

Quantifying and Understanding Plant Nitrogen Uptake for Systems Modeling

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2 Modeling Nitrogen Fixation and Its Relationship to Nitrogen Uptake in the CROPGRO Model

*Kenneth J. Boote, Gerrit Hoogenboom,
James W. Jones, and Keith T. Ingram*

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2.1 INTRODUCTION

One of the main differences between the simulation of grain legumes and grain cereals is the prediction of nitrogen (N) fixation. The objective of this chapter is to describe how nodule growth and N fixation are simulated in the CROPGRO-legume model in relation to N-uptake processes. We introduce the theory of N deficit that causes the increased carbohydrate availability that is used to drive nodule growth and nitrogenase activity. Where feasible, literature values are used for setting parameters, and where information does not exist, sensitivity analyses are used to set relationships to obtain accurate and reasonable crop growth, N concentration, carbohydrate concentrations, and nodule growth under various temperature and water-deficit conditions. Simulations of nodule growth, N-fixation rate, specific nitrogenase activity, tissue N concentrations, crop N accumulation, and crop dry-matter accumulation are compared with available data for soybean under water-limited versus fully irrigated conditions. Sensitivity of processes, growth, and yield to N fertilization, temperature, water deficit, and source-sink treatments are also shown.

2.1.1 BACKGROUND TO THE CROPGRO-LEGUME MODEL

The CROPGRO-legume model is a process-oriented, mechanistic model with sub-routines that simulate crop development, carbon (C) balance, crop and soil nitrogen (N) balance, and soil water balance, which has been described in detail by Boote et al. (1998a, 1998b). For full details on the CROPGRO growth and partitioning modules, see the 2004 DSSAT V4 crop model documentation (Boote et al. 2004, 1–102). Crop development includes processes such as vegetative and reproductive development, which determine life cycle duration, the duration of root and leaf growth, and the onset and duration of reproductive organ growth. Thus, crop development processes influence dry-matter partitioning among plant organs over time. Crop C balance includes daily inputs from photosynthesis, conversion of C into crop tissues, C losses through abscission, and growth and maintenance respiration. The C balance also includes leaf area expansion, growth of vegetative tissues, pod addition, seed addition, shell growth, seed growth, nodule growth, tissue senescence, and carbohydrate mobilization. The crop N balance includes daily soil N uptake, N₂ fixation, mobilization and translocation of N from old vegetative tissues to new growth of vegetative or reproductive tissues, rate of N use for new tissue growth, and rate of N loss in abscised parts. Soil N balance processes are those described by Godwin and Jones (1991) and Godwin and Singh (1998).

Soil water balance processes include infiltration of rainfall and irrigation, runoff, soil evaporation, distribution of root water uptake from soil layers, drainage of water below the root zone, and crop transpiration (Ritchie 1998). The time step in CROPGRO is mostly daily for carbon and nitrogen balance processes, but is hourly for some processes, such as calculation of thermal time and leaf-to-canopy assimilation. The time step for nodule growth and N fixation is daily, and matches the timing of daily C/N balance and dry-matter growth. Model state variables are predicted and output on a daily basis for crop, soil water, and soil N balance processes.

CROPGRO is a generic model that uses one common FORTRAN code to predict the growth of a number of different grain legumes, including soybean (*Glycine max* L. Merr.), peanut (*Arachis hypogaea* L.), dry bean (*Phaseolus vulgaris* L.) (Boote et al. 1998a, 1998b), cowpea (*Vigna unguiculata* L.) (Boote 1998, unpublished), faba bean (*Vicia faba* L.) (Boote et al. 2002), velvet bean (*Mucuna pruriens* L.) (Hartkamp et al. 2002a, 2002b), and chickpea (*Cicer arietinum* L.) (Singh and Virmani 1994). This versatility is achieved through input files that define species traits and cultivar attributes. The species file includes cardinal temperatures, tissue compositions, conversion costs, coefficients, relationships, and sensitivities to stresses for processes such as photosynthesis, nodule growth, N₂ fixation, maintenance respiration, leaf area growth, pod addition, and seed growth. The model code, along with information input from the species, ecotype, and cultivar files, is based on our understanding of crop–soil–weather relationships. More information on CROPGRO's generic nature and file input structure is available in Hoogenboom et al. (1994), Boote et al. (1998a, 1998b), and chapter 2 of the DSSAT V4 CROPGRO crop growth and partitioning module (Boote et al. 2004, 1–102).

The CROPGRO model originated from the SOYGRO 4.2 model developed by Wilkerson et al. (1983). The SOYGRO model did not explicitly grow nodules or fix N, nor did it explicitly take up mineral N, although it did account for the cost of N assimilation (cost of mineral N and N fixation was the same). Between 1989 and 1994, major model innovation occurred; the soil N balance and N-uptake features as well as N fixation were added (Hoogenboom et al. 1989), resulting in the release of the first version of CROPGRO V3.0 in 1994 (Hoogenboom et al. 1991, 1992, 1993). This version of CROPGRO was made a generic model capable of simulating several different legumes (soybean, peanut, and dry bean) with the same common FORTRAN source code, thus eliminating the need to make parallel changes in source code of multiple grain legume models. To the extent possible, species-related features were removed from the code and placed into a species parameter file along with a cultivar traits file, both of which are read as external input files. Major code improvements in nodule growth and N fixation were made by K. J. Boote for the V3.1 release of the CROPGRO model, followed by additional minor changes, culminating in the 1998 release of CROPGRO V3.5. Concurrent with the 1994 release of CROPGRO V3.0, all DSSAT models including CROPGRO began to use the same soil N balance (Godwin and Singh 1998) and soil water balance models (Ritchie 1998). Information on the N-fixation module is available in the CROPGRO documentation (Boote et al. 2004). Appendix 2.1 at the end of this chapter reprints pp. 44–47 on the N-fixation module from that documentation. The latest release of CROPGRO, V4.0, as a generic grain legume module in the Crop-

ping System Model (CSM) has no further improvements to nodule growth and N fixation (Jones et al. 2003; Hoogenboom et al. 2004).

2.1.2 SCHEME AND ORDER OF PLANT N BALANCE AND N FIXATION IN CROPGRO

It is important to present the overall scheme and order of C and N balance processes in the CROPGRO model before we describe the particular processes of nodule growth, N fixation, and N uptake (Figure 2.1). Daily N supply, which is N available for new growth, is the sum of soil N uptake by roots, N fixation by nodules, and N mobilized from vegetative tissues. Daily C supply is the sum of gross canopy assimilation minus maintenance respiration, plus carbohydrate mobilized today, minus the costs of N assimilation and N fixation. These processes occur daily, and there is a daily update of the state variables of N mass and N concentration in different organs. The DSSAT V4 documentation (Boote et al. 2004) gives the various state variables associated with dry matter (mass), N mass, and N concentration, as well as the sub-routines and calling orders.

The soil N balance processes in CROPGRO are identical for all the DSSAT models, and include root N uptake, mineralization, immobilization, nitrification, denitrification, and N leaching processes, with options of using either the Godwin (Godwin and Singh 1998) or the CENTURY soil N balance, the latter of which was incorporated by Gijsman et al. (2002). Daily uptake of nitrate and ammonium by roots depends on soil and root factors and on crop N demand, as described below.

The order of C and N balance operations and order of called subroutines in CROPGRO (Figure 2.1) are as follows:

1. Simulate C mobilization, photosynthesis, and maintenance respiration.
2. Compute N demand from today's dry-matter growth increment and "target" N concentrations in each tissue (in DEMAND).
3. Compute potential N mobilization from vegetative tissues as a function of thermal time. The N demand is decreased by the amount of N mobilization that can go to seed growth (in DEMAND).
4. Simulate N uptake, which depends on soil and root factors, but with the constraint that actual N uptake cannot exceed N demand (NUPTAK).
5. Compute actual N mobilization for seed growth (MOBIL), which can be less than potential N mobilization if C gain and thus N demand are low on a given day.
6. Simulate C allocation to nodules, which is the amount of carbohydrate sufficient to fix N needed to meet the computed daily N deficit. In addition, a continuous, but small fraction of root assimilates goes to nodule growth and N fixation (in CROPGRO main).
7. Simulate N fixation (nitrogenase activity), possibly limited by nodule mass and temperature effect on specific activity (NFIX).
8. Simulate nodule growth using carbohydrate that is not used for N fixation, but this is limited by temperature and maximum relative growth rate. Nodule growth is limited if water deficit is concurrently limiting nitrogenase activity (NFIX).

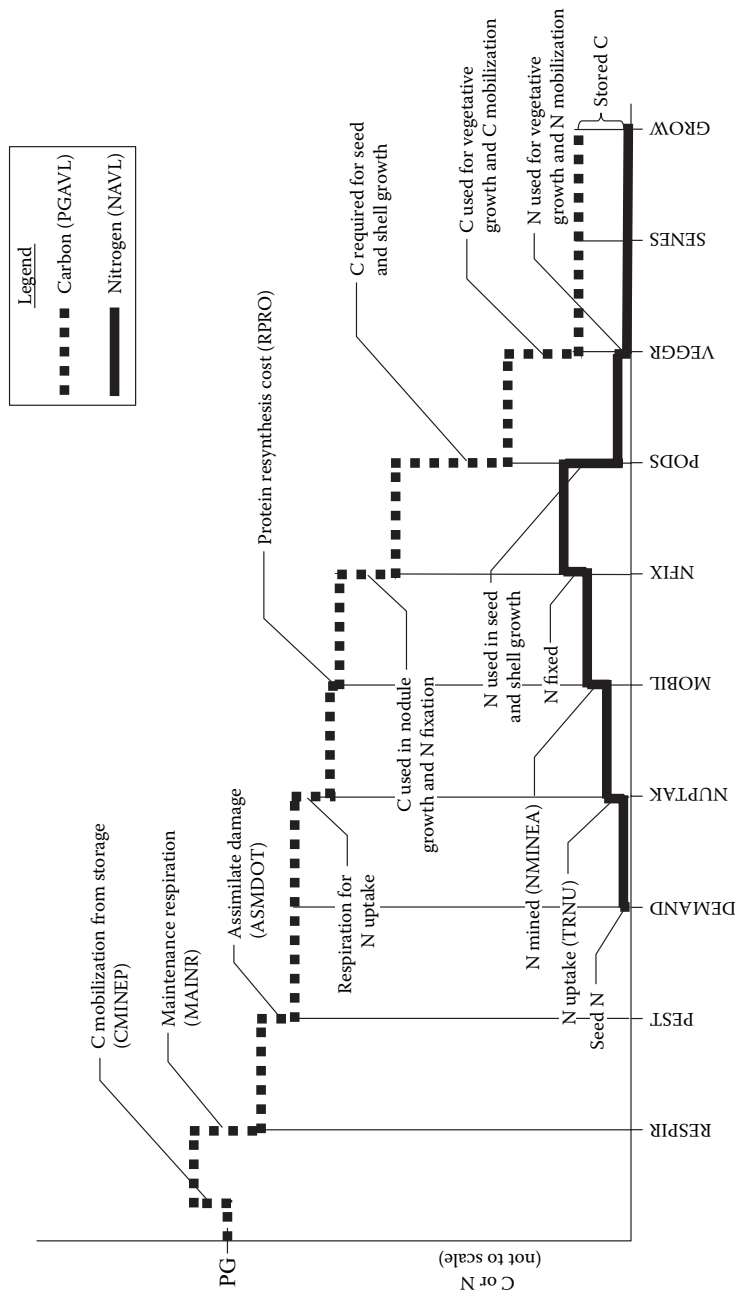


FIGURE 2.1 Schematic of the flow of C (PGAVL) and N (NAVL). The calculations for each process are shown in the order that they are computed through subroutine calls to appropriate modules. PG is gross photosynthesis per land area per day. [Figure from Boote et al. (2004). With permission.]

9. Simulate tissue growth, which depends on C and N supplies that are allocated in order of priority to seeds, pods, then to vegetative tissues (PODS and VEGGR).

The order of N balance operations, taken from the DSSAT V4 documentation (Boote et al. 2004, Figure 1), follows the logic that today's photosynthesis, maintenance respiration, and C mobilization are based on the values of state variables at the end of yesterday, but using today's environmental conditions to compute rates. On an hourly step, leaf photosynthesis is simulated and scaled to canopy assimilation as described by Boote and Pickering (1994), and depends on leaf area index, canopy height, canopy width, row spacing, leaf N concentration, specific leaf weight, genetic potential leaf rate, solar radiation, temperature, and crop water status. Crop water status is computed from the ratio of actual crop transpiration to potential transpiration. The C mobilization depends on the current carbohydrate pool and a mobilization rate that is crop-specific and temperature-dependent, and that accelerates after seeds begin to grow. The rate of N mobilization depends on the size of the available protein pool and a crop-specific, temperature-dependent, day-length-dependent mobilization rate. The N mobilization rate increases up to twofold as actual partitioning of assimilate to seed reaches 100%, but mobilization is restricted if there is insufficient C for seed growth to use that mobilized N. Using today's C supply, the model calculates the potential growth of each type of tissue. Then crop N demand is computed based on the growth increment of each tissue today, multiplied by a "target" high N concentration of each tissue, which assumes that N is nonlimiting. The target N concentration for each tissue type is given in the species file. Potential growth is summed over all tissue types. In addition, crop N demand includes N to replenish any N deficiencies in vegetative tissues, which occur if N concentration in vegetative tissue is less than the target N concentration. This deficiency demand or ability to refill vegetative tissue N deficit declines after setting seeds. In principle, N deficiency demand is an attractive feature that is similar in theory and approach to CERES models (Ritchie et al. 1998), but its construction differs from CERES models and its functionality in CROPGRO has not been well tested.

With the computed crop N demand as an upper limit, the model computes root uptake of N from the soil. The N uptake per unit root length is a Michaelis–Menten function of concentration of nitrate and ammonium in each soil layer. Potential crop N uptake per unit land area is thus computed from the nitrate and ammonium concentration of each soil layer, the root length density in each layer, and the soil water availability of that layer. Actual N uptake is the minimum of potential N uptake and N demand. Thus, actual N uptake from each layer is proportionately scaled back from potential N uptake per layer. An alternative mechanism for nitrate uptake could be one based on mass flow of solution nitrate arriving at the roots, as the model computes water uptake for each individual soil layer, and the nitrate concentration of the water in that layer is known. Uptake of ammonium, being an exchangeable cation, would still need to remain as a function of root length density. Potential model improvements in CROPGRO that should be evaluated include: (a) the use of a mass flow mechanism for root N uptake, (b) N deficiency demand for N uptake, and (c) alternative methods of computing N stress.

2.1.3 N FIXATION AND NODULE GROWTH IN CROPGRO

If actual N uptake meets the N demand, there will be no N fixation today. If N uptake is less than N demand, the amount of today's N deficit is computed and then multiplied by the glucose equivalent cost of fixing N ($7.06 \text{ g glucose g}^{-1} \text{ N fixed}$) to compute the amount of carbohydrate partitioned to nodules for N fixation today. The mineral N uptake is likewise charged a cost of N reduction and assimilation into amino acids. The N fixation (NFIXN, see appendix 2.1) occurs up to the limit of allocated carbohydrate supply, nodule mass, a species-defined nodule-specific activity, and soil temperature. The N fixation is a two-stage computation, in which the first step is to calculate the potential rate of N fixation, considering the minimum of either limiting C supply or limiting the rate of nitrogenase (considering both nodule mass and soil temperature). In the second step, this potential rate was limited to actual, depending on minimum of either flooding or plant turgor effect. If nodule mass is too low to use all the carbohydrate for N fixation at the temperature-limited specific activity, then that "leftover" carbohydrate is used for nodule mass growth (NODGRO, see appendix 2.1) at a species-defined and temperature-dependent relative growth rate, a defined tissue cost, and the minimum of plant water stress or excess water stress. The relative growth rate for nodules is $0.17 \text{ g g}^{-1} \text{ d}^{-1}$ for soybean. The effects of environmental factors of temperature, water deficit, flooding, and nodule age act on the nodule growth or N fixation on a land-area basis, rather than affecting just nodule growth rate (RGR) or N fixation (SNA).

The code allows a thermal lag phase after plant emergence for infection and nodule growth, after which nodule mass is initialized at a species-dependent initial nodule mass. The current thermal lag of zero physiological days after emergence for nodule infection is consistent with data of Bergersen and Goodchild (1973) showing that small nodules were present on soybean at 8 days after sowing, leghemoglobin was observed at 10 days after sowing, and N fixation began at 12 days after sowing. Model initiation of nodule mass occurs at emergence, which is typically 5 to 8 days after sowing, so any time difference between simulated and actual onset of N fixation would be small. Sensitivity analyses conducted early during model development showed that we needed to create a continuous partial allocation of assimilate to nodules in order to prevent excessive delay in nodule growth and N fixation. Thus, we currently have a partial allocation (bypass) to nodules that amounts to 5% of the assimilate allocated to root growth. The specific nitrogenase activity (SNA) is $45 \text{ g N kg DW nod}^{-1} \text{ d}^{-1}$ for soybean. Nitrogenase activity, in summary, is dependent on soil temperature, plant water status (TURFAC), soil aeration (excess soil water), and nodule age.

2.1.4 CONSEQUENCES OF N DEFICIENCY ON TISSUE N LEVELS, VEGETATIVE GROWTH, PARTITIONING, PHOTOSYNTHESIS, AND SEED GROWTH

What if today's N supply is deficient for today's growth, even after considering today's N fixation? Vegetative tissues are grown at a normal rate, but with a lower N concentration, so long as N concentration in new tissues remains above the minimum N level required for growth (N_g). To the extent that N concentration of new

tissue would fall below N_g , dry-matter growth of tissues is limited proportionately to maintain tissue N equal to N_g . CROPGRO allows any excess carbohydrate from photosynthesis to accumulate in leaves, petioles, and stems, and this carbohydrate is slowly mobilized for later use. In addition, a ratio called NSTRES is computed from the ratio of today's N supply/(N demand \times 0.70). The NSTRES factor causes increased partitioning of dry matter to root when the ratio of today's N supply/N demand falls below 0.7. NSTRES in CROPGRO is computed very differently from that in the cereal models, as it is based on today's supply-to-demand ratio, while that in CERES is computed on cumulative vegetative N concentration relative to upper and lower critical limits. For CERES models, the NSTRES is used to directly reduce dry-matter growth (PCARB). In contrast, in CROPGRO, the decline in leaf N concentration causes a decline in leaf and canopy photosynthesis. The photosynthesis response follows a quadratic function defined by the minimum N concentration at which the rate is zero and the optimum N concentration at which the rate is maximum, based on leaf photosynthesis versus leaf N concentration, with data for soybean coming from Boote et al. (1978), Boote et al. (1977, unpublished), and Boon-Long et al. (1983).

What is the priority for N, in the event of N deficiency, and does this change during seed filling? Nodule growth and N fixation have priority over seed growth for both assimilate (for fixation and growth) and N (to grow nodules), in order to make up any N deficit during seed filling. While nodules have high priority for N, their mass is so small that this is unimportant relative to reproductive use of N. CROPGRO gives seed growth priority over pod wall growth, which, in turn, has priority over vegetative tissue. If N deficiency is large, then seeds are grown at lower N concentration, an approach justified by data of Hayati et al. (1996). Under N deficiency, the reduction in seed N concentration is primary, but seed growth rate is also progressively reduced, following a Michaelis–Menten growth response to the N supply/N demand ratio. On the other hand, seed N concentration is allowed to increase if N is surplus, which can happen during seed fill if a stress, such as a severe drought, reduces C supply when N is available from N mobilization. The rate of N mobilization during grain filling in CROPGRO is a function of the photothermal age of the crop canopy (and is faster during grain filling), but it is not regulated (demanded) by seed filling rate, nor can luxury N fertilization substantially reduce this N mobilization from foliage. As a consequence of the decline in foliar N concentration, the leaf and canopy photosynthesis will decline during grain filling, regardless of N fertilization.

2.1.5 INITIALIZATION AND PARAMETERS FOR NODULE GROWTH AND N FIXATION IN CROPGRO

Parameters for nodule growth and N fixation for soybean consist of an initialized nodule mass per plant (0.14 g) at emergence, a thermal lag time of zero physiological days after emergence, a relative growth rate of $0.17 \text{ g g}^{-1} \text{ d}^{-1}$, and a specific nitrogenase activity (SNA) of $45 \text{ g N kg}^{-1} \text{ d}^{-1}$ for soybean, based on the mean of two literature values, 368 and 552 $\text{mmol e}^{-} (\text{kg nodule DW h})^{-1}$ for soybean nodule activity measured in flow-through systems (Layzell and Moloney 1994). The conversion is

based on 1 mole N_2 (28 g) fixed per 6 mole of e^- . Converting to a daily rate gives a range from 41.2 to 61.8 (mean 51.5) g N fixed kg DW $nod^{-1} d^{-1}$. We initially used a value of 50 g N fixed kg DW $nod^{-1} d^{-1}$, which we reduced to 45 in 1995 to improve the match of simulated-to-observed nodule mass over time for a 1984 Bragg soybean data set. The cost of N fixation is 7.06 g glucose g^{-1} N fixed, which is halfway between the measured values of 6.75 and 7.43 g glucose g^{-1} N fixed as reported for soybean by LaRue and Patterson (1981) and Ryle et al. (1979). Based on theory, the cost should be 5.18 g glucose g^{-1} N fixed for Hup^+ and 6.43 g glucose g^{-1} N fixed for Hup^- . Going from Hup^- to Hup^+ increases simulated soybean yield 2.7%. So, the cost we use is higher than even the maximum efficiency of Hup^- . The species file actually defines the cost of N assimilation or N fixation in terms of glucose cost per gram of protein synthesized (2.556 or 2.830 g glucose per g protein, respectively). Thus, the model effectively sends glucose to nodules, and nodules return the full complement of amino acids (we do not simulate amides or production of C-skeletons explicitly). The growth synthesis cost of growing nodules is charged from the glucose allocated to nodules, but the maintenance costs are charged elsewhere “off the top.”

2.2 MODEL PERFORMANCE

A major goal in testing model performance was to demonstrate reasonable behavior of the individual model processes (N_2 fixation, N-uptake rate) and model state variables (nodule mass, total biomass, N accumulation, N concentration, carbohydrate concentrations) under a range of climatic and soil conditions. We particularly wanted robust model behavior on soils with a full range of soil N supply from very limiting (sands with no N fertilization) to less N limiting, under different levels of soil water deficit and soil temperature. In addition, model performance was tested, where possible, against actual data on nodule mass, nitrogenase activity, N-fixation rate, N accumulation, and tissue N concentrations measured in field studies on Bragg soybean conducted on a Millhopper fine sand at Gainesville, Florida, by DeVries et al. (1989a, 1989b) and Albrecht et al. (1984). These studies satisfied our goal to evaluate potential N fixation on a fine sand with no N fertilization, and also under rain-fed versus irrigated conditions.

2.2.1 DYNAMICS—N DEFICIT IS NEEDED TO TRIGGER NODULE GROWTH AND N FIXATION

Our first goal in sensitivity analyses was to determine the type and robustness of simulated response for an N-limited situation. Therefore, we simulated the time-course dynamics of nodule growth, N fixation, N concentration, and nonstructural carbohydrate accumulation under a developing N deficiency for Bragg soybean sown on 5 May 1976 at 13 $pl m^{-2}$ in 30-cm rows on an unfertilized sandy soil at Gainesville, Florida (Figures 2.2A and 2.2B). At emergence, initial nodule mass is small, N fixation is insufficient, and daily N uptake from the soil soon becomes insufficient. Thus the model attempts to send sufficient assimilate to nodules to fix the required N, but N fixation is still insufficient because nodule mass is small and SNA is saturated. This carryover assimilate is used for nodule growth, but this is

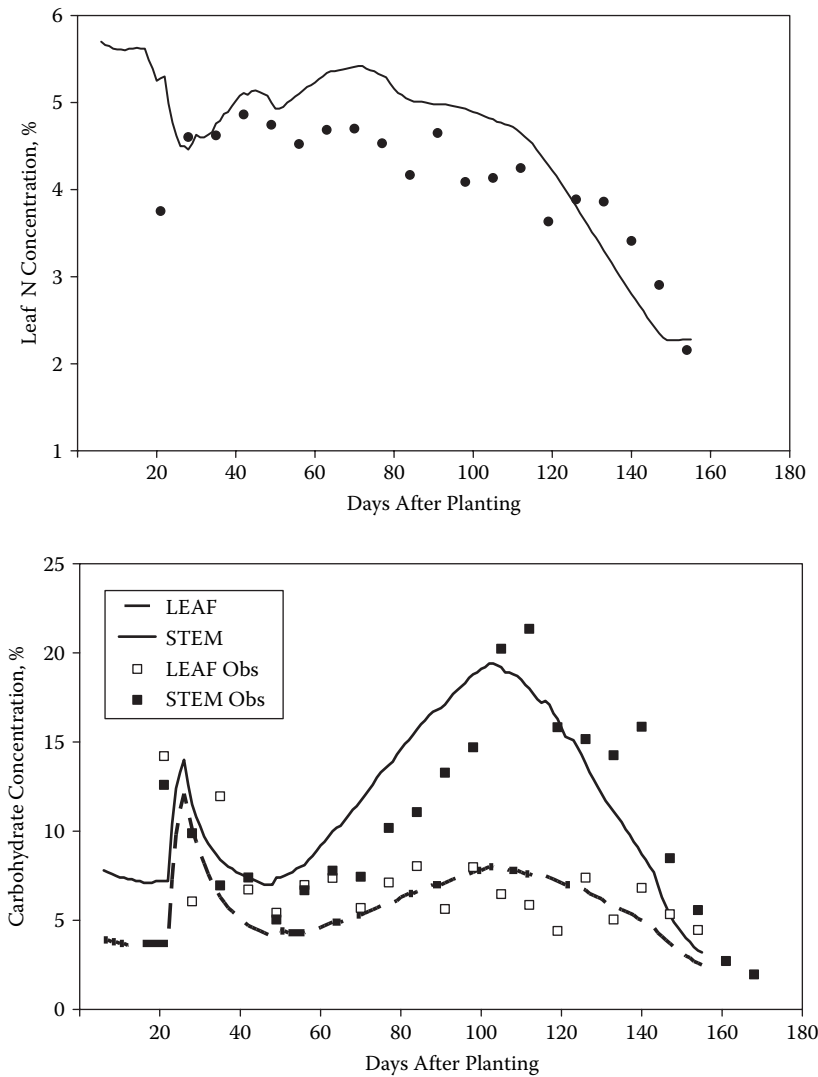


FIGURE 2.2 (A) Leaf N concentration and (B) leaf total nonstructural carbohydrate concentration of irrigated Bragg soybean grown with no fertilizer N on a fine sand soil at Gainesville, Florida, in 1976. [Adapted using data points from Boote et al. (1998b) with updated simulated values from CROPGRO V4.0.]

limited by nodule RGR, existing nodule mass, and soil temperature. As a result, there is an N deficiency, new tissue is grown at less than “target” N concentrations, and carbohydrate that cannot be used for growth or N fixation begins to accumulate in leaves and stems. While that carbohydrate pool is mobilized daily at a temperature-dependent rate, the net carbohydrate accumulation will continue to increase until N fixation and nodule growth catches up. Two characteristic responses occur, as shown in Figure 2.2:

1. There is a dip in leaf N concentration caused by growing tissue at less than “target” N concentration.
2. There is a peak in carbohydrate accumulation in the leaf and stem that concurrently matches the dip in leaf N concentration.

Once the crop has grown sufficient nodule mass to fix N at the defined SNA, then leaf N concentration begins to recover and the carbohydrate concentration begins to decline. This dip in leaf N concentration, peak in carbohydrate, and beginning recovery occurs about 24–28 days after sowing, but nodule growth and total N-fixation rate continue to increase over time because the plant is still in its exponential growth phase. The accumulation of carbohydrate starting at 50 days in Figure 2.2 is not related to N deficit, but rather is a “programmed” accumulation of carbohydrate that begins at anthesis and slows only when a full seed load has been set. Beginning at anthesis, there is a ramp function that allows up to 26% of the growth allocated to stems after anthesis to be stored as mobilizable carbohydrate in stems by the time the last pod is set, although there is concurrent mobilization as well.

2.2.2 DYNAMICS OF NODULE GROWTH AND N FIXATION: PRIORITY FOR ASSIMILATE

Early in model formulation, we had allowed carbohydrate to nodules only when there was a “daily” shortage of N supply, and this carbohydrate was used for SNA first, and then for growth. But sensitivity analysis by James Hansen during his Ph.D. program (Hansen 1996) showed that this approach caused too much delay in onset of nodule growth and N fixation, excessive dip in N concentration and accumulation of carbohydrate, and slow early growth. To solve this, we provided a continuous partial allocation of assimilate to nodules every day, amounting to a fraction of the daily assimilate allocated to roots. Based on sensitivity analyses, this allocation fraction was set at 0.05 of assimilate allocated to roots, and the initial nodule mass was increased to 0.014 g/plant, sufficient to minimize the dip in leaf N concentration and to keep the carbohydrate accumulation in leaf and stem to less than 30% by comparison with data from 1976 (see Figure 2.2B), 1979, and 1984 at Gainesville. The change was also needed to minimize dip in SLA, which was not seen during that time in our data, and to minimize decline in leaf photosynthesis as a result of low N concentration, which we also did not see (Boote 1987, unpublished data). The amount of “bypass” flow depends on root growth and is added to the amount of assimilate computed to be sent to nodules to fix sufficient N to make up today’s deficit if nodule mass is adequate and if stresses do not limit SNA. The logic to justify this “bypass” allocation is that nodules are somewhat like parasites that directly access the phloem and can grow slowly, even with low but sufficient root N uptake for the crop. There is scientific literature to support limited nodule growth despite the presence of adequate N for crop growth.

We also learned via sensitivity analyses that we had to give nodule growth and N fixation first priority for assimilate over seed growth. The senior author discovered this more than 20 years ago, in interactions with Dr. Basil Acock during programming sessions to develop the GLYCIM soybean model. The GLYCIM model runs

hourly, with hourly partitioning to organs including seeds. During one of these modeling sessions, Dr. Acock found that the model's seeds were aborting every night for lack of N. We decided that his model was giving seeds first priority for carbohydrate, thereby starving the nodules and, thus, running out of N for seed growth at night. Later work by Dr. Dennis Egli and his students also showed that seeds were not the "demanding" organs as suggested by the self-destruct hypothesis of Sinclair and deWit (1975), but were rather more passive receptacles for arriving assimilate (Hayati et al. 1995, 1996). Hayati et al. (1996) showed that under N-limiting conditions, seeds continued growing nearly as rapidly as under N-sufficient conditions, but with reduced N concentration. We also concluded that nodules were similar in some ways to root-knot nematodes (*Meloidogyne* spp.) that were shown by Stanton (1986) to be strongly plumbed into the root phloem and which were found to be first-priority users of assimilate, over seed or vegetative growth.

2.2.3 SENSITIVITY OF NODULE GROWTH AND N FIXATION TO WATER DEFICIT

For general use at multiple locations around the world, we wanted to have a crop model that responds appropriately over a range of temperatures and soil water levels, but primary data on relationships for sensitivity to those parameters were lacking. Initially for model V3.1 of CROPGRO, we had the nodule growth rate (RGR) and N fixation (SNA) sensitive to the fraction of available soil water in the nodule zone. A current hypothesis prevailing at that time was that soil water had a direct effect on nodule function. This approach did not work well because the upper nodule zone of topsoil (upper 30 cm) is very prone to drying, even when there is adequate water below 30 cm to meet plant needs for transpiration. For V3.5 of CROPGRO, we changed the nodule growth and nitrogenase activity to be sensitive only to plant water status as shown in Figure 2.3. This gave a more stable and better response and continues to be used in the most recent model, version V4.0. Plant TURFAC (affecting vegetative growth) is now the driver of the SWFACT variable and the 8-day running-memory variable, SWMEM8, as discussed in Appendix 2.1. The goal of the 8-day running memory is to allow a damage effect of past plant water deficit. Having nodules sensitive to plant water status is consistent with the data of Sprent (1972), who found that nodules in dry soil gained water from roots in moist soil. In addition, Albrecht et al. (1984) reported that SNA and nodule relative water content did not fully recover until the plant water status was fully recovered by irrigating deeply, despite good water status in the nodule zone. CROPGRO allows crop species to have differential sensitivity of nodule RGR and SNA to plant water status (Figure 2.3). For soybean, the sensitivity of nodules to water deficit is intermediate to the sensitivities of photosynthesis (SWFAC) and vegetative growth (TURFAC). On the other hand, peanut nodule sensitivity to water deficit is presumed to have the same sensitivity as photosynthesis response to SWFAC.

Nodule growth and N fixation are sensitive to excess soil water (flooding) through anaerobic stress computed from the portion of pore space that is filled with water (EPORS and FLDSUM, discussed in Appendix 2.1). At present, when the pore space becomes completely water-filled, both nodule growth and N fixation are restricted, and nodule senescence is enhanced. The flood sensitivity aspects of the model have

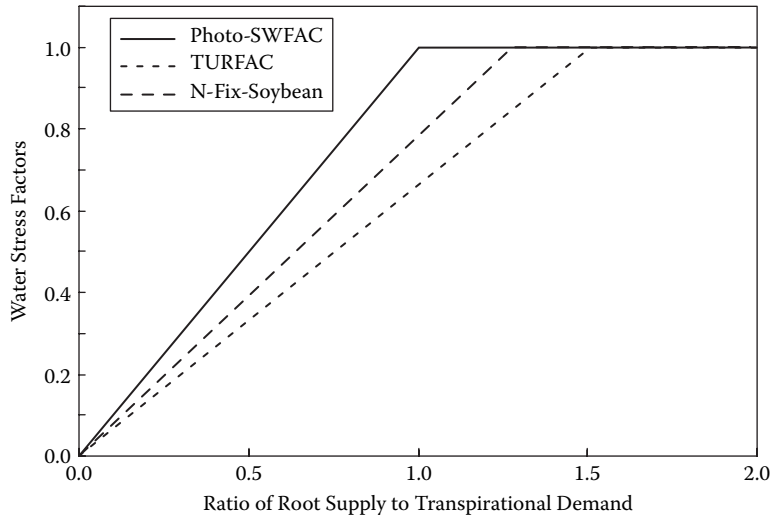


FIGURE 2.3 Sensitivity of photosynthesis (SWFAC), nodule growth, and nitrogenase activity (N-Fix-Soybean), and expansive growth (TURFAC) to ratio of root water supply to transpirational demand for water.

not been tested sufficiently to set the minimum pore space that must remain air-filled in the nodule zone to prevent anaerobic stress.

Nodule death rate (RNDTH, discussed in Appendix 2.1) was set to a given daily fraction under stress, and this fraction is modified by the maximum of flooding (anaerobic) stress, water stress, or C shortage stress effects. Nodule death rate under irrigated and water deficit conditions was calibrated to the nodule mass of the 1984 rain-fed Bragg soybean experiment (Figure 2.4).

2.2.4 SEASONAL PATTERN OF NODULE GROWTH, N FIXATION, AND N ACCUMULATION IN RAIN-FED VS. IRRIGATED CONDITIONS

We tested the CROPGRO-Soybean model against data on nodule dry-matter growth, N fixation, crop dry-matter growth, and N accumulation from a 1984 experiment that had irrigated and rain-fed treatments (DeVries et al. 1989a, 1989b). Figure 2.4 shows the simulated nodule mass accumulation over time for the two treatments compared with observed nodule mass. With the value of maximum SNA from the literature, the predicted nodule mass was within 20% of observed nodule mass for the soybean crop, although we did reduce the potential SNA from 50 to 45 g N fixed kg DW nod⁻¹ d⁻¹ in order to increase simulated nodule mass about 10%. The code is designed to allow “carryover” carbohydrate left over from nitrogenase to be used for nodule growth as a way of catching up on nodule mass if N is limiting. This feature worked poorly under water deficit, allowing excessive nodule growth that affected future nitrogenase capacity. Therefore, when water deficit limited specific nitrogenase activity, we had to concurrently limit nodule growth to use only 10% of that “carryover” carbohydrate (that not used for SNA if the plant is under water deficit). This was a feature learned by sensitivity analyses and calibration against N fixation

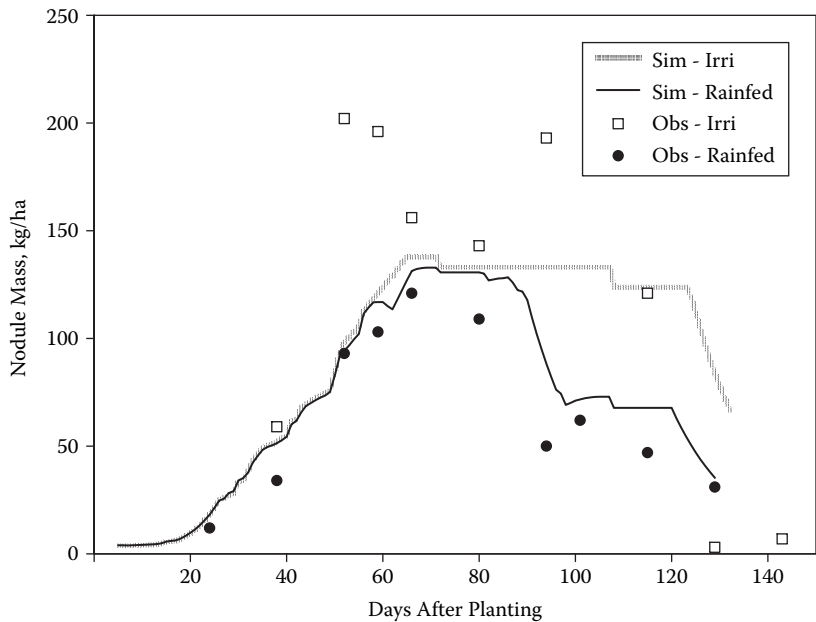


FIGURE 2.4 Simulated and observed nodule mass over time for irrigated and rain-fed Bragg soybean grown on a fine sand at Gainesville, Florida, in 1984. [Observed data are from DeVries et al. (1989a, 1989b).]

and nodule mass over time measured in the 1984 rain-fed Bragg soybean study. Nodule senescence under water deficit functioned well, but required minor adjustments to stress sensitivity.

The simulated N fixation closely matched the magnitude and life-cycle pattern of measured N fixation over time (Figure 2.5). The very rapid 1-day or 2-day dips in N fixation simulated for both irrigated and rain-fed crops is caused by cloudy, low-radiation days. Maximum N-fixation rate was 4 to 5 kg N [ha·day]⁻¹. This agreement was good to see in two respects: First, from a modeling standpoint, we were able to use a specific activity from the literature that predicted nodule mass within 20% of observed values. Second, the simulated rates of N₂ fixation were close to field measurements of N fixation despite using excavated whole root systems of individual plants and simply correcting (multiplying) from acetylene reduction to N₂ fixation (DeVries et al. 1989a). The model correctly simulated the decrease in N fixation during the 21-day water deficit period (78–99 days after sowing) during reproductive growth. However, it did not predict the low rate measured on rain-fed plants during days 61–65, when a transient water deficit period occurred, although the model did not indicate much stress. Perhaps the good prediction of N fixation under irrigation could have been anticipated, since the sandy soil provided a low N supply, and the model was already known to accurately predict dry matter and N accumulation over time for this site (Figure 2.6 shows N accumulation over time). Thus, the model should have predicted that N fixation would contribute the remaining (major) amount of N required.

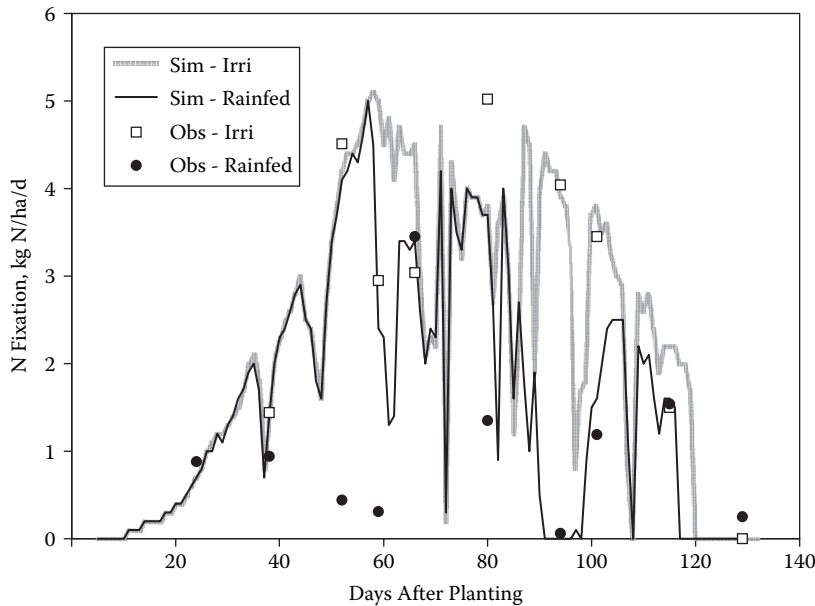


FIGURE 2.5 Simulated and observed N-fixation rate over time for irrigated and rain-fed Bragg soybean grown on a fine sand at Gainesville, Florida, in 1984. Sharp but short dips are usually associated with cloudy days. [Observed data are computed from DeVries et al. (1989a).]

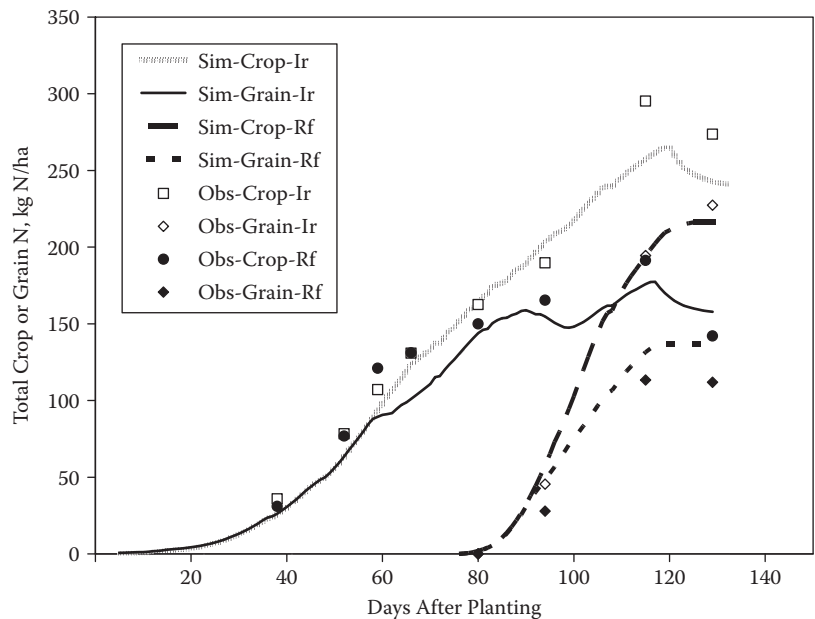


FIGURE 2.6 Simulated and observed crop and grain N accumulation over time for irrigated and rain-fed Bragg soybean grown on a fine sand at Gainesville, Florida, in 1984. [Observed data are from DeVries et al. (1989b).]

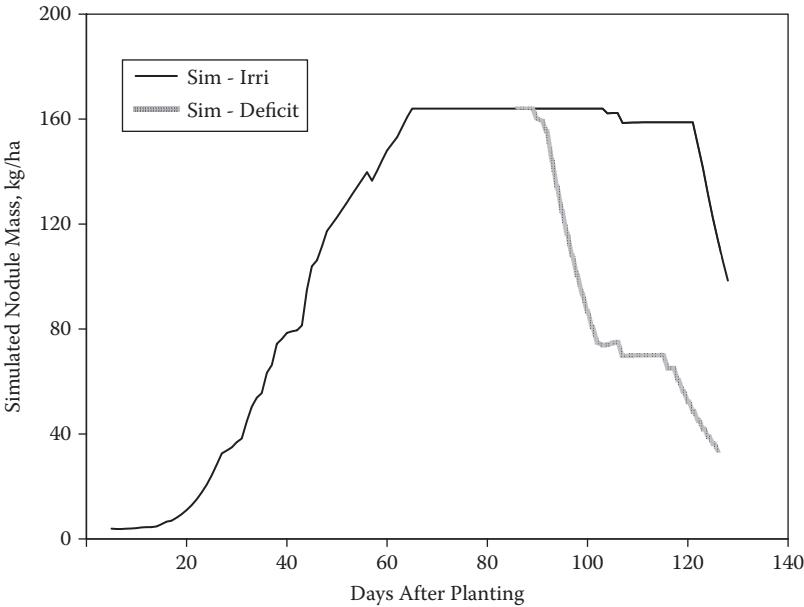


FIGURE 2.7 Simulated nodule mass over time for irrigated treatment versus a 19-day water deficit during seed filling for Bragg soybean grown on a fine sand at Gainesville, Florida, in 1980.

Model simulations were also compared with data from a 1980 experiment in which nitrogenase activity, canopy CER, stomatal conductance, and plant water status of Bragg soybean were measured periodically during a 19-day water deficit period initiated after the R5 beginning seed stage (Albrecht et al. 1984). This crop was sown 13 June 1980 at 30 plants per m² in 76-cm rows in Millhopper fine sand soil with no N fertilizer. In this experiment, simulated nodule mass reached a peak of 160 kg ha⁻¹ and then senesced rapidly during the 19-day water deficit period to about 60 kg ha⁻¹ (Figure 2.7). Simulated N fixation, initially at about 5 kg N [ha·d]⁻¹, first began to decline 8 days after water-withholding (in concert with simulated onset of water deficit), and then fell to zero by 11 days after water-withholding, and recovered to about 1.3 kg N [ha·d]⁻¹ after water deficit was relieved (Figure 2.8). Albrecht et al. (1984) measured specific nitrogenase activity on recovered nodules, but did not measure total nodule mass nor total N fixation. The simulated SNA approached 40 g N kg⁻¹ d⁻¹ during vegetative growth while nodule mass was still increasing. The predicted and observed SNA were still about 30 g N kg⁻¹ d⁻¹ prior to start of the water deficit experiment. Simulated SNA fell to zero at 11 days after water-withholding, but the observed SNA maintained somewhat longer, only reaching zero at 15 days after withholding (Figure 2.9). Based on these findings, we may need to decrease the sensitivity of soybean SNA to plant turgor, making its sensitivity more like the sensitivity of photosynthesis to plant turgor. After re-irrigating, the observed and simulated SNA recovered to about 20 g N kg⁻¹ d⁻¹ within 3 days of re-irrigating, and reached a value as high as the irrigated control. However, both SNA and N fixation

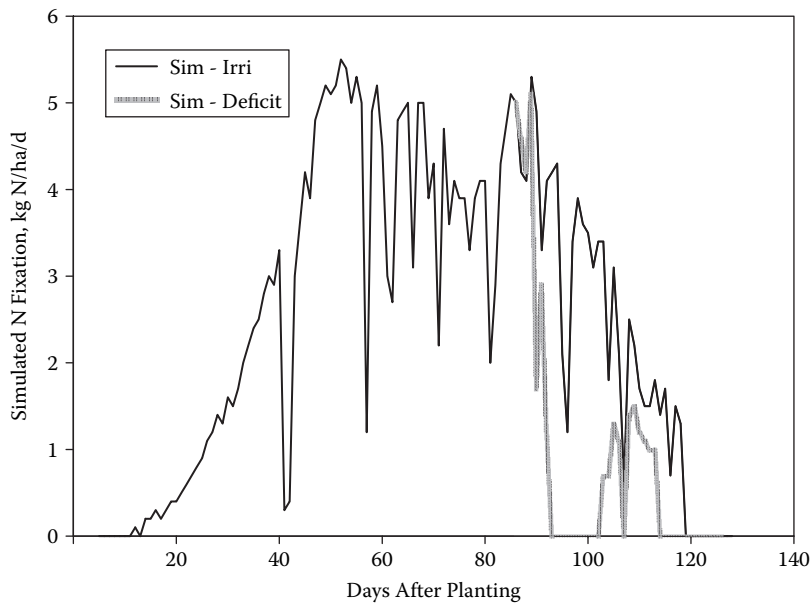


FIGURE 2.8 Simulated N fixation over time for irrigated treatment versus 19-day water deficit during seed filling for Bragg soybean grown on a fine sand at Gainesville, Florida, in 1980.

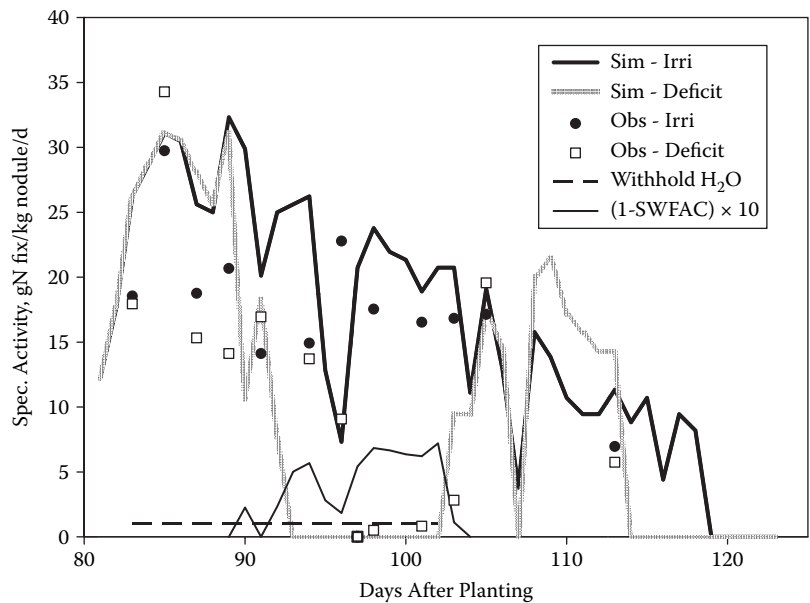


FIGURE 2.9 Simulated and observed specific nitrogenase activity over time for irrigated treatment versus 19-day water deficit during seed filling for Bragg soybean grown on a fine sand at Gainesville, Florida, in 1980. The value “1-SWFAC” is the degree of water deficit, where 0.0 is no stress and 1.0 is total stress. [Observed data are computed from Albrecht et al. (1984).]

were also declining in the irrigated control over time, as the crop was more than halfway through seed fill and had only another 15–20 days to maturity.

2.2.5 SENSITIVITY ANALYSIS TO DISCOVER PROBABLE TEMPERATURE SENSITIVITIES OF NODULE GROWTH AND N FIXATION

As shown in Appendix 2.1, potential N fixation is a function of C supply, nodule mass times specific activity, and soil temperature. Likewise, nodule growth rate is a function of C supply (left after N fixation), nodule mass times relative growth rate, and soil temperature. Both are also sensitive to TURFAC and excess water. ACSTF and ACSTG, discussed in Appendix 2.1, are functions of soil temperature in the nodule zone and are used to affect N fixation and nodule growth rate, as shown in Figure 2.10. There was inadequate published data to parameterize the sensitivity of nodule growth rate (RGR) and specific nitrogenase activity (SNA) to soil temperature. Therefore, we used sensitivity analyses of model performance to parameterize the sensitivity of nodule growth and specific nitrogenase activity to soil temperature; particularly since the first release of CROPGRO-Soybean with N fixation (V3.1) was initially developed with data from warm locations, such as Florida. Subsequently, version 3.1 of the model was tested with four seasons of data on growth, tissue N concentration, and N accumulation from relatively cool seasons at Ames, Iowa (Sexton et al. 1998), and in a high-elevation location in northwest Spain where the nighttime minimum temperatures frequently reached 13°C (Sau et al. 1999). We discovered, for moderately cool seasons in Iowa, that model version 3.1 simulated large dips in leaf N concentration (as low as 3.0%), large nodule mass (exceeding 600 kg ha⁻¹), leaf carbohydrate pools of 34% to 40%, and very inhibited early growth associated with low leaf N, which caused low photosynthesis, resulting in low biomass accumulation and low yield in 3 of 4 years (Sexton et al. 1998). Simulated early crop growth

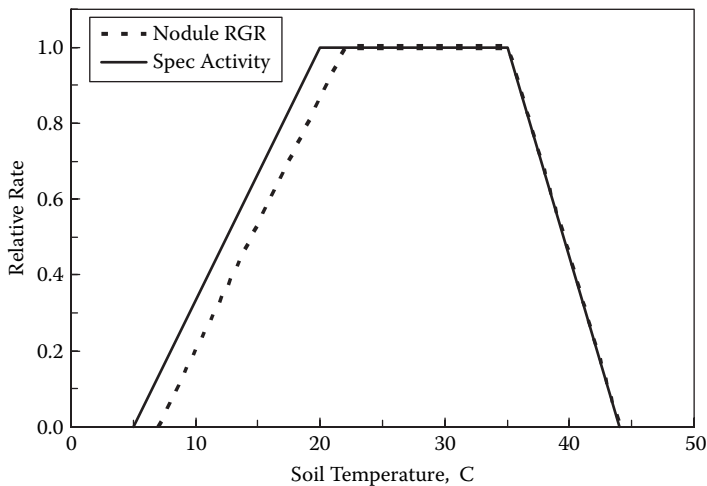


FIGURE 2.10 Sensitivity of nodule growth rate (Nodule RGR) and specific nitrogenase activity (Spec. Activity) to soil temperature for soybean.

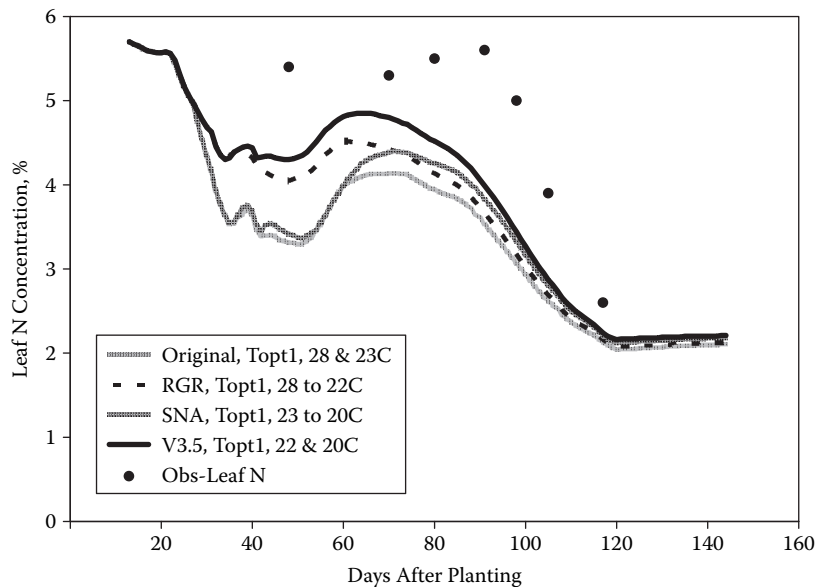


FIGURE 2.11. Simulated leaf N concentration for Kenwood soybean grown in Ames, Iowa, in 1995 with different temperature functions affecting nodule RGR or nodule SNA. [Observed data are from Sexton et al. (1998).]

in those fields was much less than observed growth, and simulated leaf N dipped much more than in the Sexton et al. (1998) data.

We know that soybean grows well in that location, as shown in the observed growth measurements. Therefore, as part of the recalibration for the 1998 V3.5 model release, we reduced the cardinal temperatures for the lowest limit of optimum temperature (Topt1) for RGR from 28°C to 22°C, and for SNA, the Topt1 from 23°C to 20°C (Sexton et al. 1998). Figure 2.10 shows the values for temperature sensitivity of nodule growth and SNA currently used in V3.5 and V4.0 model releases, which resulted in the improved simulation (see solid line for V3.5–4.0) of leaf N concentration (Figure 2.11), leaf nonstructural carbohydrate (Figure 2.12), nodule mass (Figure 2.13), and crop N accumulation (Figure 2.14).

Our goals in setting these cardinal temperatures were to hold nodule mass at a maximum of 200 to 300 kg ha⁻¹, to minimize the drop in leaf N concentration, to limit the carbohydrate accumulation to less than about 25%, and to mimic the actual dry-matter growth rate observed in those fields where soybean grew well (Sexton et al. 1998; Sau et al. 1999). While Sau et al. (1999) also tested other temperature-dependent functions such as photosynthesis, they found the temperature effects on nodule RGR and SNA were the dominant temperature-response functions with respect to effects on dry-matter growth and yield.

We also learned that the modification of those temperature functions on RGR and SNA had to be balanced. Poor model behavior, such as lower leaf N concentration (Figure 2.11) or high leaf carbohydrate accumulation (Figure 2.12) remained even if we only reduced the Topt1 for SNA. Excessive simulated nodule growth

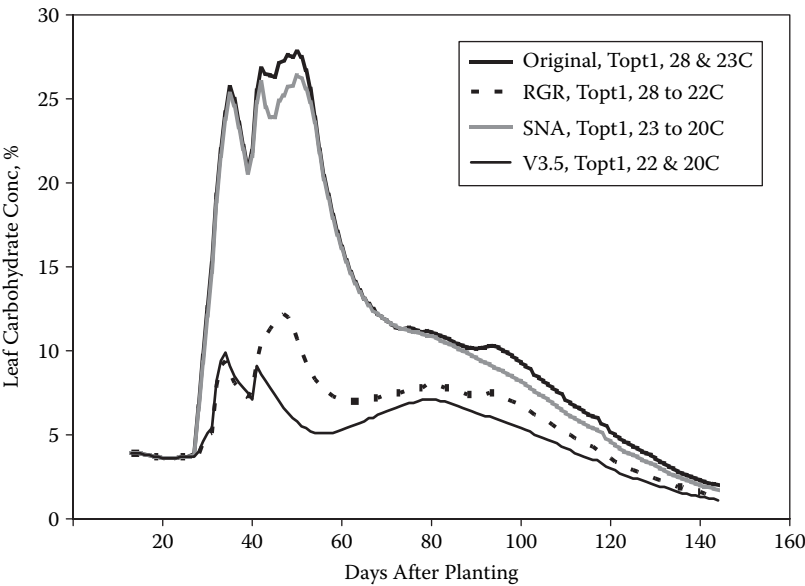


FIGURE 2.12 Simulated leaf nonstructural carbohydrate concentration for Kenwood soybean grown in Ames, Iowa, in 1995 with different temperature functions affecting nodule RGR or nodule SNA.

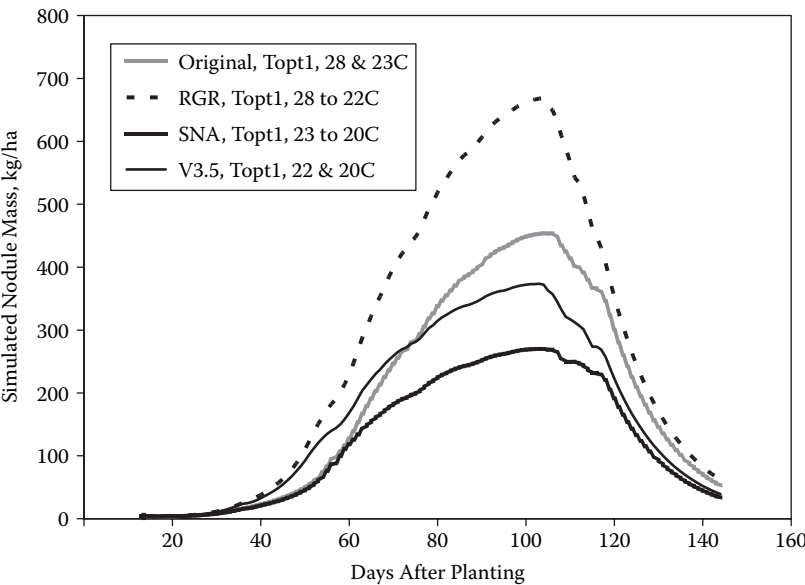


FIGURE 2.13 Simulated nodule mass for Kenwood soybean grown in Ames, Iowa, in 1995 with different temperature functions affecting nodule RGR or nodule SNA.

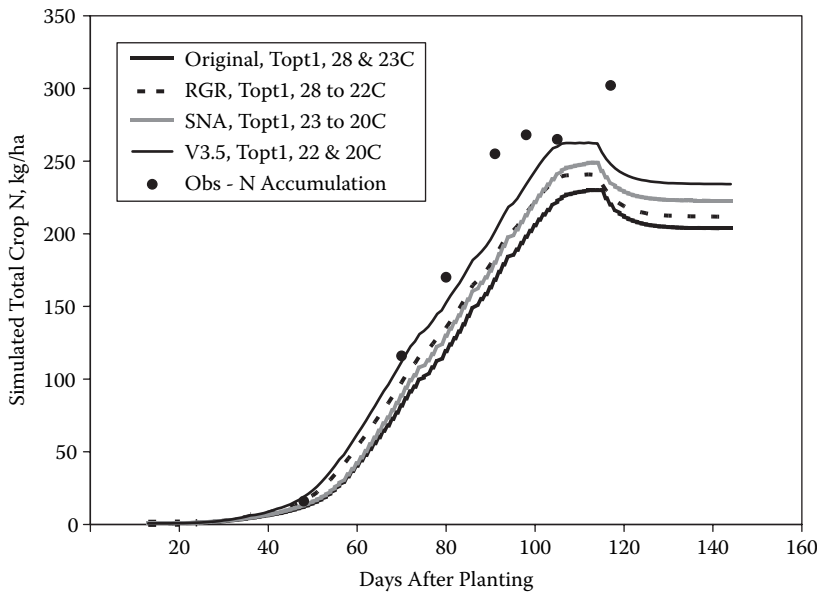


FIGURE 2.14 Simulated and observed total crop N accumulation for Kenwood soybean grown in Ames, Iowa, in 1995 with different temperature functions affecting nodule RGR or nodule SNA. [Observed data are from Sexton et al. (1998).]

as large as 1000 kg ha⁻¹ occurred if we only reduced the Topt1 for RGR (Figure 2.13). But combining the changes to both temperature functions gave more balanced behavior and increased yield by 362 kg ha⁻¹, biomass by 612 kg ha⁻¹, leaf area index by 0.59 units, and harvest index by 0.009, and improved the prediction of N accumulation for the Iowa soybean data sets (Figure 2.14).

2.2.6 COMPARATIVE ANALYSIS OF TEMPERATURE SENSITIVITIES OF DIFFERENT GRAIN LEGUMES

Since the CROPGRO model simulates a number of different grain legumes, there is a similar problem of how to estimate the temperature sensitivities and other parameters for the various legumes in the absence of data. Data limitations forced the same type of sensitivity analyses for the other legumes to ensure reasonable early season growth, nodule mass, minimal decline in leaf N concentration, and carbohydrate accumulation under various scenarios of soil N supply and soil temperature (climatic regions). Boote et al. (2002) reviewed how the process was done during the modification of the CROPGRO model for the ability to predict growth and yield of faba bean. They showed data on nodule mass and leaf N concentration predictions of faba bean in that paper. Table 2.1 shows comparative cardinal temperatures for nodule growth rate and specific nitrogenase activity for the grain legume species simulated by the CROPGRO model. It is important to note that faba bean is a cool-season, somewhat frost-hardy grain legume grown in the winter season, while dry bean and soybean are relatively cool-tolerant species, and peanut and velvet bean are warm-season legumes. The cardinal temperatures reflect these differences.

TABLE 2.1
Cardinal Temperatures for Nodule Growth Rate and Specific Nitrogenase Activity for Several Crops Simulated by the CROPGRO V4 Grain Legume Model

Crop	Temperature (°C)							
	Nodule Growth Rate				Specific Nitrogenase Activity			
	Tbase	Topt1	Topt2	Tceiling	Tbase	Topt1	Topt2	Tceiling
Faba bean	1	16	25	40	1	16	25	40
Dry bean	6	21	35	44	4	19	35	44
Soybean	7	22	35	44	5	20	35	44
Cowpea	7	22	35	44	5	20	35	44
Peanut	9	25	34	44	7	23	34	44
Velvet bean	7	26	35	44	5	23	35	44

2.2.7 SENSITIVITY ANALYSIS: EFFECT OF SOURCE:SINK RELATIONS ON N FIXATION

It is also important to document that simulated nodule growth and N fixation respond realistically to variation in source supply (light, CO₂, insect defoliation) as well as variation in sink strength, such as insect depodding, that may occur under field conditions. Therefore, we evaluated how the CROPGRO-Soybean model performed relative to the published data of Lawn and Brun (1974), who measured nodule mass and N fixation under these treatments. They sowed Clay (MG 0) and Chippewa (MG I) soybean cultivars at 25 plants m⁻² in 0.5-m row spacing on 28 May 1974 at Saint Paul, Minnesota. The Waukegan silt loam soil, having 1.5% organic carbon, was amended with 11,200 kg ha⁻¹ of corn cobs one month prior to sowing to immobilize mineral N to ensure complete reliance of the soybean crop on N fixation. The DSSAT soil organic matter module (Godwin and Singh 1998) linked to CROPGRO simulated that there was no net release of mineral N until the end of the season, in general agreement with aims of the researchers. On 11 August, four source:sink treatments were applied:

- 1. supplemental light (12,500 lux all day long, estimated equal to 4.5 MJ m⁻² d⁻¹)
- 2. partial shade (50%)
- 3. partial depodding (50%, although the net amounted to 25%)
- 4. partial defoliation (60%)

Figures 2.15A and 2.15B illustrate model simulations of N fixation over time for these five treatments on both cultivars. Data were converted from acetylene reduction per plant to N₂-fixation rate per unit land area, using the plant population and the same conversion assumptions as described for the data of deVries et al. (1989a, 1989b). The simulated nodule mass was more than 500 kg ha⁻¹ (data not shown), which was nearly twofold higher than observed (assuming 20% dry matter for fresh nodules). Possibly the temperature adjustments on nodule mass and N fixation need further modification, as this is a cool location. The simulated N fixation was 5 to 6 kg N ha⁻¹ d⁻¹ and was comparable to that observed (Figure 2.15). The model per-

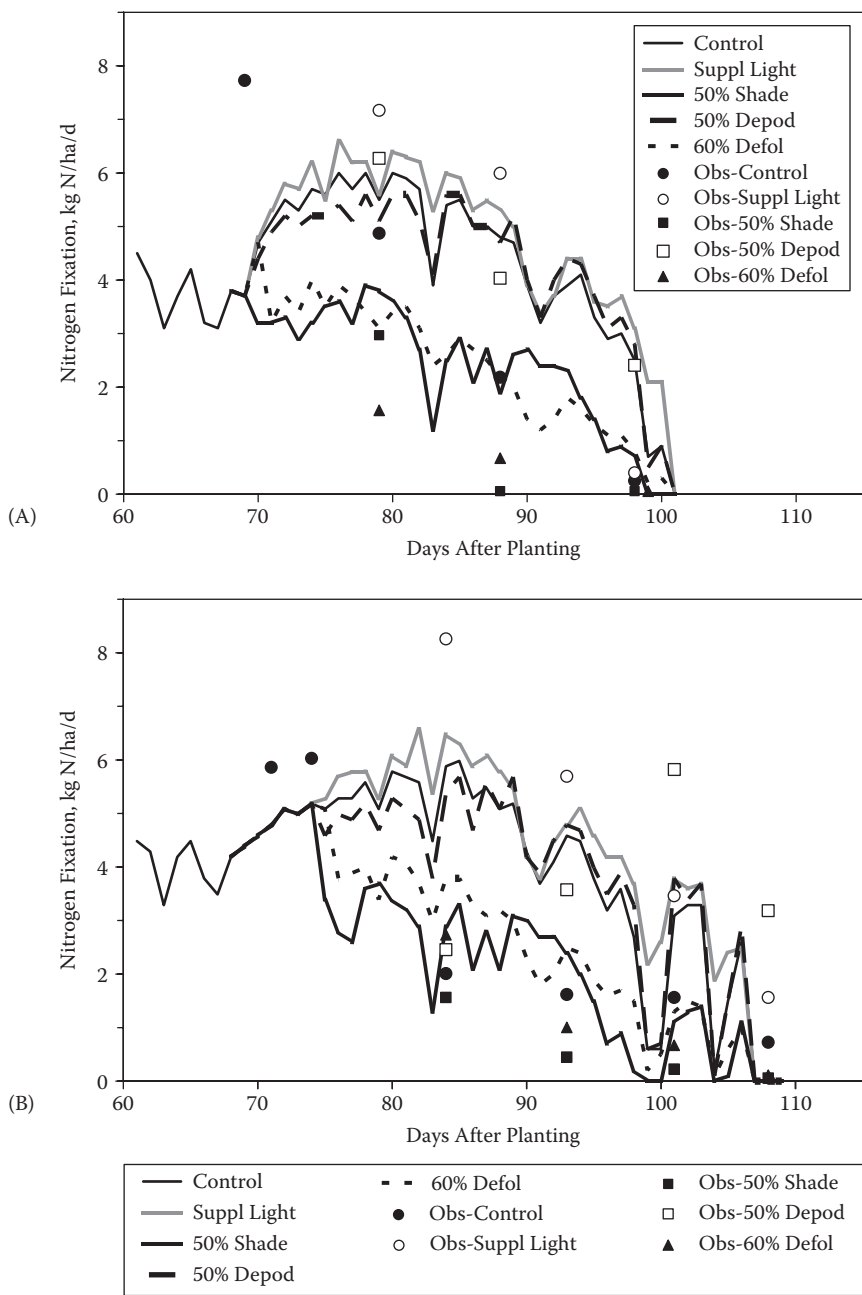


FIGURE 2.15 Simulated rate of N fixation of: (A) Clay and (B) Chippewa Upper soybean sown on 28 May 1974 at Saint Paul, Minnesota, and exposed to five source:sink treatments on 11 August: (1) control, (2) supplemental light (12,500 lux all day long, equal to 4.5 MJ m⁻² d⁻¹), (3) partial shade (50%), (4) partial depodding (50%), and (5) partial defoliation (60%). [Points are observed data from Lawn and Brun (1974).]

formed generally as expected in response to variation in source (supplemental light, shading, and defoliation), with better maintenance of N fixation with supplemental light, and severe rapid reductions under shading and defoliation. While the observed depodding treatment enhanced N fixation, the simulated depodding initially did not enhance N fixation because of lack of sink tissues, but later N fixation was higher.

2.2.8 SENSITIVITY ANALYSIS: GROWTH AND YIELD RESPONSE TO APPLIED N FERTILIZATION

Another important sensitivity analysis was to evaluate seed yield response to applied N fertilizer, to document the consistency of response, and to verify that simulated soybean seed yield is not increased too much by fertilizer N application. This was done to mimic the reality that exists in field situations where nodulation is effective. It was important to set the N-fixation responsiveness of the legume model such that it did not show any “stumbles,” i.e., reduced growth rates or low leaf N situations for variable initial soil mineral N, for variable N fertilization, or for variable soil N mineralization situations. Having robustness of this response is important to modeling of soybean growth because model users typically do not know the residual mineral N in a soil, and they may have a poor description of the amount of N mineralized over time for their particular soil. This robust model response of N fixation in a very-low-N sandy soil in Florida was illustrated in Figures 2.2 through 2.9. Robust response to soil water deficits (Figures 2.4 to 2.9) and regional variation in temperature (Figures 2.10 to 2.14) were shown. Figure 2.16 illustrates the CROPGRO-Soybean model response to application of N fertilization on Millhopper fine sand soil in Florida. Soybean grain yield was increased from 3650 to about 3860 kg ha⁻¹ as N fertilizer increased from zero to 640 kg N ha⁻¹. There are two reasons the soybean model predicted this small 5%–6% yield increase with high N fertilization:

1. The cost of nitrate reduction is less than the cost of N fixation (5.36 versus 7.06 g carbohydrate [g N fixed]⁻¹)
2. The extra N uptake allows leaf N to increase slightly as in luxury consumption above the N concentrations of a strictly N-fixing soybean plant (Figure 2.17), and this additional N both increases photosynthesis and maintains photosynthesis longer when plants mobilize N during seed-filling

The simulations show delayed onset of nodule growth and N fixation with higher N fertilization application (Figure 2.18). For this sandy soil, the simulated uptake of “native” mineral N coming from soil organic matter mineralization was only 16 kg N ha⁻¹, which is very small compared with 331 kg N ha⁻¹ from N fixation. For a higher organic matter soil in the midwestern United States, simulated mineral N uptake would be much higher.

With these modifications, the CROPGRO model potentially can simulate the amount of N fixed in most fields in the midwestern United States, with the proviso that the prediction is only as good as the user’s description of the initial mineral N (nitrate and ammonium), the soil organic matter (SOM) concentration, and the appropriate fractionation of SOM into the three pools of soil organic matter to

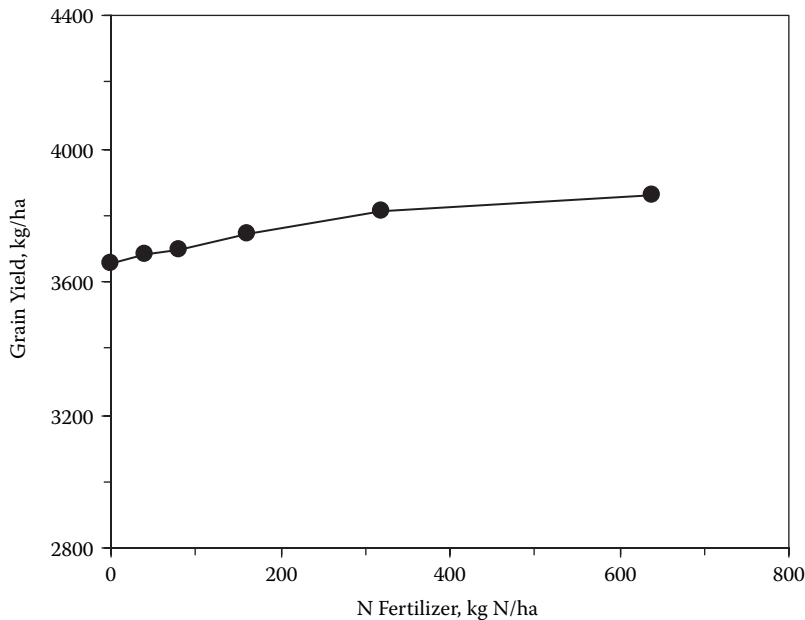


FIGURE 2.16 Simulated grain yield of Bragg soybean in response to N fertilization on Millhopper fine sand soil in Gainesville, Florida, with 1979 weather.

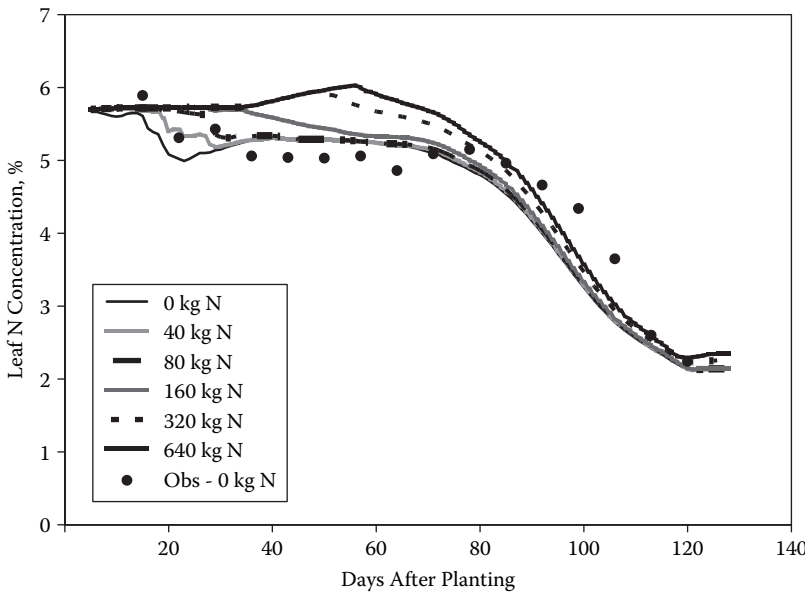


FIGURE 2.17 Simulated leaf N concentration over time for Bragg soybean in response to N fertilization on Millhopper fine sand soil in Gainesville, Florida, with 1979 weather. This shows luxury uptake where fertilizer N is applied. Observed leaf N concentration values are for unfertilized control.

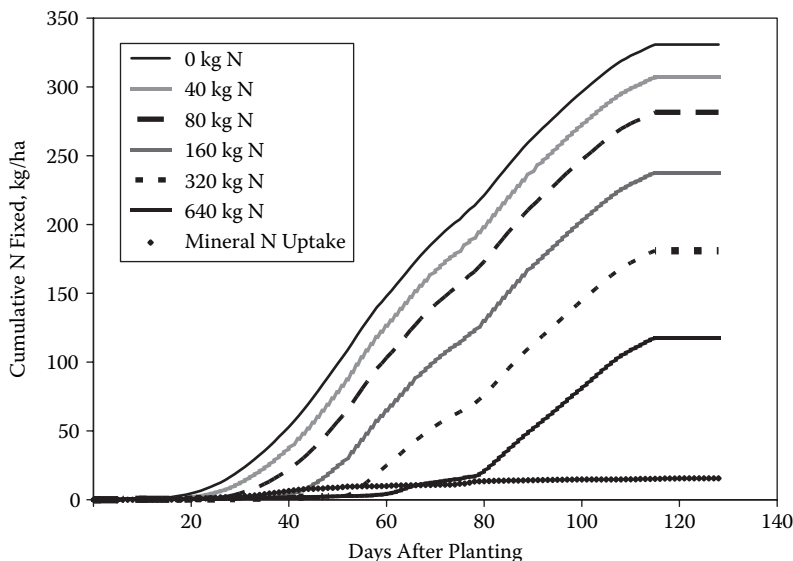


FIGURE 2.18 Simulated cumulative N fixation over time for Bragg soybean as affected by N fertilization on Millhopper fine sand soil in Gainesville, Florida, with 1979 weather. The dashed line is the simulated mineral N uptake without N fertilizer application.

adequately simulate the CENTURY SOM module that is linked to the DSSAT crop models (Gijssman et al. 2002).

2.2.9 ROBUSTNESS FOR DIFFERENT GRAIN LEGUMES, SOILS, AND CLIMATE CONDITIONS

The CROPGRO-Legume model has been tested extensively and been found to work well with N fixation “turned on” under low N fertilization and low N soils for 40 to 50 data sets on soybean, 30 or more on peanut, and 12 or more on faba bean. Nearly all of these data are for legumes grown without fertilizer N, but only a few have data on actual nodule growth or N fixation. The 1984 Bragg data, including nodule mass, N fixation, N concentrations, and N accumulation, are part of the DSSAT V4.0 database (Jones et al. 2003). The N-fixation and nodule mass data for the 1980 Bragg study (Albrecht et al. 1984) and the Minnesota study of Lawn and Brun (1974) are not yet in that database. In the case of faba bean, Boote et al. (2002) tested simulations of treatments relying on only N fixation compared with N fertilization only and found that the model worked well under both situations. Parameterizations of the cardinal temperatures for nodule growth and specific activity of faba bean are, of course, very different. The model has also been used successfully for simulating chickpea, cowpea, and velvet bean under N-fixing situations. While the model will simulate adequate N fixation for dry bean under N limitation, we are less certain that this approach is correct for dry bean, which is generally considered to be a poor N-fixing plant. In most available studies, N fertilizer was applied, and for this reason, the simulations were usually made with N considered nonlimiting.

2.3 SUMMARY AND FUTURE IMPROVEMENTS

In summary, we attempted to model N_2 fixation as mechanistically as practical in the CROPGRO model by considering explicit nodule growth and specific nitrogenase activity. The strategy is built around carbohydrate being sent to nodules for N fixation and/or nodule growth if today's N supply is deficient. Some of the lessons we learned along the way, with sensitivity analyses and by comparison with data, show that to properly simulate N fixation:

1. The processes need to be on a land-area basis.
2. There is a zero thermal lag time from emergence to initializing nodule mass.
3. There needs to be a direct partial allocation of assimilate to nodules to minimize lags and ensure minimal nodule growth.
4. Temperature functions can be solved by comparison with dynamics of processes under cool soil regions when there is insufficient data to minimize the extent of leaf N decline and leaf carbohydrate accumulation.
5. Nodules need first priority for assimilate over seeds.
6. Water stress must be based on plant water status rather than nodule-zone soil water.
7. If water stress limits nitrogenase activity, only a small fraction of the "carryover" carbohydrate sent to nodules can be used for nodule growth.
8. Responsiveness to low or high soil mineral N and fertilizer N must be programmed such that lags in nodule growth, N fixation, and crop growth are minimized.
9. The benefit of N fertilization on yield must mimic the rather minor benefit observed in field situations.

Future improvements are needed to include the effects of soil pH on nodulation, nodule growth, and N fixation. The crop models do not yet consider soil pH or salinity effects on growth and yield. Flooding effects also need to be better parameterized and considered. There is a strategy (and input) in the model to set degree of "ineffective" versus "effective" nodulation, but it is limited to a decimal value between 0 and 1, and it has not been tested well for such intermediate cases. This is needed for dry bean cultivars and some peanut cultivars.

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APPENDIX 2.1*

A2.0 NITROGEN FIXATION (NFIX)

Subroutine NFIX calculates nitrogen fixation by nodules and is called if both the ISWNIT (nitrogen simulation) and ISWSYM (nitrogen fixation) switches are set to “Y.” The routine contains sections for data “Run Initialization,” “Seasonal Initialization,” and “Rate/Integration,” and is thus called three times from the CROPGRO routine. Table A2.1 lists input parameters used by NFIX, and Table A2.2 lists input and output arguments used by NFIX.

A2.1 RUN INITIALIZATION

Table A2.1 lists input parameters that are read from FILEIO and FILEC by the NFIX routine. Variable definitions and units can be found in Appendices Q and I of the DSSAT V4 documentation. The input data includes curve information for determining the effect of temperature, canopy age, dry soil, and wet soil on N fixation and nodule growth rates.

A2.2 SEASONAL INITIALIZATION

Several variables are set to zero at the beginning of each season of simulation in the “Seasonal Initialization” section.

A2.3 RATE/INTEGRATION

The N₂ fixation component in CROPGRO has been changed considerably since the earlier versions in 1992–1993. There is a thermal-time requirement for initiating first-nodule mass. When N uptake is sufficient, nodule growth is slow, receiving a minimum fraction (bypass flow) of the total assimilate that is allocated to roots.

TABLE A2.1
Input Parameters Read by NFIX Routine

FILEIO Parameters (e.g., DSSAT30.INP):			
	EFINOC	EFNFIX	
FILEC Parameters (e.g., SBGRO030.SPE):			
CNODCR	FNFXW	PRONOD	TYPFXD
DWNODI	FNNGT	RFIXN	TYPFXT
FNFXA	NDTHMX	SNACTM	TYPFXW
FNFXD	NODRGM	TYPFXA	TYPNGT
FNEXT			

* Reprinted from pp. 44–47, DSSAT V4 Crop Growth and Partitioning Module (Boote et al. 2004).

TABLE A2.2
Interface for NFIX Routine

Variable Name	Definition	Units
Input Arguments		
AGRNOD	CH ₂ O requirement for nodule growth	g[CH ₂ O]/g[nodule]
CNODMN	Minimum CH ₂ O reserved for nodule growth	g[CH ₂ O]/m ² /day
CTONOD	CH ₂ O to allocate to nodules to fix N needed for reproductive and vegetative growth	g[CH ₂ O]/m ² /day
DLAYR(L)	Soil depth in layer L	cm
DXR57	Relative time between first seed (NR5) and physiological maturity (NR7)	—
FILECC	Pathname plus filename for SPE file	—
FILEIO	Filename for INP file	—
NLAYR	Number of soil layers	—
NR7	Day when 50% of plants first have yellowing or maturing pods	days
PLTPOP	Plant population	# plants/m ²
SAT(L)	Saturated soil water content in layer L	cm ³ /cm ³
ST(L)	Soil temperature by soil layer	°C
SW(L)	Soil water content in layer L	cm ³ /cm ³
TURFAC	Water stress factor for expansion	—
YRDOY	Current day of simulation	YYDDD
YRSIM	Beginning date of simulation	YYDDD
Output Arguments		
CNOD	CH ₂ O used in N fixation and nodule growth (including respiration costs) today	g[CH ₂ O]/m ² /day
DWNOD	Nodule mass	g[nodule]/m ²
DWNODA	Nodule mass	g[nodule]/m ²
NDTH	Nodule death rate	g[nodule]/m ² /day
NFIXN	Amount of N fixed during the day	g[N]/m ² /day
NODGR	New nodule growth	g[nodule]/m ² /day
SENNOD	Daily senesced matter from nodules in soil layer L	kg[dry matter]/ha
WTNFX	Cumulative weight of N fixed	g[N]/m ²

When N uptake is deficient (less than N demand) for growth of new tissues, carbohydrates are used for N₂ fixation to the extent of the nodule mass and the species-defined nodule-specific activity. If nodule mass is insufficient, then assimilates are used for nodule growth at a rate that is dependent on soil temperature and species-defined nodule relative growth rate. The N₂-fixation rate is further influenced by soil temperature, soil water deficit, soil aeration (flooding), and plant reproductive age. The N₂-fixation process is decreased as the plant water stress factor (TURFAC) is decreased below a species-dependent value.

The first call to the “Rate/Integration” section of NFIX occurs when plant development has reached a specified physiological age (VSTAGE greater than TTFIX). On this first call, the nodule mass is initialized based on user-supplied initial nodule mass (DWNODI) and the current plant population (PLTPOP).

Next, three factors (ACSTF, ACSTG, and FLDSUM) are summed over the layers of the soil profile. These factors affect the N-fixation rates and/or nodule growth rates. All three are computed using the CURV function, which returns a factor between 0.0 and 1.0 based on four critical curve definition points. ACSTF is a soil temperature factor that affects potential and actual N-fixation rates. ACSTG is a soil temperature factor that affects nodule growth rate. FLDSUM is related to excess soil moisture and affects N-fixation rates.

```
ACSTF = ACSTF + DLAYR(I) * FLAYR *
CURV(TYPFXT, FNFXT(1), FNFXT(2), FNFXT(3), FNFXT(4), ST(I))
```

```
ACSTG = ACSTG + DLAYR(I) * FLAYR *
CURV(TYPNGT, FNNGT(1), FNNGT(2), FNNGT(3), FNNGT(4), ST(I))
```

```
EPORS = MAX(SAT(I) - SW(I), 0.0)
FLDSUM = FLDSUM + DLAYR(I) * FLAYR *
CURV(TYPFXW, FNFXT(1), FNFXT(2), FNFXT(3), FNFXT(4), EPORS)
```

These factors are then divided by DNOD, the depth of the nodule zone, to yield the nodule growth and fixation factors, TNFIX, TNGRO, and FLDACT:

```
TNFIK = ACSTF / DNOD
TNGRO = ACSTG / DNOD
FLDACT = FLDSUM / DNOD
```

Other factors that are computed are SWFACT, a drought factor based on TURFAC (water stress factor), and NFXAGE, which determines the effect of canopy age on N growth rates:

```
SWFACT = CURV(TYPFXD, FNFXT(1), FNFXT(2), FNFXT(3),
FNFXT(4), TURFAC)
```

```
NFXAGE = CURV(TYPFXA, FNFXT(1), FNFXT(2), FNFXT(3),
FNFXT(4), DXR57)
```

A running average of the last 8 days of water deficit factor (SWFACT) is kept. Both the 8-day average and the current day's value of SWFACT are used to reduce the N-fixation rate.

CLEFT is a running value of CH₂O left over as the various processes occur in the following order:

1. Set aside a minimum (CNODMN) for nodule growth,
2. Fix N₂,
3. Grow nodule mass with any CH₂O not used.

The CH_2O left for nodule growth after N fixation is:

$$\text{CLEFT} = \text{CTONOD} - \text{CNODMN}$$

The specific nodule activity (SNACT) is computed taking into account the maximum activity of the nodules (SNACTM) and strain effects (EFNFIX) for N fixation plus the amount CNODMN (except in the case where N_2 fixation was limited by water deficit).

The nodule death rate, RNDTH is computed as a function of the soil water deficit factor (SWFACT), soil water excess factor (FLDACT), and carbon deficit factor (CNFACT):

$$\begin{aligned} \text{RNDTH} &= \text{NDTHMX} * \text{MAX}((1. - \text{FLDACT}), (1. - \text{SWFACT}), \\ &\quad (1. - \text{CNFACT})) \\ \text{NDTH} &= \text{MIN}(1.0, \text{RNDTH}) * \text{DWNOD} \end{aligned}$$

NDTHMX is the maximum nodule death rate for flooded or dry soil conditions. NDTH is the nodule death rate per unit area.

If physiological maturity has not been reached ($\text{DAS} < \text{NR7}$), potential N fixation is computed

$$\text{PNFIXN} = \text{MIN}((\text{CLEFT} * 0.16 / \text{RFIXN}), (\text{DWNOD} * \text{SNACT})) * \text{TNFIX}$$

RFIXN is defined as the respiration required for biological N fixation in $\text{g}[\text{CH}_2\text{O}]/\text{g}[\text{protein}]$. The 0.16 factor converts from $\text{g}[\text{protein}]$ to $\text{g}[\text{N}]$. TNFIX is the soil temperature factor affecting N fixation. So, the potential rate of N fixation is the nodule activity rate, limited by available carbon and soil temperature.

Actual N fixation, NFIXN, is computed with the soil water drought factors (SWFACT and SWMEM8) and soil water excess factor (FLDACT).

$$\text{NFIXN} = \text{PNFIXN} * \text{MIN}(\text{SWFACT}, \text{SWMEM8}, \text{FLDACT})$$

Normally, CH_2O not used for N fixation (because of limited nodule mass or activity) can be used to grow more nodule mass, thereby growing the mass needed to overcome this limitation. In the case of plant water deficit that decreases N-fixation-specific activity, we do not want the extra CH_2O to be used for nodule growth. For this purpose, we compute actual N fixation (NFIXN) limited by water deficit and potential N fixation with no water deficit (PNFIXN) and their respective CH_2O costs, CUSFIX and PCSFIX.

$$\begin{aligned} \text{PCSFIX} &= (\text{PNFIXN} / 0.16) * \text{RFIXN} \\ \text{CUSFIX} &= (\text{NFIXN} / 0.16) * \text{RFIXN} \end{aligned}$$

The amount of CH_2O not used for potential N fixation (CNOFIX) is set aside and is not used for nodule growth in the case of water stress.

$$\text{CNOFIX} = \text{PCSFIX} - \text{CUSFIX}$$

Actually, 10% of it can be used for nodule growth plus the amount CNODMN.

$$\text{CLEFT} = \text{MAX}(0.0, \text{CLEFT} - \text{CUSFIX} - 0.9 * \text{CNOFIX}) + \text{CNODMN}$$

The maximum nodule relative growth rate is reduced by EFINOC, the inoculation effectiveness (or rhizobium density factor), and EFNFIX, the strain efficiency to obtain the effective nodule relative growth rate (NODRGR).

```

IF (DAS .LT. NR7) THEN
    NODRGR = NODRGM * EFNFIX * EFINOC
ELSE
    NODRGR = 0.0
ENDIF

```

The new nodule growth rate (NODGR) is limited by either supply or demand for C.

$$\text{NODGR} = \text{MIN}(\text{CLEFT} / \text{AGRNOD}, \text{DWNOD} * \text{NODRGR}) \\ * \text{TNGRO} * \text{MIN}(\text{SWFACT}, \text{FLDACT}) * \text{NFXAGE}$$

The C required for new nodule growth today and the C used in N fixation and nodule growth (including respiration costs) today are calculated as:

$$\text{CNODGR} = \text{NODGR} * \text{AGRNOD} \\ \text{CNOD} = \text{CUSFIX} + \text{CNODGR}$$