Published May, 1983

Application of GOSSYM to Genetic Feasibility Studies. I. Analyses of Fruit Abscission and Yield in Okra-Leaf Cottons[1]

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ABSTRACT

The cotton (*Gossypium hirsutum* L.) model GOSSYM was used to demonstrate how a computerized crop simulation model can be used in a breeding or in an agronomic research program to predict the performance of cottons such as okra leaf when grown under various environmental conditions. The GOSSYM computer simulations indicated that the higher fruit load produced in okra-leaf compared to normal-leaf cottons results from the carbohydrate (not used in leaf material) being used in the initiation of more fruiting sites. Then, as the fruit load increases late in the fruiting period, larger carbohydrate stresses develop in the okra-leaf type than in the normal-leaf crop. The plant simulated by GOSSYM balances those shortages of materials by aborting fruit. The abortion of fruit is higher in okra-leaf than in normal-leaf cotton because it develops a higher fruit load. GOSSYM predicted that the percent fruit retention in okra-leaf cottons was not correlated with N-application rate; however, as the application rate increased, the number of fruiting positions produced also increased. Increasing carbohydrate supply by increasing the photosynthetic rate by 50% improved percent fruit retention at all rates of N. Okra-leaf cottons perform inconsistently under field conditions apparently because the plants fail to produce and maintain sufficient leaf area index (LAI) to intercept enough solar radiation and provide the photosynthate required to meet the fruit growth requirements under adverse growing conditions. Under favorable growing conditions, both normal and okra-leaf types produced a dense canopy; however, the LAI was larger in the normal-leaf type. The more efficient distribution of carbohydrates into the fruits by the okra-leaf type resulted in higher yield. Under adverse conditions, the LAI was lower in both genotypes. However, it remained higher in the normal than in the okra-leaf type, which thereby intercepted more solar radiation and resulted in higher yield. Okra leaf appears superior for yield under optimum conditions, normal leaf under adverse conditions. An intermediate leaf type such as sub okra may be valuable in increasing the stability of cottons to adverse environmental conditions.

Additional index words: Gossypium hirsutum L., Cotton breeding, Crop simulation, Carbohydrate balance, Nitrogen balance, Light interception.

MODERN digital computers have made it possible to compress large amounts of information concerning the cotton (*Gossypium hirsutum* L.) plant into a series of logical and mathematical expressions called simulation models. These models can predict (within limits) the growth of the cotton plant from emergence to open boll, account for major physiological and morphogenetic processes, and describe the primary relationships in the soil-plant system.

Applications of simulation models in research management, plant breeding, yield forecasting, farm management, and in insect, disease, and weed control were recently discussed by Baker (4). Other applications are well documented in the literature of disciplines such as crop management (4, 28), entomology (10, 16), crop physiology (5, 7), and host-plant resistance (17). Recently, a number of plant breeders have envisioned models as tools for predicting the effects and economic benefits of various genetic combinations. Breeders are also interested in predicting response of particular genotypes to specified environments and how the crop can best be managed to maximize yields.

The purpose of this series of papers is to demonstrate how a computerized crop-simulation model can be useful in a breeding or agronomic research program to predict the response of genotypes to given environments. In this study, we chose to investigate the okra-leaf character of cotton; a subsequent paper includes an analysis of the photosynthetic efficiency of cotton. The okra-leaf character in cotton, which is controlled by a single, partially dominant gene, is expressed phenotypically by considerable reduction in leaf area as compared to normal-leaf cotton. Researchers have demonstrated that okra leaf is associated with considerable reduction in boll rot (2, 3, 18, 25). Large increases in lint yield have been observed in okra-leaf compared to normal-leaf cultivars, especially where boll rot is a problem (2, 18). However, Andries et al. (1) found that the normal-leaf type produced higher yields, followed in order by the okra and super okra-leaf types. Karami and Weaver (18) reported that squares were initiated earlier in okra-leaf than in normal-leaf cotton and that this difference in fruiting periods resulted in 5 to 6 days earlier maturity in okra-leaf. This agrees with the work of Andries et al. (2, 3) and Rao and Weaver (25). Higher lint percentages, micronaires, and harvest indexes were also associated with the okra-leaf character (18).

The desirable characteristics of okra leaf are partially overshadowed, however, by its higher abortion rate of fruiting forms. Kerby and Buxton (19) found that M-8 super okra leaf and 'Stoneville 7A' okra leaf produced 95 and 111% more fruiting positions, respectively, than 'Deltapine 16' normal leaf, but later aborted 180 and 207% more bolls, respectively. When near-isogenic lines of Stoneville 7A were used, 8 and 26% more fruiting positions were observed in okra and super okra-leaf types, but later they aborted 33 and 72% more bolls than their normal-leaf counterparts. The high fruit abortion in okra-leaf types was correlated with a general reduction in leaf area index (LAI) which presumably results in reduced carbohydrate production/fruiting position.

Guinn (15) found that factors which increase photosynthesis, such as high CO_2 level, long photoperiod, and high light intensity; decreased abscission of squares and young bolls. Conversely, factors which increase respiration, such as warm nights, increased abscission. These results support the classical papers by Mason (23) and Wadleigh (27) which strongly stated a nutritional theory for fruit abscission in cotton. The theory states that the cotton plant seeks to balance boll demand for carbohydrates and other nutrients against supply by abscising fruit. Pegelow et al. (24) proposed that the higher abscission rates observed in okra-leaf cottons may be due to an inadequate pool of available N within the plant, resulting form the reduced leaf area of the okra-leaf type. Baker and Myhre (8) compared canopy CO_2 exchange rates/unit of ground area in 'Rex' normal and okra-leaf cottons planted in 100-cm-wide rows and found no significant difference. Their report suggested that

[1] Contribution from USDA-ARS in cooperation with the Dep. of Agronomy, Mississippi State Univ. and Mississippi Agric. & For. Exp. Stn. Received 8 June 1981.

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okra and normal-leaf cultivars should have the same abscission rate. The work of Kerby and Buxton (19), however, indicated that okra-leaf cottons initiated much more fruit than their normal-leaf counterparts; and high rates of flowering have been associated with high abortion rates in young bolls (9).

Contrary to the nutritional theory is the work of Eaton and Ergle (13) who found no correlation between boll shedding and carbohydrate or N levels in various plant tissues. Further, they noted that early-planted and late-planted cotton had similar concentrations of carbohydrate and N in mid-August and that the early-planted cotton shed fruit rapidly but that planted later did not. They suggested that fruit retention was more likely a plant hormone-controlled phenomenon.

Baker et al. (5) provide a compromise between the nutritional theory and the hormone theory by proposing that the plant adjusts to a disparity between real and potential growth and that it abscises fruit on the basis of the supply-demand ratio for carbohydrates or N rather than for supply per se. The supply-demand balance triggers abscission by shifting the hormone balance within the plant. They incorporated this hypothesis into the cotton simulation model SIMCOT II and were able to simulate the time courses of square and boll initiation and abscission.

To demonstrate how a model such as GOSSYM can be used in analyzing complex problems, a series of simulations was conducted to study fruit abscission in okra-leaf cotton as affected by N application rate and plant carbohydrate supply and to analyze the possible causes for inconsistent lint yield performance of okra-leaf genotypes observed under Mississippi environmental conditions.

MATERIALS AND METHODS

The cotton-simulation model GOSSYM was used in this study. Its dynamic physiological characteristics permit evaluation of yield components as affected by the morphological differences between

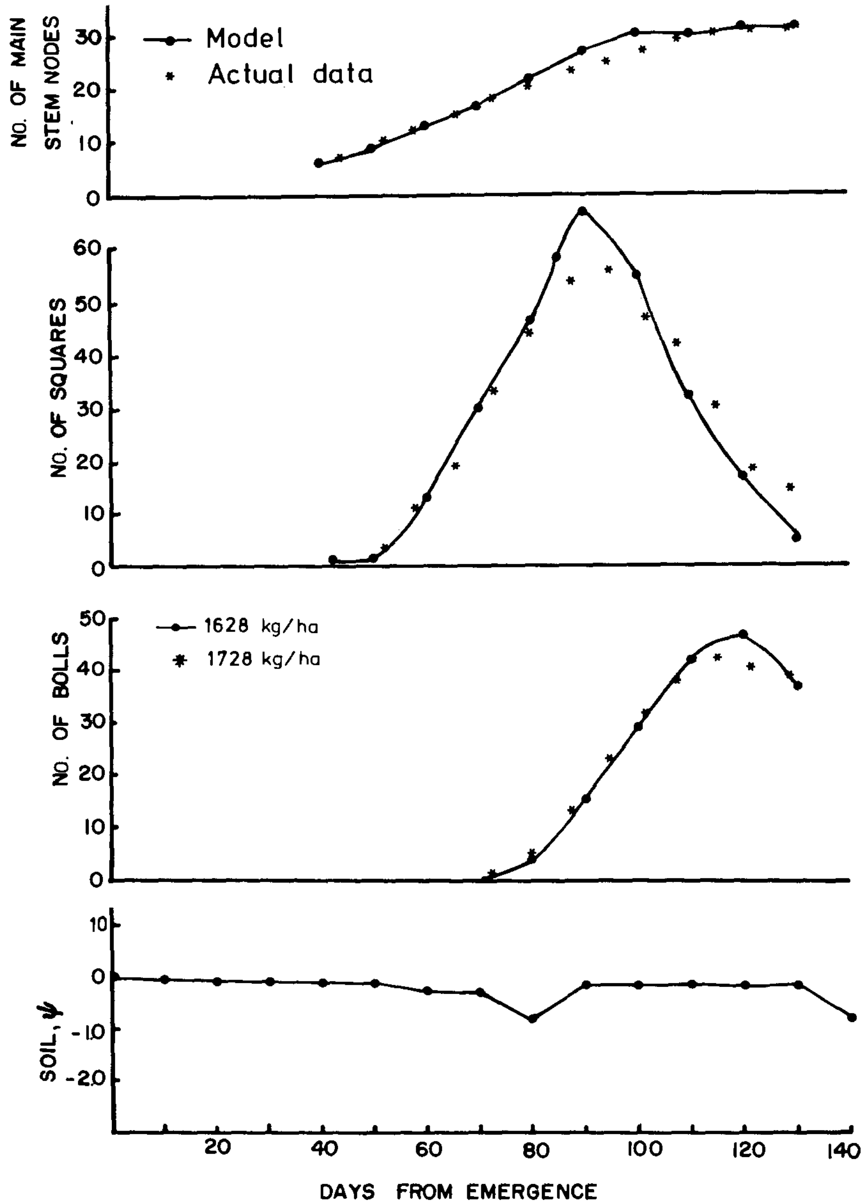

Fig. 1. Seasonal development for number of main stem nodes, number of squares, number of bolls, and soil-water potential of GOSSYM with Bruce and Römkens (11) observations in treatment AAA.

normal and okra-leaf cottons and by the various treatments used in this study.

GOSSYM was originally developed by Baker and Lambert, and its concepts have been presented in detail elsewhere by Baker et al. (6). It has been described more recently by Landivar (20). The latter description included modifications to that time. Subsequent versions have been developed by Whisler et al. (28) and Marani and Baker (22). Complete documentation of GOSSYM is in press; it includes FORTRAN[3] listing, definition of variables, description of the theory involved, and flow diagram of the model.

GOSSYM was validated using data collected by Bruce and Römkens (11) at the Plant Science Farm of Mississippi State University. Input necessary to run GOSSYM includes daily solar radiation, maximum and minimum temperatures, and rainfall (including irrigation, if any). This information was obtained from a class A weather station and provided by J. C. McWhorter[4]

Plots were grown under a rainout shelter and were planted at 50,425 plants/ha in rows 91 cm apart. Prior to planting, 167 kg/ha of P_2O_5, 335 kg/ha of K_2O, and 84 kg/ha of N were applied. At 4-week intervals after planting, three additional applications of 84 kg/ha of N were applied making a total of 335 kg/ha of N for the season. Intensive insect control practices were employed, and minimum damage was experienced. Their experiment consisted of seven irrigation treatments in 1961. We selected three of those treatments for use in our validation effort, i.e., their "AAA," "ABB," and "ADD" treatments. All were well watered from planting to first flower; then, they were irrigated when their average water potentials at 15, 30, and 45 cm depth fell below −0.3, −0.6, and −2.3 bars, respectively. The AAA plot received 375 mm of irrigation water, the ABB received 270 mm, and the ADD received 186 mm during 1961. GOSSYM predicted the development of the cotton plant reasonably well under conditions similar to those experienced by Bruce and Römkens (11); results are shown in Fig. 1, 2, and 3. In addition to that validation effort, the model has been more extensively validated by Reddy (26) who compared the model's predictions with field data collected at several locations in Mississippi (rain fed), Arizona (irrigated), and Israel (irrigated). Results for the Mississippi locations were very satisfactory; however, some changes were made to the model to simulate more closely cotton growth in the drier Arizona and Israel environments. After GOSSYM successfully simulated the data from Bruce and Römkens (11) experiment and from that of several other locations in Mississippi, we felt confident in using it to predict the growth and yield of cotton where actual data were not

[3] FORTRAN listing and dictionary of terms are available upon request from J. A. Landivar, Crop Simulation Res. Unit, P. O. Box 5367, Mississippi State, MS 39762.

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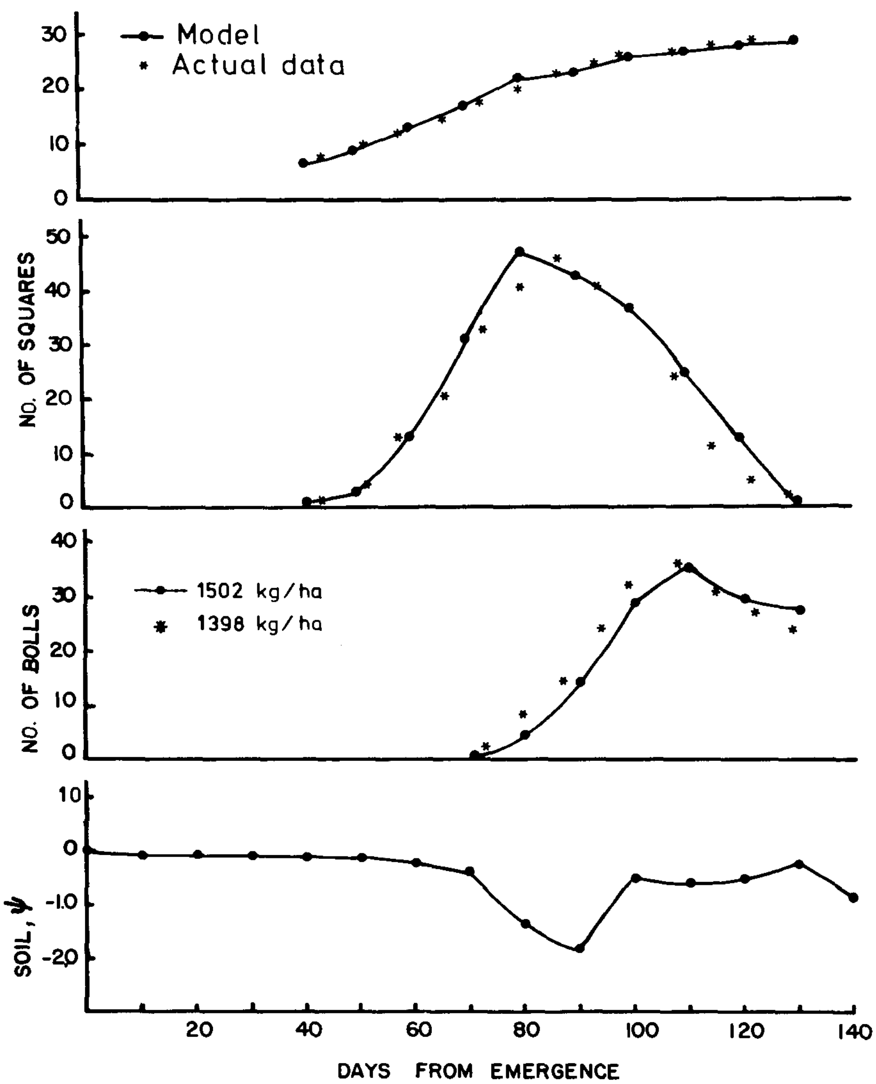

Fig. 2. Seasonal development for number of main stem nodes, number of squares, number of bolls, and soil-water potential of GOSSYM with Bruce and Römkens (11) observations in treatment ABB.

available. Changes made in GOSSYM to simulate a crop with reduced leaf area included a 30% reduction in the rate of leaf-area expansion. An equation for calculating percent light interception in okra-leaf cotton was derived empirically using data collected by Baker and Myhre (8). They demonstrated that change in LAI had no effect on canopy photosynthesis or transpiration other than that predicted from differences in light interception.

Three N treatments were simulated, i.e., 56, 112, and 224 kg N/ha. In the 56 kg/ha treatment, N was broadcast before planting. The 112 kg/ha treatment was split into two applications of 56 kg/ha broadcast at planting and 56 kg/ha side-dressed (banded) 28 days after emergence. The 224 kg/ha treatment was divided into four applications, 56 kg/ha broadcast at planting and three banded side-dressings at 28-day intervals. The crop was simulated with a planting density of 98,400 plants/ha. Two water regimes were simulated. Both were irrigated to field capacity before planting; then after first bloom, the plots were irrigated as described by Bruce and Römkens (11) for their ADD and AAA treatments. The total water applied throughout the season was 186 and 375 mm, respectively. Two levels of net photosynthetic efficiency were used to investigate possible effects of carbohydrate supply on fruit abscission, i.e., normal and 1.5 X normal.

Simulations were conducted for all possible combinations of N and irrigation regimes.

RESULTS AND DISCUSSION

Cottons with reduced leaf area, such as okra- and super okra-leaf types, produce more fruiting sites than normal-leaf cottons. Without any changes in the morphogenesis logic, GOSSYM simulated that observation (Table 1). The simulated difference in number of fruiting sites produced by okra- and normal-leaf types was on the same order of magnitude as found in the literature (19). The output indicated that cotton genotypes with reduced leaf area will invest the carbohydrate not used in leaf-area increase for the production of roots, stems, and flowers. The redistribution of carbohydrates occurring in okra-leaf types led to the production of a higher fruit load at all rates of N. As the season progressed, carbohydrate stresses developed due to increased demand as the fruit load increased. The model balanced those shortages of materials by aborting fruit. The abortion of fruit was higher in okra than in normal leaf cotton because okra leaf had developed a greater fruit load (Table 1). This result agrees with the general observation that okra-leaf genotypes abscise a higher number of fruit than normal-leaf types, but the degree of difference in num-

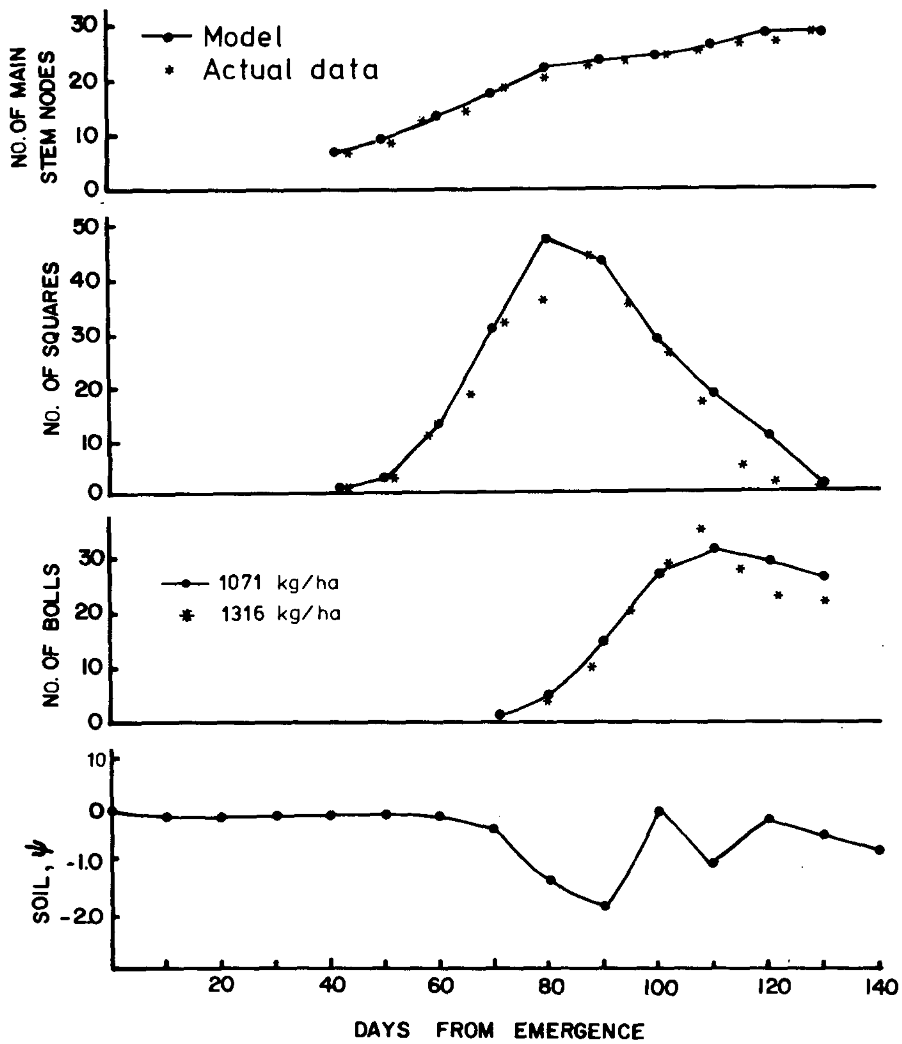

Fig. 3. Seasonal development for number of main stem nodes, number of squares, number of bolls, and soil-water potential of GOSSYM with Bruce and Römkens (11) observations in treatment ADD.

ber of aborted fruiting forms by okra- vs. normal-leaf was less than reported in the literature (19).

Percent retention of fruit in okra-leaf plants was not correlated with N-application rates (Fig. 4); however, as the N-application rate increased, lint yield increased in both moisture regimes (Fig. 5), as well as in the higher photosynthetic efficiency simulation runs (Fig. 6). The low N-application rate slowed the growth rate of the plant and delayed reproductive growth. The reduced growth rate induced by N shortages reduced the plant's demand for carbohydrates. This in turn reduced the metabolic stresses usually found in actively growing cotton plants. On the other hand, as the N-application rate increased, the rate of vegetative and reproductive growth increased, leading to an increased demand for carbohydrates. The well-fertilized, model crops developed higher LAI's which in turn led to higher photosynthetic rates as more solar radiation was intercepted. The increase in carbohydrate supply tended to balance the higher demand for carbohydrates induced by higher N-application rates. This allowed percent retention of fruit in the okra-leaf cottons to be similar at all N-application rates.

Increasing the carbohydrate supply increased percent retention in okra leaf of fruit at all stages of growth (Fig. 7). The simulated crop with the higher photosynthetic efficiency also retained a higher percentage of its fruit at all N-application rates used. This suggests that amount of pho-

Table 1. Seasonal development for number of fruiting sites/plant and cumulative number of aborted fruit resulting from GOSSYM simulations of normal vs. okra-leaf cottons.†

Days from emergence	Normal leaf: Fruiting sites	Normal leaf: Cumulative aborted fruit	Okra leaf: Fruiting sites	Okra leaf: Cumulative aborted fruit
	no./plant			
50	3	2	3	2
60	15	3	15	2
70	33	6	36	4
80	55	14	65	10
90	84	22	96	15
100	93	33	100	25
110	94	47	105	46
120	105	69	116	71
130	105	86	117	89
140	105	86	117	89
150	105	86	117	89

† These simulations assumed applications of 224 kg/ha of N, 375 mm of water, and a planting density of 98,400 plants/ha.

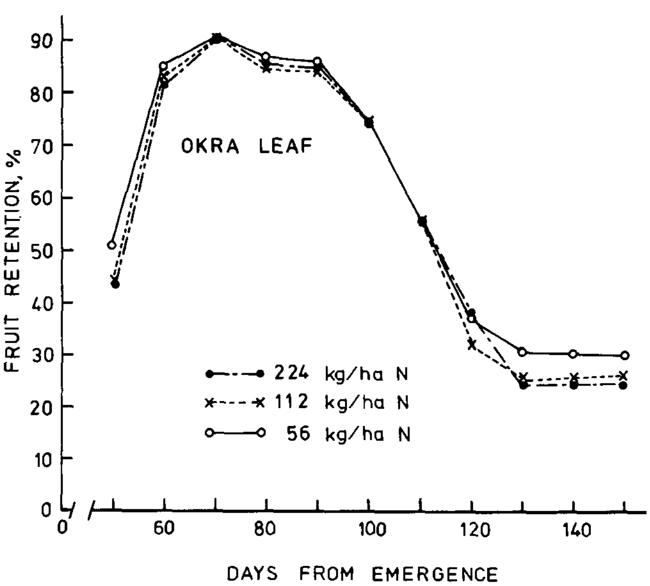

Fig. 4. Influence of N-application rates on simulated percent fruit retention of okra-leaf cotton (planted at 98,400 plants/ha and receiving 375 mm of water).

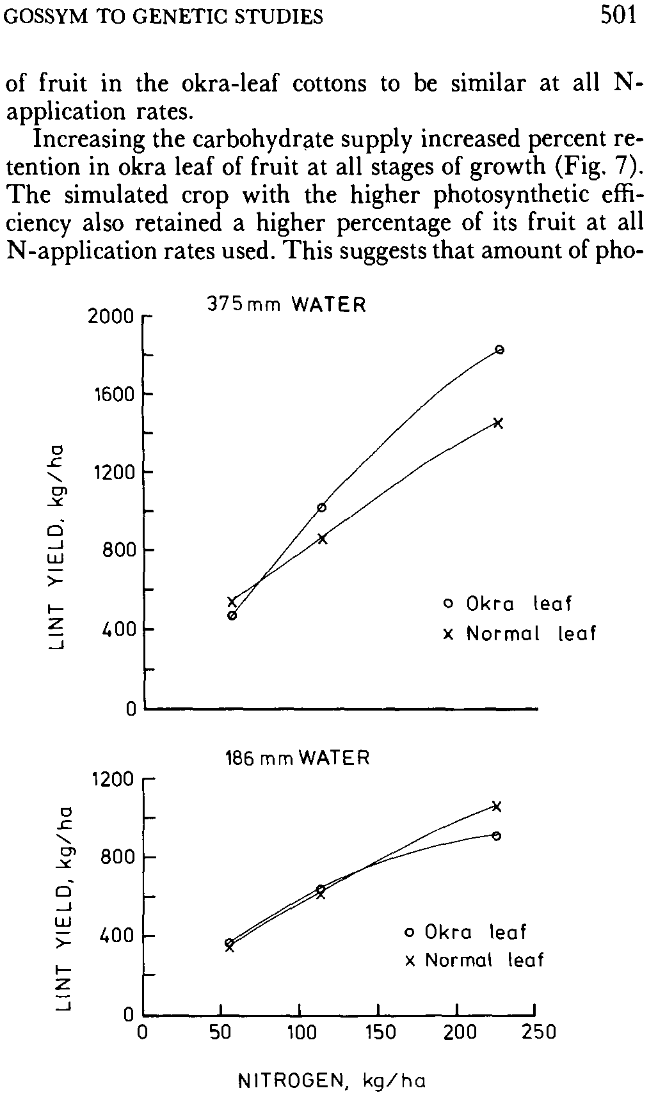

Fig. 5. Influence of N-application rates at two water levels on simulated lint yield response of okra vs. normal-leaf cotton (planted at 98,400 plants/ha).

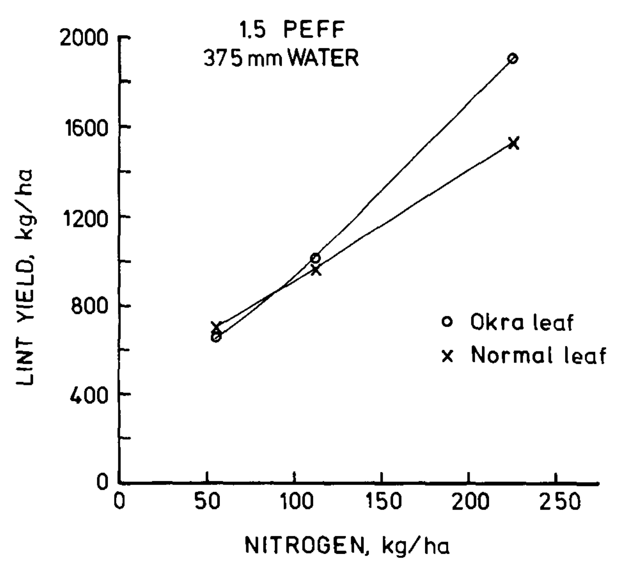

Fig. 6. Influence of N-application rates on simulated lint yield response of okra- vs. normal-leaf cotton with photosynthetic efficiency (PEFF) increased by 50% (planted at 98,400 plants/ha).

tosynthesis is the critical known limiting factor in okra-leaf cottons.

As the N-application rate increased, lint yield also increased. The benefit of higher rates was greater at the high water level than at the low (Fig. 5). The model accumulates water and nitrate through the transpiration stream; therefore, at low water levels, severe N stresses developed (nutritional drought) limiting the lint yield of both normal and the okra-leaf types.

Analyzing yield response at the various treatment levels, the model predicts that as growing conditions improve (i.e., higher water and N-application rates), the okra-leaf cotton will produce higher lint yields than the normal-leaf types; whereas, unfavorable conditions will favor normal-leaf cotton (Fig. 5). Field performance of okra-leaf cultivars has been observed to be very inconsistent over years. Usually, okra leaf performs comparably to normal leaf in favorable growing seasons, but worse under adverse conditions. Okra-leaf cultivars have typically averaged about 5% less lint yield than normal-leaf cultivars under Mississippi conditions (J. N. Jenkins, unpublished data). Our results suggest that the yield inconsistency of okra-leaf cotton could be due to the failure to maintain a LAI sufficient to intercept solar radiation for its requirements during adverse growing conditions (Fig. 8). The rate of leaf development is very susceptible to adverse environmental conditions. Both N deficiencies and dry growing seasons are well known factors negatively influencing vegetative development. Under favorable growing conditions, both the normal- and the okra-leaf cottons produce a leaf canopy sufficient to shade the ground surface; and in doing so, both intercept most of the incoming solar radiation. Adverse growing conditions affect the LAI of both leaf-type cottons. However, because okra-leaf has a smaller area/leaf, it produces a lower LAI at any given plant height. As leaves senesce, LAI is reduced and light interception becomes critical. This reduces rates of photosynthesis, leading ultimately to lower lint yields than in normal-leaf cotton. Because okra leaf invests a smaller proportion of its carbohydrate in leaves, it may invest relatively more in the production of fruit; and final yield may be higher than in normal-leaf cotton under favorable growing conditions. This hypothesis is illustrated in Fig. 8. Under favorable conditions (i.e., high water and high N), simulations of both okra and normal leaf produced canopies sufficiently dense to intercept most incoming solar radiation as early as 84 days after emergence (Fig. 8). [GOSSYM contains logic, based on observations of Ludwig et al. (21), that when the LAI of the crop is above 2.9, most of the incoming solar radiation will be intercepted by leaves.] The model predicts that normal leaf invests a larger fraction of its available carbohydrate in the production of leaves apparently not essential to yield production (Fig. 8). Under favorable conditions, okra leaf would produce and maintain adequate LAI to intercept most of the incoming solar ra-

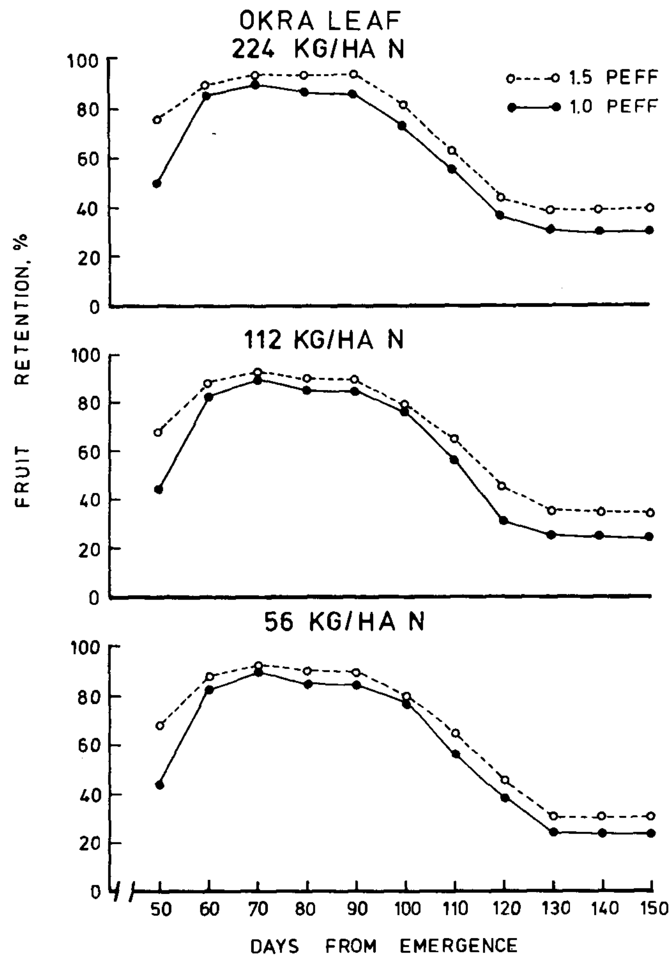

Fig. 7. Influence of N-application rates on simulated percent fruit retention of okra-leaf cotton with photosynthetic efficiency (PEFF) at standard levels and increased by 50% (planted at 98,400 plants/ha and receiving 375 mm of water).

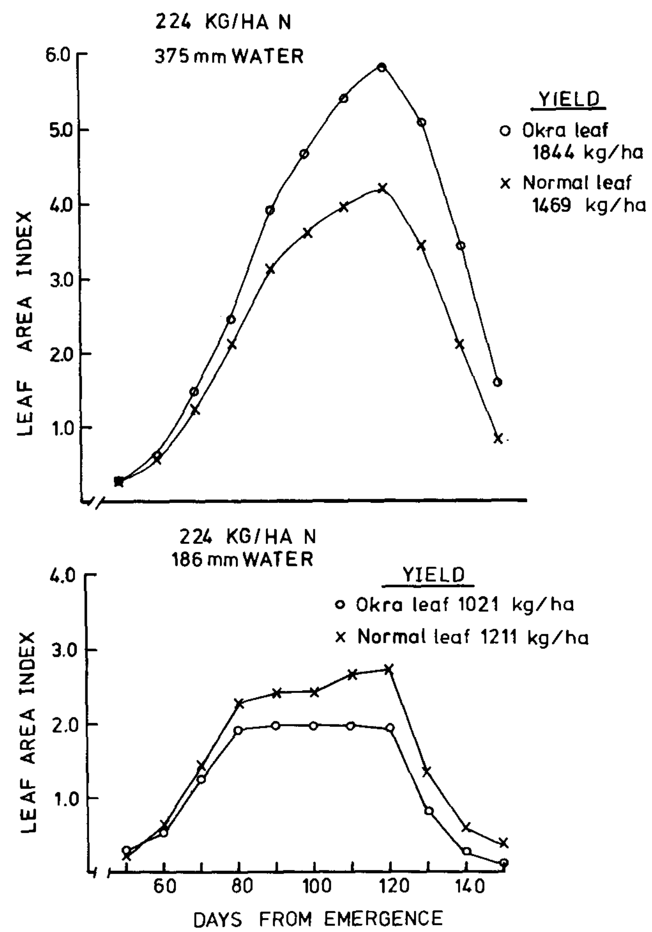

Fig. 8. Simulated leaf area index at two water levels at higher N-application rate of okra vs. normal-leaf cotton (planted at 98,400 plants/ha).

Table 2. Effects of irrigation level and leaf type on lint yield.

Leaf type	Lint yield by irrigation level			
	AAA†	ABB	ADD	Mean
	kg/ha			
Okra	1769	1429	958	1385
Intermediate	1583	1885	991	1486
Normal	1468	1719	1210	1465

† The symbols AAA, ABB, and ADD indicate irrigation regimes described in text.

diation without being wasteful. Under optimum conditions the more efficient distribution of carbohydrate in okra leaf should result in the production of 381 kg more lint/ha than in normal-leaf cotton. When growing conditions were not as favorable (i.e., reduced water supply), simulated LAI was reduced in both okra- and normal-leaf types (Fig. 8). However, it remained higher in the normal crop which intercepted more solar radiation, resulting in 190 kg/ha more lint than in okra leaf.

An intermediate leaf type, such as sub okra reported by Green (14) or such as the F_1 of crossing okra-leaf with normal-leaf parents (12), may be valuable in increasing the stability of okra-leaf cottons to adverse environmental conditions. To test this hypothesis, we made additional simulations including an intermediate-leaf type. Intermediate leaf was simulated by reducing its leaf-growth potential by 15% compared to normal leaf (okra-leaf was reduced by 30%). The estimated yields are shown in Table 2. The symbols AAA, ABB, and ADD represent Bruce and Römkens (11) irrigation inputs. The AAA treatment was maintained at field capacity throughout the season. Under that treatment, vegetative development was greatly enhanced in all three genotypes, reaching maximum LAI's of 5.8, 5.0, and 4.2 for normal, intermediate, and okra leaf, respectively. Under AAA conditions, predicted yield was negatively correlated with leaf biomass produced. The ABB treatment was somewhat drier; it was maintained at field capacity from planting to first bloom, then it was irrigated whenever root zone tensiometer readings were below −0.6 bars. This treatment represents a more typical year in the cotton-producing areas of Mississippi than does AAA. The simulated rate of LAI formation was reduced considerably in all three genotypes, affecting primarily the amount of light interception by okra leaf which reached a maximum LAI of 2.8. This resulted in reduced yield in the simulated okra-leaf cotton, but increased yield in the normal and intermediate-leaf types which produced maximum LAI's of 3.9 and 3.3, respectively. Those levels were apparently adequate for intercepting most of the incoming solar radiation, but the more efficient distribution of carbohydrates in the intermediate-leaf type yielded 166 kg/ha more lint than normal-leaf cotton.

Simulated LAI's were reduced further in the ADD treatment. This treatment was irrigated to field capacity at planting and maintained at that level to first bloom. It was then irrigated whenever soil-water potential was below −2.3 bars. The LAI's were considerably reduced in all genotypes reaching a maximum of 2.7, 2.2, and 2.0, respectively, for normal, intermediate, and okra leaf. The normal-leaf crop intercepted more solar radiation than the okra and intermediate-leaf types and produced higher yields.

Analyzing mean lint yield over the three environments, the model predicted that the intermediate-leaf type should out yield okra leaf by approximately 100 kg/ha of lint. It also should out yield normal leaf, but that difference was not large. Because most years in the cotton-producing areas of the Southeast will be similar to the ABB treatment, or drier, the intermediate-leaf type seems to have an advantage over okra and normal leaf. Our analysis suggests that the intermediate-leaf type should be considered for further cotton research in such areas. However, in drier climates, normal-leaf types appear to have a distinct advantage over okra or intermediate-leaf cottons.

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