Development of a Nitrogen Balance for Cotton Growth Models: A First Approximation[1]

J. W. Jones, J. D. Hesketh, E. J. Kamprath, and H. D. Bowen[2]

ABSTRACT

Daily growth values of cotton (*Gossypium hirsutum* L.) were calculated based on the carbohydrate balance of SIMCOT II, a simulation model of cotton growth and development. The daily N requirements for new growth of leaves, stems, roots, burrs, and seed were calculated based on maximum and minimum N concentration for these plant parts. Daily N absorption depended on the availability of N in the soil pool and new growth requirements. If the absorbed N was less than the required amount, partitioning functions determined the distribution of available N into each sink. During periods of N shortages, some N reserves were supplied for new growth from the breakdown of N compounds in the older leaves and stems. Depending on the level of N shortage, new growth was slowed, bolls and squares were abscised, and some leaves were shed.

The model shows that, based on the N balance, growth can be restricted and reproductive organs aborted after SIMCOT II runs its normal course for a day during the boll setting period. Simulated fruiting characteristics and yield curves were similar to those of real plants.

Additional index words: Modeling, Nutrition, Nitrogen stress, Partitioning function.

DUNCAN (6) developed logic for computer simulation of cotton (*Gossypium hirsutum* L.) growth and yield (SIMCOT). This model and subsequent revisions[3] shed considerable numbers of floral buds and fruit because of insufficient carbohydrate. Available carbohydrate was determined from a plant budget of daily photosynthate supply (2), the carbohydrate reserves (6), and the growth requirements (9, 10) including the energy derived from respiration needed for maintenance and growth (2).

Critics of this model suggested consideration of a daily N budget for the plant; Viets (15), in fact, anticipated a model based on both C and N budgets. In this paper we review some of the relevant literature, discuss necessary assumptions, and develop the logic for a computer simulation model for a N balance which could be inserted into SIMCOT II. In an associated paper (11), we critically analyze this computer program for the plant N budget and present a far more extensive discussion of many of the assumptions involved. The model showed that, based on the N balance, growth can be restricted and reproductive organs aborted, after SIMCOT II ran its normal course for a day during the boll-setting period, making decisions based upon a carbohydrate budget.

SUMMARY OF THE COTTON PLANT MODEL

A brief description of SIMCOT II is necessary for understanding the approach to the N balance. SIMCOT II predicts daily growth of roots, stems, leaves, and bolls. To operate the model, standard U.S. Weather Bureau daily values of rainfall, evaporation, solar radiation, and maximum and minimum temperatures are read as inputs. Planting date, row spacing, plant population, season length, geographical location, water-holding capacity of the soil, and standard daily growth increments for the various plant parts are inputs. Subroutines calculate the length of the photoperiod, the soil moisture content (depending on rainfall and evapotranspiration), the fraction of a physiological day (a variation of the degree-day concept) that occurs during the calendar day in question, and the light intercepted by the crop. Gross photosynthesis is calculated from light interception and leaf area index. The photosynthetic efficiency of the leaves is reduced during days of limiting soil moisture. Maintenance and light respiration values are calculated and subtracted from gross photosynthate which is made available for new growth of the plant parts after applying a carbohydrate-dry weight conversion factor. These relationships for photosynthesis and respiration are given elsewhere (2, 9). The distribution of net photosynthesis is based on the standard growth requirements for each plant part. If the carbohydrate supply exceeds demand, the plant accumulates reserves. If the supply is less than demand, priorities determine fruit shedding and slows the morphological development of the plant.

The model grows the plant by increasing the weights of plant parts, and by initiating new nodes on the main stem, fruiting branches, and (possibly) one vegetative branch. New nodes are initiated each 2.5 physiological days on the main stem and vegetative branch and each 6 days on fruiting branches. Temperature (as a part of the physiological day concept) and carbohydrate stresses increase the time between successive nodes (plastochrons). The daily output consists of the date, dry weight, solar radiation, squares, bolls, and a graphical schematic of the plant, showing each node and indicating whether there is a square, a boll, or no fruit at each node. SIMCOT II starts at plant emergence and ends at frost.

The model has been shown to provide favorable predictions of plant growth in preliminary comparisons with field data when moisture and nutrients were nonlimiting.

THE NITROGEN BALANCE

The logic used in developing the N balance somewhat parallels that of the carbohydrate balance. Figure 1 shows a schematic for N flow from the soil to the plants and for its distribution within the plants. Nitrogen supplied to soil through fertilizer applications and organic matter decay is stored in the soil. The organic matter decay is controlled by the soil environment (e.g. temperature, oxygen level, and moisture tension). The N uptake into the plant is controlled by the soil environment, the supply of N from the soil pool, and the plant's demand for N. If the N supply (uptake plus available reserves) is less than the demand, stress levels are set in the plant—the level of stress depending on the N reserves in the leaves, stems, and roots and on the magnitude of the N deficit. The N is then distributed to the plant parts as needed for new growth requirements and stresses. If the N supply exceeds the minimum growth requirements, the excess is added to the N reserves in the leaves, stems, and roots.

Soil Nitrogen Storage

Nitrogen available in the soil was assumed to be derived from organic matter decay and from fertilizer applications, with an initial amount of residual N. The average N concentration in organic matter was set at 5%. Thus, for each 1% of organic matter in the plow layer (24,200 kg/ha of organic matter), there is a total N content of 1210 kg/ha of which 1 to 2% becomes available over the entire growing season (1). Thus, 12.1 to 24.2 kg N/ha become available during the season for each 1% of organic matter (OM). Assuming a 160-day growing season and that an equal amount of organic matter decays each day, the average daily availability rate [D (t)] becomes:

$$D(t) = [(24.2)(1000)(OM)]/160 \text{ PPLT}$$
$$= [(151.2)(OM)(g \text{ plant}^{-1}\text{day}^{-1})]/\text{PPLT} \quad [1]$$

where PPLT = plants/ha, OM = organic matter (%), and t = day in question.
It was assumed that this organic matter N is released within the top 30.48 cm of soil.

The applied N is added to the soil pool after applying an efficiency factor which depends on the soil type and losses caused by leaching, denitrification, and volatization. For the coarse-medium- and fine-textured soils of North Carolina, 45, 55, and 65%, respectively, of the applied N was considered to be available for plant growth. (Obviously, better factors are needed). After a rainfall, the application of fertilizer increases the N in the soil pool.
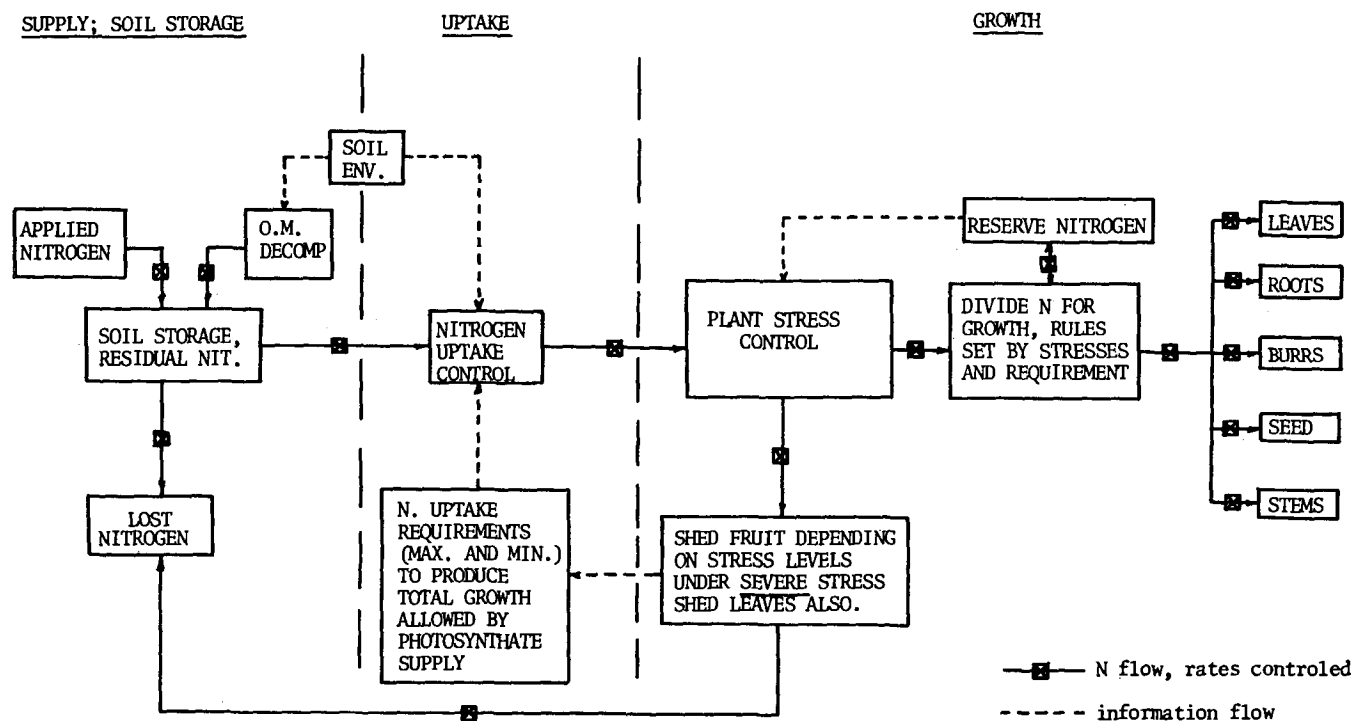
SUPPLY; SOIL STORAGE   UPTAKE   GROWTH

Fig. 1. Schematic for a N balance for a cotton growth model.

Table 1. Summary from three sources of N concentrations for cotton plant parts.

Source	N concn in plant parts									
	Leaves		Stems		Roots		Seed		Burrs	
	Early season	Late season	Early season	Late season	Early season	Late season	Early season	Late season	Early season	Late season
	%									
Bassett et al. (3)	4.2	3.0	2.0	1.0	--	--	4.2	4.0	2.0	1.0
Wadleigh (17)										
A-0.009 g N day⁻¹ plant⁻¹	2.7	1.7	0.9	0.4	0.8	--	--	2.3	--	0.7
B-0.0275 g N day⁻¹ plant⁻¹	3.2	2.3	1.2	1.1	1.0	--	--	2.7	--	1.0
C-0.0825 g N day⁻¹ plant⁻¹	3.9	2.7	1.3	1.2	1.3	--	--	2.9	--	1.5
D-0.245 g N day⁻¹ plant⁻¹	4.0	2.9	1.4	1.4	1.5	--	--	2.9	--	2.3
Morrison* (12)	--	2.4	--	0.9	--	--	--	--	--	1.4†

* No values were given for early or late concentrations. † Reported value is for bolls, including lint, seed, and burrs.

The N available in the soil on day (t) can be summarized as follows:

$$SN(t) = SN(t-1) + D(t) + E_t[AP(t)]/100 - UPTK(t-1) \qquad [2]$$

where $SN(t)$ = soil nitrogen in the soil pool on day (t) (g/plant), E_t = application efficiency (%), $AP(t)$ = amount of fertilizer applied on day (t) (g/plant), and $UPTK(t-1)$ = amount of nitrogen assimilated on the previous day (g/plant).

Nitrogen Uptake

The daily N uptake per plant was determined by N supply from the soil, demand of N for new growth, and maximum daily plant absorption for the existing conditions. The N supply was partially described by soil storage. During early growth, the root volume of the plant was considered to determine the supply of organic matter N to the plants. The available soil volume per plant (VT) and for the top 30.48 cm. was calculated by:

$$VT = (W)(L)(12)(2.54)cm^3 \qquad [3]$$

where W = row spacing (cm), and L = average distance to adjacent plants (cm). To determine the fraction of total soil volume in contact with the roots, a simple root-growth model was developed, based on data from Bassett, Stockton, and Dickens (4), and Hall et al. (7). Depth of root penetration was assumed to occur at a rate of 30.48 cm/4 weeks and lateral growth at a rate of 30.48 cm/6 weeks. The root volume VPLT (t) on day (t) was calculated by:

$$VPLT(t) = WPLT(t)LPLT(t)DPLT(t) \qquad [4]$$

for $WPLT(t) \leq W$, $DPLT(t) \leq 30.48$ cm, and $LPLT(t) \leq L$; where $WPLT(t)$ = length of lateral roots toward center of row (cm), $DPLT(t)$ = depth of tap root (cm), and $LPLT(t)$ = length of lateral roots toward next plant in the row (cm). The ratio $VPLT(t)/VT$ was formed to reduce the maximum available N from daily organic matter decay early in the season. The N from organic matter that was not available to the plant was added to the soil pool for later use. When fertilizer is applied at planting or residual N is present, this reduction will have little effect on the plant.

The demand for N was calculated from growth of leaves, stems, roots, and bolls by SIMCOT II. Table 1 summarizes data from three sources (3, 12, 16), on the N concentrations of cotton plant parts. These data agree with other reports (14) that the N concentration of the cotton plant is relatively high early in the season and decreases later in the season. The N concentration in the seed is relatively constant throughout the season. It was assumed that, as long as the absorption rate and supply were nonlimiting, the plant would maintain concentrations at the early-season or maximum level. Also, it was assumed that a minimum concentration is required in each plant part in order for it to grow. Table 2 shows the maximum values of (early season) and minimum (late season) N concentrations for various plant parts used in the model. It was assumed that there would be negligible amounts of N in the lint.

The N requirements are set by the new growth calculated by carbohydrate supply and based on the maximum concentrations for each plant part for the new growth for the day (t). The total plant requirement for the day (REQ(t)) is:

$$REQ(t) = \sum_{i=1}^{6} (M_i)[dW_i(t)] \qquad [5]$$

Table 2. Values of maximum and minimum N concentrations for various plant parts used in the model.

Plant part	N concn (g/g dry basis)	
	maximum (M_i)	minimum (m_i)
Leaves (i = 1)*	0.042	0.020
Seed (i = 2)	0.040	0.040
Burrs (i = 3)	0.020	0.007
Stems (i = 4)	0.020	0.009
Roots (i = 5)	0.015	0.008
Lint (i = 6)	0.000	0.000

* The variable i is used to identify each plant part.

where i = plant part (leaves, stems, etc.), M_i = maximum nitrogen concentration of the ith plant part (g/g, dry basis) and dW_i = growth for the day for the ith plant part set by the carbohydrate balance (g).

The N assimilation during a day then is REQ(t), unless the daily maximum absorption rate is less than REQ(t) and provided the supply in the soil pool is adequate. A(t) is the maximum allowable absorption rate for day (t), SN(t) is the amount of N in the soil pool, and UPTK(t) is the amount of N assimilation by the plant from the soil. Then

$$UPTK(t) = minimum [REQ(t), A(t), SN(t)] \qquad [6]$$

The literature was searched to find suitable data for A(t). Table 3 gives values of daily N absorption rates (g/plant/day) from Henderson (8). These values were calculated from cotton crops grown in Norfolk soil during periods of adequate soil moisture content. The average N absorption rate was 0.0516 g plant⁻¹ day⁻¹. Olson and Bledsoe's data (13) indicate that daily absorption rates were 0.08 and 0.059 g plant⁻¹ day⁻¹ during the heavy fruiting period on cotton grown in Cecil Sandy Loam two successive years. Wadleigh (16) supplied water and N to plants daily and found that when he supplied 0.0825 g N plant⁻¹ day⁻¹ (Table 4, Treatment C), absorption rate for his plants was 0.080 g N plant⁻² day⁻¹ and when he supplied 0.245 g plant⁻¹ day⁻¹ (treatment D), the absorption rate was 0.091 g plant⁻¹ day⁻¹.) (Plant population for these tests was equivalent to 14,826 plants/ha. The daily absorption rate by the plant's roots depends on factors such as plant population, soil moisture content, root volume, and nitrogen concentration. Since no data were found that develop such relationships, it was assumed for the model that the daily absorption rate for good soil moisture conditions and adequate N concentration is 0.0516 g plant⁻¹ day⁻¹ for 49,420 or more plants/ha increasing to 0.091 g plant⁻¹ day⁻¹ for populations of 14,826 plants/ha or less. If GA(t) is the maximum absorption rate per plant under favorable conditions. then:

$$GA(t) = \begin{cases} .091 \text{ g day}^{-1} \text{ plant}^{-1} \\ \quad \text{if } 0 < PPLT < 14{,}826 \\ .091 - 0.282 \times 10^{-4} \text{ (PPLT-14,} \\ \quad 826) \text{ g day}^{-1} \text{ plant}^{-1} \\ \quad \text{if } 14{,}826 < PPLT < 49{,}420 \\ .0516 \text{ g day}^{-1} \text{ plant}^{-1} \\ \quad \text{if } 49{,}410 < FPLT \end{cases} \qquad [7]$$

If the concentration of N in the soil pool (averaged over the rooting depth) dropped below a certain level, it was assumed that N absorption by roots would be reduced. The following relationship was developed:

$$A(t) = \begin{cases} GA(t) [C(t)]/\alpha \text{ if } C(t) \leq \alpha \\ GA(t) \text{ if } C(t) > \alpha \end{cases} \qquad [8]$$

where $C(t)$ = concentration of N in the soil pool on day (t) (g N/g water) and α = N concentration below which the N absorption rate would be reduced.

Table 3. Average daily N absorption rates from Henderson (9).

	N absorption rate					
	Days after planting					
Year	60	70	80	90	100	110	Avg*
	g N/plant/day						
1966	0.045	--	0.015	0.090	.090	0.080	0.058
1967	0.031	0.090	0.018	0.029	--	0.060	0.046

* Avg = 0.0516 g N plant^{-1} day^{-1}.

Table 4. Comparison of simulated plant characteristics with data from Wadleigh (17) for daily N supply rates.

Treatment (Daily supply rate)		Main stem nodes	Open bolls	Fruit/top dry weight ratio (Aug. 10)
A (0.009 g N day^{-1} plant^{-1})	Wadleigh	18	5.3	0.95
	Simulated	21	4.0	0.38
B (0.0275 g N day^{-1} plant^{-1})	Wadleigh	21	10.1	0.80
	Simulated	24	13.0	0.65
C (0.0825 g N day^{-1} plant^{-1})	Wadleigh	25	18.6	0.68
	Simulated	32	18.0	0.54
D (0.245 g N day^{-1} plant^{-1})	Wadleigh	29	23.1	0.71
	Simulated	32	18.0	0.54

Using this relationship absorbed N is decreased by low soil moisture levels and by low N concentrations in the soil solution.

NITROGEN IN THE PLANT

The N is taken from the soil on day (t) at the amount of UPTK (t) and absorbed into the plant. If UPTK (t)≥REQ (t), or, in other words, if the N supply is greater than or equal to the demand, the N is added to the N levels of various plant parts at the rate of $M_i dW_i$ (t). Thus, nitrogen is not a limiting factor for new growth. The N in each plant part on day (t) is defined by N_i (t), and the reserve nitrogen RESN (t) is defined as:

$$RESN (t) = \sum_{\substack{i=1 \\ i \neq 2}}^{6} (N_i (t) - m_i W_i (t)) \qquad [9]$$

where m_i is the minimum N concentration of the ith plant part and W_i (t) is the weight of the ith plant part on day (t). In other words, we are assuming the N concentration of each plant part, except the seed, can be reduced to its minimum concentration in order to supply N for new growth when necessary. A reserve N supply factor limits the rate at which this reserve N can be used in new growth.

If the N absorption is less than demand [UPTK (t) < REQ (t)], then N is distributed for new growth in the various plant parts according to the model[4] shown in Fig. 2. (There is no data base for this part of the model). The relative utilization strength of each plant part is read as input and is assumed to be a constant rate for all N absorption values. The slope of each curve in Fig. 2 represents the relative utilization strength for each particular plant part and represents maximum percentages of N absorption that can be assimilated by each plant part when supply is limited. For example, the slope of the seed utilization curve is S_m. If the supply of N on day (t) is less than the demand, then a maximum of S_m (UPTK (t)) can be utilized by the seed. Similarly B_m (burr or boll capsule utilization rate), L_m (leaf utilization rate), ST_m (stem utilization rate), and R_m (root utilization rate) are used to distribute N within the plant on a day of N shortage, with the heaviest demand calculated first in all cases.

Nitrogen stress levels, depending on the magnitude of the the deficiency, were defined. These stress levels are used to specify plant response to N shortages. Wadleigh (16) reported that after a plant has set enough bolls to deplete its N reserves, all subsequently formed bolls abscised. Soon after, the terminal buds of the fruiting branches aborted and squares were shed. He also reported that after plants blossomed, terminal growth ceased in plants that received the lowest level of nitrogen whereas terminal growth only slowed in plants that received higher levels. Premature leaf shedding was also associated with
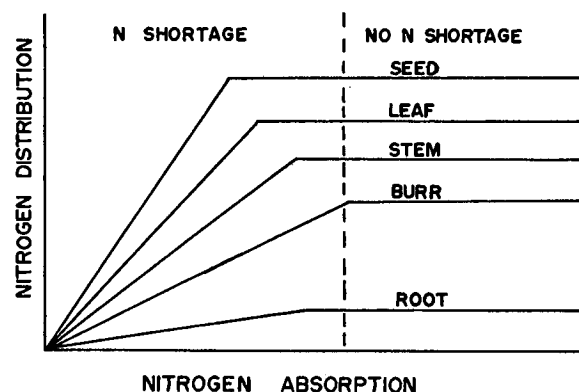
[4] This N partitioning model resulted from a discussion with Dr. Lloyd T. Evans, CSIRO, Canberra, Australia.

Fig. 2. Nitrogen distribution model showing N utilization as a function of the amount absorbed by the plant.

a N shortage. Tucker and Tucker (14) report the following N deficiency symptoms:

1. Internode elongation is reduced.
2. Number of nodes and vegetative branches is decreased.
3. Number of fruiting sites is decreased.
4. Fruiting period is decreased.
5. Yield is decreased.
6. Red pigment anthocyanin that forms in leaves when nitrogen deficiency is acute results in premature leaf shedding.

Therefore, any stress factors defined need to relate to plant responses consistently with the results reported above. Stress factors can therefore be defined as set functions that map describable events into real numbers for the purpose of quantifying the plants' responses to such events. Nitrogen stress factors were defined as follows:

Stress = 0. No N shortage stress.

Stress = 1. Not enough N was taken from the soil to keep all plant concentrations at the maximum level [UPTK (t) < REQ (t)], but all seed requirements were satisfied [M (t)dW (t) UPTK (t)]. As a result, the plastochrone increases in main shoot and vegetable branch apices, i.e., new mode initiation is slowed which results in slower vegetative growth.

Stress = 2. Not enough N is distributed to the seed to satisfy seed requirements (satisfying between 70 and 100% of the seed requirements). Reserve N may be used at a maximum rate of RESF (nitrogen reserve supply factor). Also if the N supply to the leaves is less than 10% of the leaves' requirements, *Stress* is set to 2. As a result, new square initiation is slowed by an increase in plastochrones of 20%/day; some N is taken from reserves (leaves, stems, roots), and some squares are shed.

Stress = 3. Same as *Stress 2*; however, between 35 and 70% of the boll demand is supplied. As a result, new square initiation is slowed by an increase in plastochrones of 30%/ day (which practically stops new growth), and some bolls and squares are shed. Leaf shedding (arbitrarily) occurs at a rate of one leaf/2 days. (No quantitative data were found to support this figure.)

Stress = 4. Most severe stress. This stress occurs if deficiency is greater than any listed for *Stress 1, 2* or *3*; also, if UPTK (t) is less than 10% of REQ (t). As a result, square and boll shedding is heavier, and new square initiation is stopped. Leaf shedding occurs at the rate of 1 leaf/day.

Depending on the stress level, new growth is added to the plant and N is accumulated in accordance with priorities for N as expressed in Fig. 2. Of course the plant loses N through the shedding of fruit and leaves. The simulation then goes to the next day and the process is repeated.

PRELIMINARY RESULTS

The following results are offered to show the relative effect of the N balance on some important growth measurements simulated by SIMCOT II. Wadleigh's
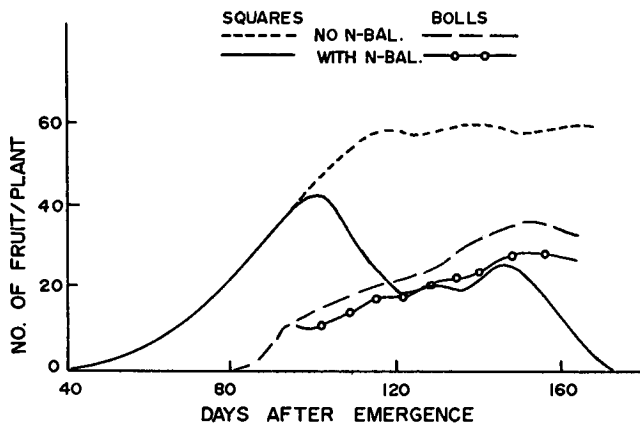
Fig. 3. Comparison of number of squares and bolls generated by SIMCOT II with and without the N balance. Plant population was 49,420/ha and N application rate was 364 kg/ha.
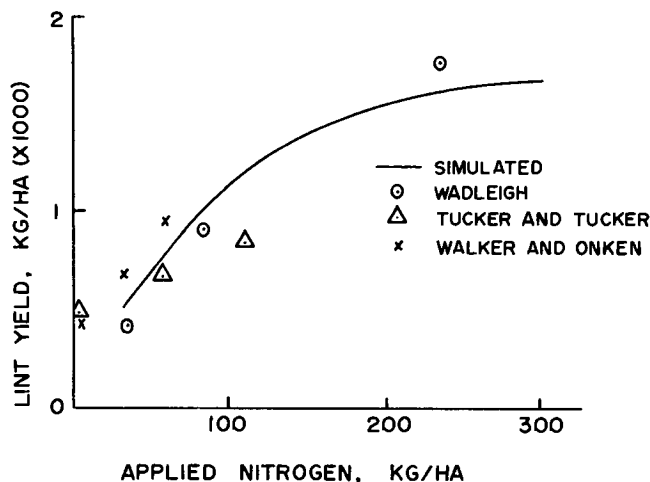

Fig. 4. Nitrogen application and yield responses for observed vs. predicted results. Water-holding capacity of soil for simulated results was 3.18 cm per one-tenth of root depth.

daily N supply rates (Table 4) were used in the model for comparing simulated growth patterns with measured plant responses. Although actual weather data were not available for the experiments, the simulated results do indicate that growth and reproduction patterns are similar for corresponding N rates. Table 4 gives comparisons for number of main stem nodes and open bolls and the fruit/top dry weight ratio. The results of simulated treatments C and D were the same, which indicates that treatment C provides sufficient N for growth and reproduction. Plants that received simulated treatments A and B were smaller, weighed less, and produced less fruit than those that received treatments C or D. Similar results were measured by Wadleigh.

A comparison is offered in Fig. 3 that shows the effect of the N balance on the fruiting of the simulated plant. The number of squares on the plant were decreased, even though the 364 kg N/ha application was more than adequate to produce the yield obtained. In this case both the N stresses caused by the limited daily N absorption rate by the plant, as well as by carbohydrate stresses, reduced the fruit on the plant to a level that the plant could support. The

fruiting pattern on the plant having the N balance more closely follows the fruiting cycle of plants observed under field conditions (5).

Fig. 4 shows a N-yield response curve for simulated vs. experimental results. The simulated curve was produced by using a heavy soil with a large water-holding capacity, no residual N, and 49,420 plants/ha. Any residual N would shift the curve to the left. Although this curve shows that yield levels off at high levels of N, it does not show a decrease in yield at very high levels. No special mechanism for that response was included in the simulation, although with lower waterholding capacities of the soil, there was a tendency for simulated yields to show this response. Yield values reported by Wadleigh (16), Walker and Onken (17), and Tucker and Tucker (14) were included on the graph to show the relative magnitudes of simulated vs. observed results.

These examples (Fig. 3 and 4) were not attempts to test the model. It is obvious that the magnitude and shape of the N yield response curve depends on the weather, soil type, residual N, cotton variety, and many other factors that were not available in sufficient detail in the literature to try to duplicate a particular set of results. However, the shapes and magnitudes of the simulated curves shows promise for this approach.

SUMMARY AND CONCLUSIONS

A brief description was given of a cotton growth model, and a N balance was developed for the cotton model. If water, carbohydrate supply, and N are all sufficient for growth, the plant grows at a standard growth rate for its environment. Water and carbohydrate stresses reduce the growth rate. Nitrogen requirements are based on the growth allowed by the carbohydrate balance. Depending on the N supply in the soil and the daily absorption rate and on the maximum and minimum concentrations of N for growth of each plant part, N is absorbed by the plant to meet the carbohydrate growth requirements. If absorbed N is less than the requirements, growth is reduced by N stresses. Carbohydrate and N stresses cause fruit shedding; severe N stress also causes leaf shedding.

It becomes important now to calibrate the model in the field, noting that the plant model has defined carbohydrate, water, and N stress terms. It will be necessary to monitor more closely the plant's response to carefully controlled levels of carbohydrate, water, and N supply throughout the season and to observe the effects of shortages of any combination of these factors. When the plant's responses to the defined stress levels are calibrated, a much better understanding of the plant's control system will be attained. To accomplish the calibration, better results will be needed for predicting daily absorption rates for N based on N concentration in the soil water, water and N flow through the soil by convection and diffusion and the absorption of water and N by the root system. More sophisticated methods for predicting denitrification, organic matter decay and leaching of soil N caused by drainage are needed. Many details were omitted in the first attempt to model the N balance, but a framework has been established. More work

should be done on defining maximum and minimum concentrations of N for plant growth, from a biochemical approach. In this work, consideration should be given to various N stress levels. Comparisons of simulation results with measured field results over a range of conditions will provide the ultimate test of merit for the N balance and the cotton plant model.

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