8) \quad (1)$$

The rate of leaf appearance calculated from Eq. (1) resulted in a more rapid increase in leaf area than was observed with Embrapa 48 (Fig. 1). Leaf area increase was found to be more accurately simulated for this cultivar by slowing the rate of leaf appearance. This was done by changing the coefficient 0.018 to 0.014 and the base temperature from 8 to 10 °C. The resultant simulation of leaf area matched with experimental observations (Fig. 1), and was used for all succeeding simulations.

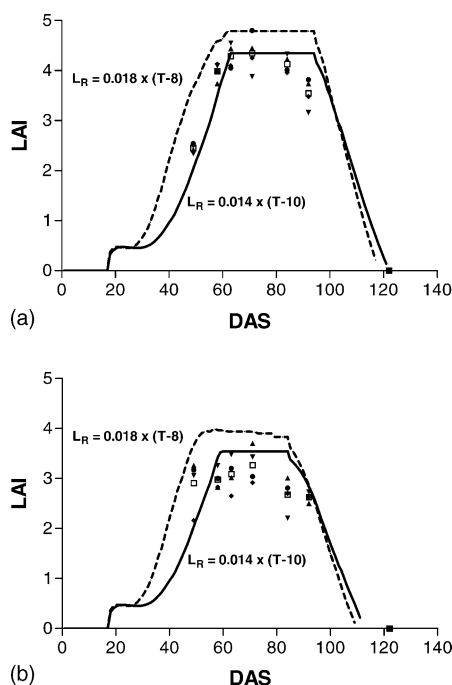


Fig. 1. Experimental observations for days after sowing (DAS) in the 1991/1992 growing season of observed LAI for five cultivars and simulation results using two equations describing rate of leaf appearance.

4.1. 1998/1999 N experiment

Tillage treatments had no large influence on results from this experiment (Zotarelli, 2000), so the results from both tillage treatments are presented in the comparisons with the model. Using the revised approach for calculating the N budget of the crop and the new coefficients for Eq. (1), crop growth and yield was simulated for the weather conditions of the 1998/1999 season.

The critical feature of the revised model was simulation of N accumulation by the crop. Comparison of the time course of N accumulation between the simulations and observations showed a close correspondence (Fig. 2). In this case, the crop was mainly dependent on N_2 fixation, and the accumulation of N from this source appears to be well captured by the conceptual simplifications that were incorporated into the model.

Simulated changes in dry weight of the vegetative material generally matched well with observations (Fig. 3). Both the simulation and the observations indicate a peak vegetative dry weight of 10,000

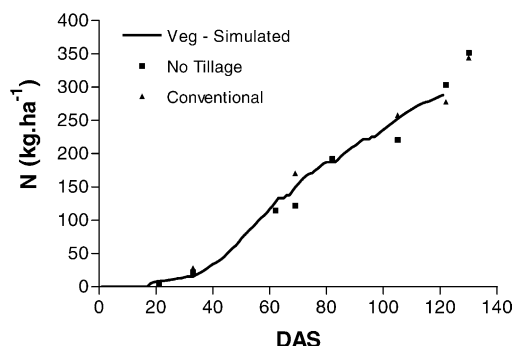


Fig. 2. Nitrogen accumulation observed for DAS: the 1998/1999 tillage experiment and that simulated with the modified model.

kg ha⁻¹. While the intensity of the data collection does not allow a clear resolution of the timing of maximum mass, it appears the model achieved a maximum vegetative mass somewhat earlier than was observed. There is a clear difference, however, in the decrease in vegetative mass during seed fill. The model simulated a steady decrease in vegetative mass during seed fill while this was not observed experimentally. This difference seems to have resulted because in the model senesced vegetative tissue is immediately removed from the crop while in reality there is a retention of low N and senesced tissue on the plants resulting in a greater amount of measured 'standing' vegetative mass.

There was no difference in experimental seed yield between the two tillage treatments in the experiment with a mean yield of 4400 kg ha⁻¹ (Zotarelli, 2000). The simulated yield was 4540 kg ha⁻¹.

4.2. 1991/1992 to 1999/2000 irrigation experiments

A key aspect of the original soybean model was the inclusion of the sensitivity of N_2 fixation to soil drying. Therefore, comparison of the revised model with the irrigation experiment allowed a test of whether this capability was retained in the revised model. However, there was generally not a large difference in the experiments between irrigated and non-irrigated treatments in mass accumulation. For example, a comparison of the observations in 1997/1998 for the irrigated (Fig. 4a) and rainfed (Fig. 4b) showed little overall difference in mass through the growing season. The simulations showed a similar response with only a slightly greater mass accumulation for the irrigated treatment

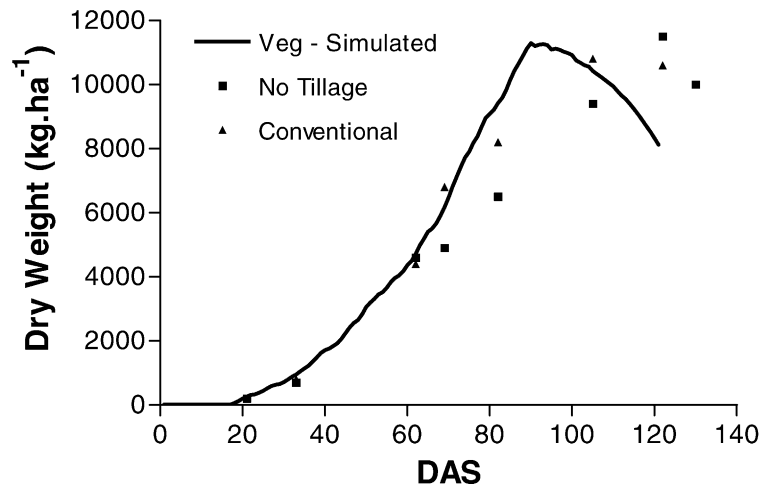
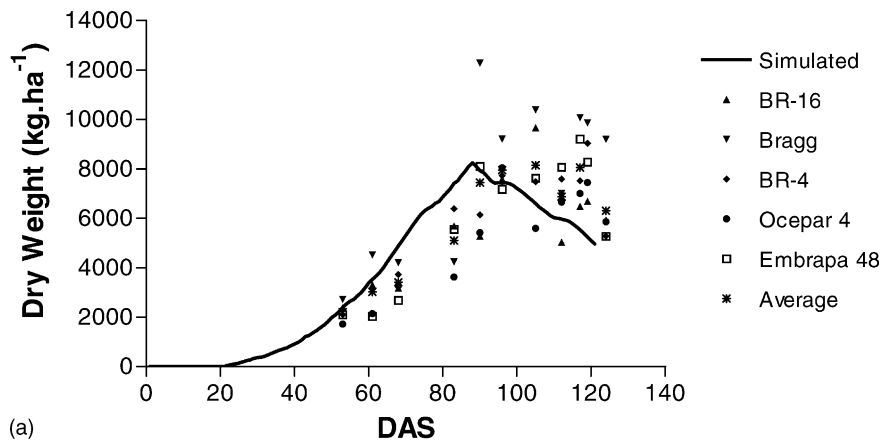
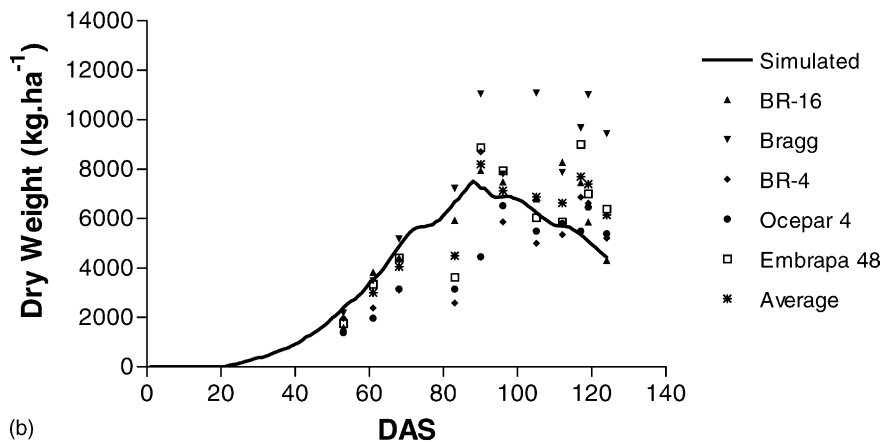


Fig. 3. Dry weight accumulation observed for DAS: the 1998/1999 tillage experiment and that simulated with the modified model.



(a)



(b)

Fig. 4. Dry weight accumulation observed for DAS: the 1997/1998 yield experiment with five cultivars for: (a) the irrigated treatment and (b) the rainfed treatment. The simulated dry weight accumulation for each treatment is shown by the solid line.

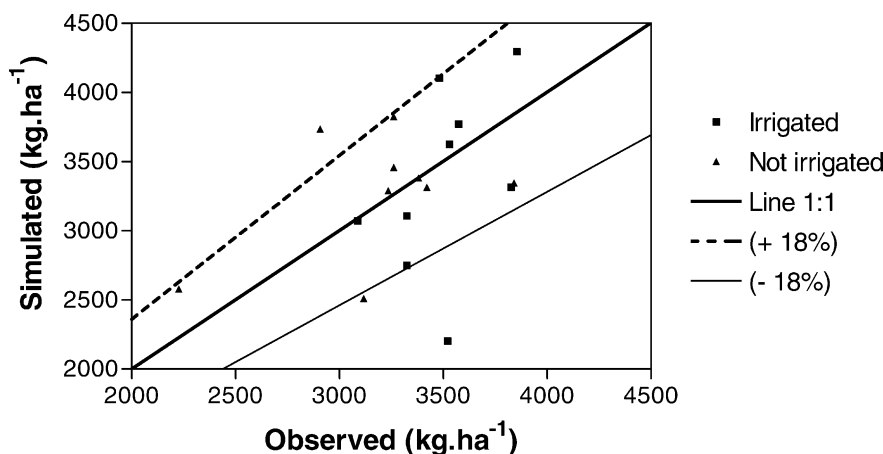


Fig. 5. Plot of simulated yield against observed yield in 9 years of irrigated and rainfed treatments. The 18% range of discrepancy between simulated and observed is indicated by dotted lines.

as compared to the rainfed treatment (Fig. 4). Similar to the results in Fig. 2, the simulated vegetative mass decreased during seed fill. The observed vegetative mass was not found to decrease to the same extent as simulated, likely a result of retention of low N tissue as part of the harvested plant material.

The yield was simulated for both irrigated and non-irrigated conditions in each of the nine growing seasons. A plot of the simulated yields and observed yield (Fig. 5) showed that, except three cases, simulated yields agreed within 18% of the experimental results. In most cases, the deviation between simulated yield and observed yield was 13% or less. The regression forced through the origin between simulated yields and observed yields resulted in a slope of 1.010 and an $r^2 = 0.22$ ($P = 0.05$).

The one major failure to simulate yield occurred for the 1996/1997 irrigated experiment where simulated yield was 37% less than observed. In this case, irrigation was simulated to have resulted in several episodes of flooding that decreased N_2 fixation, and hence, lowered yield. Experimentally, it appears the irrigation did not have the negative effect on the observed yield as was simulated since a relatively high yield was obtained in the experiment.

4.3. Sensitivity analysis

The sensitivity analysis considered the implications on yield of variations in the N content of leaves and

stem during growth and at senescence. Since the uptake of N was calculated from the development of new leaf area and the growth of new stem mass, increasing these variables increases the N concentration to be achieved and hence an increased daily N uptake. Increased N uptake results, of course, in a larger N resource in the crop to support seed growth, and consequently, yields are simulated to increase. The yield increase in response to increasing leaf N contents (Fig. 6) was greater than the response to increasing stem N concentration (Fig. 7). The simulated response to increasing leaf N content, in particular, indicated that ensuring high leaf N may be a useful criterion to assess various management options

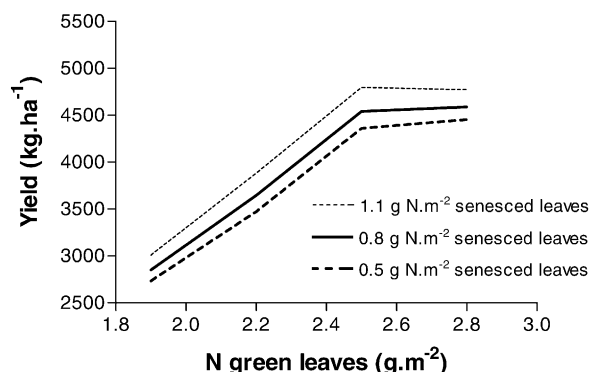


Fig. 6. Results of a sensitivity analysis showing simulated yield plotted against leaf nitrogen contents per unit leaf area. Three levels of senesced leaf nitrogen per unit leaf area are shown.

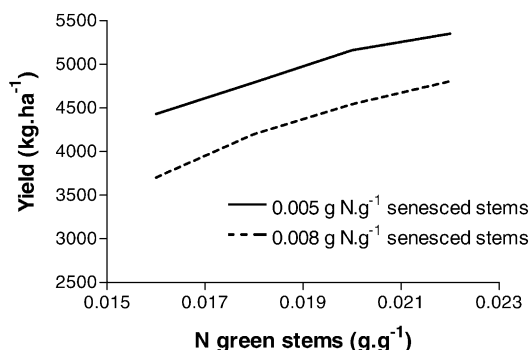


Fig. 7. Results of a sensitivity analysis showing simulated yield plotted against nitrogen concentration in developing stems. Two levels of minimum stem nitrogen content at maturity are shown.

and cultivar selections. There appears to be little information on the genetic variation of maximum leaf N content per unit area. However, the simulated yield response essentially plateaued at a leaf N content greater than 2.5 g N m^{-2} because of the limit imposed in the model on daily N uptake.

The N concentration of senesced tissue is required in the model to calculate the amount of N that can be transported from the senescing tissue to the growing seeds. Therefore, decreases in the N concentration of senesced tissue was expected to increase yield. Indeed, this response was observed in the comparison of the leaves (Fig. 6), but the response was small. Decreasing senesced leaf N from 0.8 to 0.5 g N m^{-2} increased yields only by $100\text{--}150 \text{ kg ha}^{-1}$. Considering, however, that changing the senesced leaf N from 0.8 to 0.5 g N m^{-2} increases available N by less than 20% and leaves usually provide only half or less of the seed nitrogen, minimal increases in yield should be expected. On the other hand, decreasing the N content of senesced stem resulted in yield increases of $550\text{--}700 \text{ kg ha}^{-1}$ (Fig. 7).

5. Discussion and conclusions

The proposal of Jamieson and Semonov (2000) to calculate soil N uptake of wheat from the development of new leaf area and the growth of stem was found to be readily adapted to simulating soybean N accumulation. In fact, the calculations of N uptake by soybean were made easier than in wheat because it was assumed that N_2 fixation in soybean could replace

any deficiencies of N in the soil. Currently, the model does not make an attempt to include a lag in the initiation of N_2 fixation activity once soil nitrate levels are decreased. Simulation of such a lag phase may be necessary in circumstances where soil N levels are initially high and N_2 fixation is initiated late in crop growth only after soil nitrate levels are decreased. Nitrogen accumulation, however, was inhibited with soil drying.

The advantage of the Jamieson and Semonov (2000) approach in the soybean model is that the empirical coefficients concerning soil N availability and N_2 fixation rate were eliminated from the original soybean model. In place of these two 'calibrated' coefficients, it is necessary only to use the input variables about tissue leaf N content and these variables were components of the original model of Sinclair (1986). The variables of N content of growing and senesced leaves and stem can be readily measured and are likely to be conservative within a cultivar. Consequently, the mechanistic basis of the N calculations has been enhanced in the process of simplification that eliminated two empirical coefficients.

The revised approach to calculating soybean N accumulation matched well with observations. In direct comparisons of N accumulation, the time course and amount of N in the crop matched observations (Fig. 2). Further, simulated crop mass until the beginning of seed growth compared favorably with observations (Figs. 3 and 4). Vegetative mass during seed fill in the model tended to decline to a greater extent than observed, but this seems likely a result of senesced mass being removed from the crop in the simulations while the observations represent 'standing mass'. Finally, yield simulated with the revised N model matched within 13% for 11 of the 18 simulated cases in the irrigation experiment and within 18% for 15 cases (Fig. 5).

The sensitivity analysis demonstrated the relative sensitivity of the four critical variables used to calculate the N content of growing and senescing leaves and stems. The model was sensitive to the N content per unit leaf area of the developing leaves, but relatively insensitive to the senescing leaf N content (Fig. 6). There are apparently no observations of variations among cultivars in leaf N content per unit area, and the simulated range of this trait may be much larger than actually exists. Certainly, these simulations indicated

an yield advantage for those cultivars that have high leaf N content.

The storage of N in the stem seems to be particularly important in defining yield potential in this revised model. The highest yields were obtained when the growing stem had high N concentration and the senescing stem had low N concentration (Fig. 7). Again, the range of these variables within the soybean germplasm is not known, and whether these traits can be genetically manipulated would need to be investigated. The sensitivity analysis indicates that yield increases may be possible if these traits can be genetically altered.

Tests of the revised approach to simulate the N budget of soybean appears to be a solid improvement over what was done previously. The revised model eliminates the need to do ‘calibrations’ of the model in each new environment to determine empirical coefficients for N uptake. Further, the model is based on clearly defined variables that can be readily measured for individual cultivars. Since empiricism has been removed from the model, the accuracy of the yield simulations may be somewhat less but the simulations do not require any direct information from the environment in which the predictions are being made.

References

- Alves, B.J.R., Santons, J.C.F., Boddey, R.M., 1994. Metodos de determinacao do nitrogenio em solo e planta. In: Hungria, M., Araugo, R.S. (Eds.), Manual de Metodos Empregados em Estudos de Microbiologia Agricola. Embrapa, Brasilia.
- Bindi, M., Sinclair, T.R., Harrison, J., 1999. Analysis of seed growth by linear increase in harvest index. *Crop Sci.* 39, 486–493.
- Boote, K.J., Jones, J.W., Hoogenboom, G., 1998. Simulation of crop growth: CROPGRO model. In: Peart, R.M., Curry, R.B. (Eds.), Agricultural Systems Modeling and Simulation. Marcel Dekker, New York, pp. 651–692.
- Denison, R.F., Weisz, P.R., Sinclair, T.R., 1985. Variability among plants in dinitrogen fixation (acetylene reduction) rates by field-grown soybean. *Agron. J.* 77, 947–950.
- Hanway, J.J., Weber, C.R., 1971. N, P, and K percentages in soybean [*Glycine max* (L.) Merrill] plant parts. *Agron. J.* 63, 286–290.
- Hanway, J.J., Dunphy, E.J., Loberg, G.L., Shibles, R.M., 1984. Dry weights and chemical composition of soybean plant parts throughout the growing season. *J. Plant Nutr.* 7, 1453–1475.
- Harper, J.E., 1971. Seasonal nutrient uptake and accumulation patterns in soybeans. *Crop Sci.* 11, 347–350.
- Jamieson, P.D., Semonov, M.A., 2000. Modelling nitrogen uptake and redistribution in wheat. *Field Crops Res.* 68, 21–29.
- Justes, E., Jeuffroy, M.H., Mary, B., 1997. Wheat, barley, and durum wheat. In: Lemaire, G. (Ed.), Diagnosis of the Nitrogen Status in Crops. Springer, Berlin, pp. 73–91.
- Lugg, D.G., Sinclair, T.R., 1981. Seasonal changes in photosynthesis of field-grown soybean leaflets. 2. Relation to nitrogen content. *Photosynthetica* 15, 138–144.
- Muchow, R.C., Sinclair, T.R., 1986. Water and nitrogen limitations in soybean grain production. I. Field and model analyses. *Field Crops Res.* 15, 143–156.
- Ney, B., Dore, T., Sagan, M., 1997. Grain legumes. In: Lemaire, G. (Ed.), Diagnosis of the Nitrogen Status in Crops. Springer, Berlin, pp. 107–117.
- Serraj, R., Sinclair, T.R., Purcell, L.C., 1999. Symbiotic N₂ fixation response to drought. *J. Exp. Bot.* 50, 143–155.
- Sinclair, T.R., 1984. Leaf area development in field-grown soybeans. *Agron. J.* 76, 141–146.
- Sinclair, T.R., 1986. Water and nitrogen limitations in soybean grain production. I. Model development. *Field Crops Res.* 15, 125–141.
- Sinclair, T.R., deWit, 1976. Analysis of the carbon and nitrogen limitations to soybean yield. *Agron. J.* 68, 319–324.
- Sinclair, T.R., Muchow, R.C., Ludlow, M.M., Leach, G.J., Lawn, R.J., Foale, M.A., 1987. Field and model analysis of the effect of water deficits on carbon and nitrogen accumulation by soybean. *Field Crops Res.* 17, 121–140.
- Sinclair, T.R., Salado-Navarro, L., Morandi, E.N., Bodrero, M.L., Martignone, R.A., 1992. Soybean yield in Argentina in response to weather variation among cropping seasons. *Field Crops Res.* 30, 1–11.
- Sinclair, T.R., 2003. Improved carbon and nitrogen assimilation for increased yield. In: Specht, J.E., Boerma (Eds.), Soybean Monograph. American Society of Agronomy, Madison, WI, in press.
- Spaeth, S.C., Sinclair, T.R., 1985. Linear increase in soybean harvest index during seed-filling. *Agron. J.* 77, 207–211.
- Spaeth, S.C., Sinclair, T.R., Ohnuma, T., Konno, S., 1987. Temperature, radiation, and duration dependence of high soybean yields: measurement and simulation. *Field Crops Res.* 16, 297–307.
- Zotarelli, L., 2000. Balanco do nitrogenio na rotacao de culturas em sistema de plantio direto e convencional na regioao de Londrina-PR. M.Sc. Dissertation. Universidade Federal Rural Do Rio de Janeiro.