

# Application of GOSSYM to Genetic Feasibility Studies.

## II. Analyses of Increasing Photosynthesis, Specific Leaf Weight and Longevity of Leaves in Cotton<sup>1</sup>

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### ABSTRACT

The model GOSSYM was used to demonstrate how a computerized crop simulation model can be used in a breeding or agronomic research program to simulate the performances of genotypes with different physiological response when grown under various environmental conditions. Results of simulating a cotton (*Gossypium hirsutum* L.) crop with higher leaf photosynthetic rate indicated that cotton lint yield could be increased up to 54% by increasing photosynthetic rate by 30%, providing that adequate N and water were available. With 30% increase in photosynthetic rate the high water (375 mm) input outyielded the low water (186 mm) treatment in both 56 and 112 kg/ha of N treatment, however, no difference in lint yield was obtained between the water regimes at 336 kg/ha of N. Maturity was delayed in the higher water treatment. Simulation results indicated a higher N requirement to obtain maximum lint yields with a cultivar having increased photosynthetic rate. It was concluded that if the increased CO<sub>2</sub> exchange rate observed in a genotype were associated with increased specific leaf weight, more of the CO<sub>2</sub> fixed would be used in the production of thicker leaf rather than lint production. This suggests caution in using specific leaf weight to select indirectly for higher leaf photosynthetic rates in cotton. Keeping the leaves photosynthetically active for a period of up to 70 days resulted in a higher leaf area index (LAI), the crop intercepted a higher fraction of the incoming solar radiation, and produced a higher lint yield. This seems to be a more promising characteristic to be used as criteria in a breeding or agronomic research program oriented toward increasing lint yield.

*Additional index words:* *Gossypium hirsutum*, Cotton breeding, Crop simulation, Nitrogen rates, Watering rates.

THIS is the second of a series of papers to demonstrate how a crop simulator such as GOSSYM can be useful in a breeding program. Plant breeders envision the use of models as tools for predicting the effects and economic benefit of various genetic combinations and how the proposed genotype will respond to a given environment (21). In part I of this series, we analyzed fruit abscission and yield in

okra and normal leaf cottons (*Gossypium hirsutum* L.) (24). In the present paper we analyze the photosynthetic efficiency of cotton.

Considerable differences among cultivars in their photosynthetic rate per unit of leaf area have been found in tall fescue (*Festuca arundinacea* Schreb.) (1), alfalfa (*Medicago sativa* L.) (7, 31), oats (*Avena sativa* L.) (9), corn (*Zea mays* L.) (10, 17), soybeans [*Glycine max* L. Merr.] (11), cotton (12), sugarcane (*Saccharum* spp. L.) (18) and common bean (*Phaseolus vulgaris* L.) (20). Evidence has been presented of a relation between rates of photosynthesis and crop yield. Peet et al. (32) found that photosynthetic rates during the pod filling period were well correlated with both biological and seed yield in all but one of nine cultivars of dry beans. Similar results were obtained by Harrison et al. (16) who reported that canopy apparent photosynthesis during pod filling in soybeans was correlated with higher seed yield. Hardman and Brun (15), and Mauney et al. (26) demonstrated that providing additional CO<sub>2</sub> to crops strongly affects yield by sustaining greater rates of photosynthesis.

Krenzer and Moss (23) observed that providing additional CO<sub>2</sub> to wheat (*Triticum aestivum* L.) during the floral initiation and grain development resulted in significant yield increases. They concluded that a screening procedure for higher photosynthetic rates during these stages might be an effective technique for increasing wheat yield. Moss (27) observed a rapid decline in net photosynthesis during the grain filling period. His data suggest the possibility of increasing grain yield by delaying leaf senescence.

Other researchers report a correlation between specific leaf weight and leaf photosynthetic rates. Pearce et al. (31) found that photosynthetic capability of alfalfa was positively related to specific leaf weight. Their analysis showed that variation in specific leaf weight accounted for about 64% of the variation in photosynthesis. Barnes et al. (7) reported that significant variation in specific leaf weight occurred within and among alfalfa cultivars, and suggest that it was a convenient, economical, and rapid method to select for genotypes with higher photosynthetic rates. This agrees with

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the work of Dornhoff and Shibles (11) and Kerby et al. (22). They found that photosynthetic rates of leaves were highly correlated with specific leaf weight. They also suggested that specific leaf weight may be acceptable as a selection index for leaf photosynthesis.

Izhar and Wallace (20) studied the inheritance of observed cultivar differences in photosynthetic efficiency of dry beans. They concluded that the photosynthetic efficiency of the cultivars, 'Red Kidney' and 'Michelite-62', their  $F_1$  and  $F_2$  progenies, and backcross to Red Kidney suggest that the genetic mechanism controlling the cultivar differences in net  $CO_2$  exchange rate is quantitative, that there may be relatively few genes involved, and that there is some dominance for the low photosynthetic efficiency of Red Kidney.

Despite this evidence several reports have questioned the value of breeding for increased photosynthetic rates as a means of increasing yields. Nelson et al. (30), failed to find a positive relationship between net  $CO_2$  exchange rate measurements, obtained during a regrowth period of tall fescue and subsequent forage yield.

Irvine (19) found that photosynthetic rates per unit of leaf area in sugarcane did not increase with increasing yields and concluded that differences in leaf photosynthetic rates would be of little practical value to breeders selecting for higher yields. He suggested that photosynthetic rates per unit of land area are more likely to be related to yield.

Muramoto et al. (29) studied several growth characteristics of the cotton plant, including photosynthetic rate. They failed to find consistent differences in photosynthesis among cultivars and  $F_1$  crosses of *G. barbadense* L. and *G. hirsutum* L. El-Sharkawy et al. (13) measured the photosynthetic rate of 26 species of cotton. Although differences in photosynthesis were large, they were not significant.

Large cultivar differences in net  $CO_2$  exchange rate of maize have been reported (17). Five generations of selection for high and low photosynthetic rates have been carried out. Although heritability is high, the effect on yield was not established (28). In reviewing the physiological basis for crop yield, Evans (14) commented that until more progress is made on the relationship of high  $CO_2$  exchange rate to yield, there is little point in selecting crop plants for high leaf photosynthetic rates.

In order to provide insight into the controversy of the reports discussed, a series of simulation runs were made with the following objectives: 1) to study the effects of increasing the photosynthetic rate on cotton lint yield, 2) to study the effects of water and N on a genotype with higher photosynthetic rates, and 3) to analyze two criteria for improving crop photosynthesis.

## MATERIALS AND METHODS

The GOSSYM model in its various versions has been described elsewhere (4, 5, 6, 33). Therefore, only the detail of the model associated with photosynthesis will be described here.

The PNET (net photosynthesis) subprogram of GOSSYM calculates total carbohydrate available for redistribution among the growing points of the plant. The photosynthetic process creates the carbohydrate supply as a function of light interception, based on the data of Baker et al. (3). This value is adjusted by plant population and moisture stress. Provisions have been made in the model for carbohydrate losses due to maintenance and light respiration. After these losses have been accounted for, the model arrives at the day's increment of available carbohydrate (AC) for distribution among the growing points of the plant structure.

To simulate crops with different photosynthetic rates (PR) we simply multiplied AC by 0.5, 1.0 or 1.3 representing a genotype with low, average and high PR, respectively. Environmental inputs necessary to run GOSSYM including solar radiation, maximum and minimum temperatures, rainfall and/or irrigation amounts were obtained from a class-A weather station at the Plant Science Farm of Mississippi State University. The data collected by Bruce and Römken (8) were previously used to validate GOSSYM (24). The model predicted the development of the cotton plant reasonably well under conditions similar to those of Bruce and Römken.

Three N levels were used in the experiment. All the N was in the form of  $NO_3$ . In the 56 kg/ha treatment it was applied at planting. The 112 kg/ha treatment was split into two applications, 56 kg at planting and 56 kg sidedressed 28 days after emergence. The 336 kg N/ha treatment was divided into four applications, 84 kg at planting and three sidedressings of 84 kg at 28 day intervals.

Two water regimes were used. The simulated crops were well watered from planting to the time of the first flower, then they were irrigated whenever the average soil water potential at 15, 20, and 45 cm depth fell below  $-0.3$  and  $-2.3$  bars respectively for the high and low water treatments. The high water treatment received 375 mm of water and the low water treatment received 186 mm of water during the growing season. Runs were made in all possible combinations of PR, N application rates, and water regimes.

Additional simulation runs were made to examine some plant characteristics which could possibly be used by plant breeders to increase crop dry weight gain and hence yield. Variation in photosynthetic rate per unit leaf area has been reported to be accompanied by variation in specific leaf weight (dry wt/area) (7, 11, 22, 31), three simulation runs were made to study these characteristics in various combinations. Simulation A (Fig. 7) represented a normal crop simulation, B a crop with a 15% higher photosynthetic rate (1.15 PR) and a 10% higher specific leaf weight, simulation C represents a crop with 15% higher photosynthetic rate (1.15 PR) but normal specific leaf weight.

Another plant characteristic that was examined was the length of time for which leaves remain viable on the plant. A total of 4 simulation runs were made with the leaves programmed to senesce at 60, 65, 70 and 75 days after they were initiated.

Simulations of specific leaf weight and delayed senescence effects used the weather data and cultural inputs of Bruce and Römken (8). The plant population was 98,400 plant/ha and a total of 336 kg/ha of N and 375 mm of water was applied to the crop during the season. Under conditions similar to those of Bruce and Römken (high N and water input), GOSSYM assumes that leaves senesce 70 days after being initiated.

## RESULTS AND DISCUSSION

The simulated total dry matter produced per plant increased as photosynthetic rate (PR) increased in all treatments. However, lint yield did not respond in the same manner to changes in PR.

At low N application rates (56 kg/ha of N) and low water, the model predicted a small increment increase in lint yield as PR increased from 0.5 to 1.0 (Fig. 1). The response nearly leveled as the PR increased to 1.3. The yield response in the high water treatment was somewhat larger as PR increased from 0.5 to 1.0, but it also changed little with an additional increment of PR. These treatments were characterized by severe N stresses throughout the season. These stresses were the main factor limiting yield. Most of the extra carbohydrate available for growth in the 1.3 PR treatment was used in the production of woody tissue.

Potential plant growth was greatly reduced due to N stresses, consequently the extra carbohydrate was not used in either vegetative (larger plants) or reproductive growth.

The 112 kg/ha of N treatment responded somewhat similarly to the low N treatment (Fig. 2). However, greater increases in yield were obtained as PR increased from 0.5 to 1.0, in the low water treatment as well as the high water treatment, but again there was little response to greater PR than 1.0. The increased photosynthetic efficiency led to a higher demand for N. Consequently, the plant rapidly depleted the available soil N. Nitrogen stresses were predicted by the model as early as 40 days after emergence. Nitrogen stresses were more severe in the high water treatment, in which the rate of vegetative development was greater, further increasing the demand for N.

The high-water treatment out-yielded the low-water treatment at the various levels of PR, developed a larger leaf area index (LAI) and was able to intercept a larger fraction of the incoming solar radiation. However, lint yield was limited by N shortage, even when 112 kg/ha was applied.

When sufficient N was applied to avoid an adverse effect of N deficiency (336 kg N/ha, Fig. 3), the model predicted substantial yield increases as the PR increased from 0.5 to 1.0, in both the high and low water treatments. The high

water treatment developed a larger LAI and intercepted more solar radiation than the low water treatment resulting in a larger number of the fruit being initiated and set. As the PR increased from 1.0 to 1.3, further increases in lint yield were obtained; however, at 1.3 PR the influence of water treatment became negligible. Although total dry matter produced was greater in the high water treatment, most of it went to the vegetative organs. This delayed maturity and reduced yields. Nitrogen stresses were seldom observed at this N level; however, early in the vegetative development of the plant, mild N stresses developed due to an increase in the organ growth potential caused by the higher availability of carbohydrates. Real plants may not show any symptoms of N shortage at 336 kg/ha application rate, possibly due to the active N uptake process, which GOSSYM does not account for. However, as the season progressed the passive N uptake process which GOSSYM does account for was sufficient to supply the needs of the plant.

As the photosynthetic efficiency increased, the percent of fruit retained increased. Figures 4a, 4b, and 5 show the time course of development of the plants at the three levels of PR used. The 0.5 PR crop was stressed for carbohydrates through the season, consequently the production of fruiting sites was delayed early in its reproductive cycle (Fig. 4a). As the PR increased to 1.0, the carbohydrate stresses (carbohydrate supply/demand)<sup>3</sup> were relaxed. This led to a higher production of fruiting positions. The 1.3 PR crop

<sup>3</sup> GOSSYM calculates the supply of carbohydrate as discussed in Materials and Methods. The demand for carbohydrate is calculated as the sum of potential growth increments of all the plant organs. Potential growth of organs is calculated as a function of temperature, assuming no shortage of photosynthate or N.

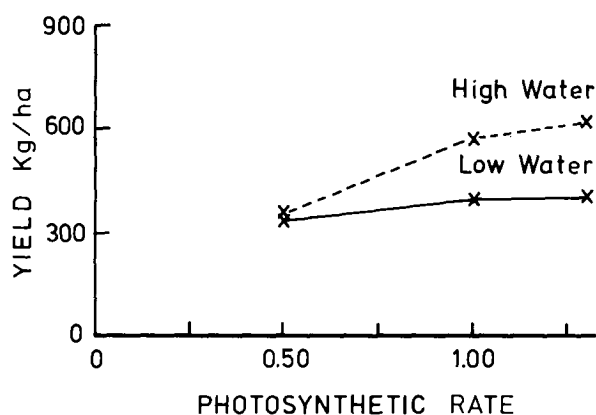


Fig. 1. The simulated influence of photosynthetic rate on cotton lint yield per ha with 56 kg N/ha at low water and high water (186 and 375 mm total water applied, respectively).

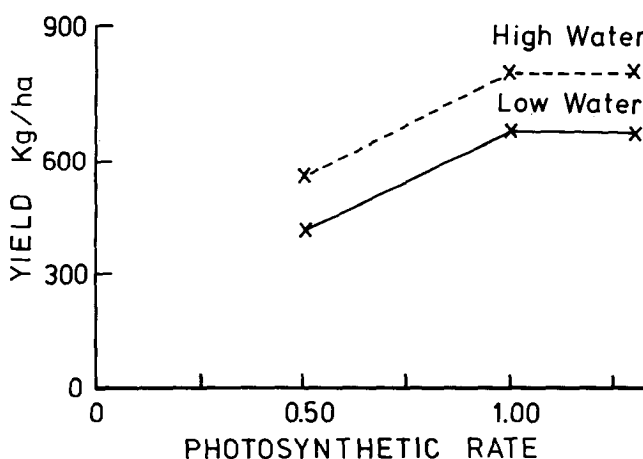


Fig. 2. The simulated influence of photosynthetic rate on cotton lint yield per ha with 112 kg N/ha at low water and high water applications (186 and 375 mm total water applied, respectively).

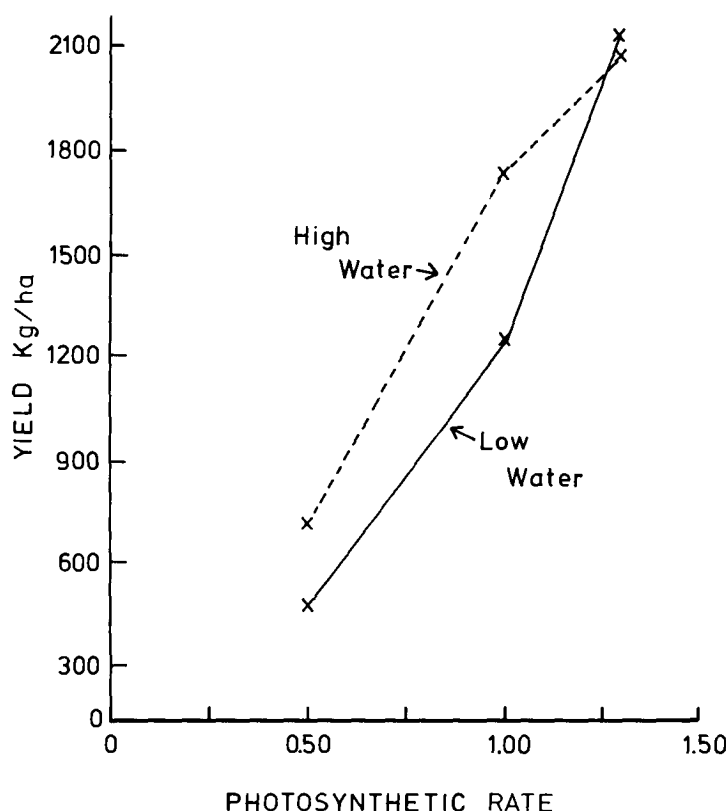


Fig. 3. The simulated influence of photosynthetic rate on cotton lint yield per ha with 335 kg N/ha at low water and high water applications (186 and 375 mm total water applied, respectively).

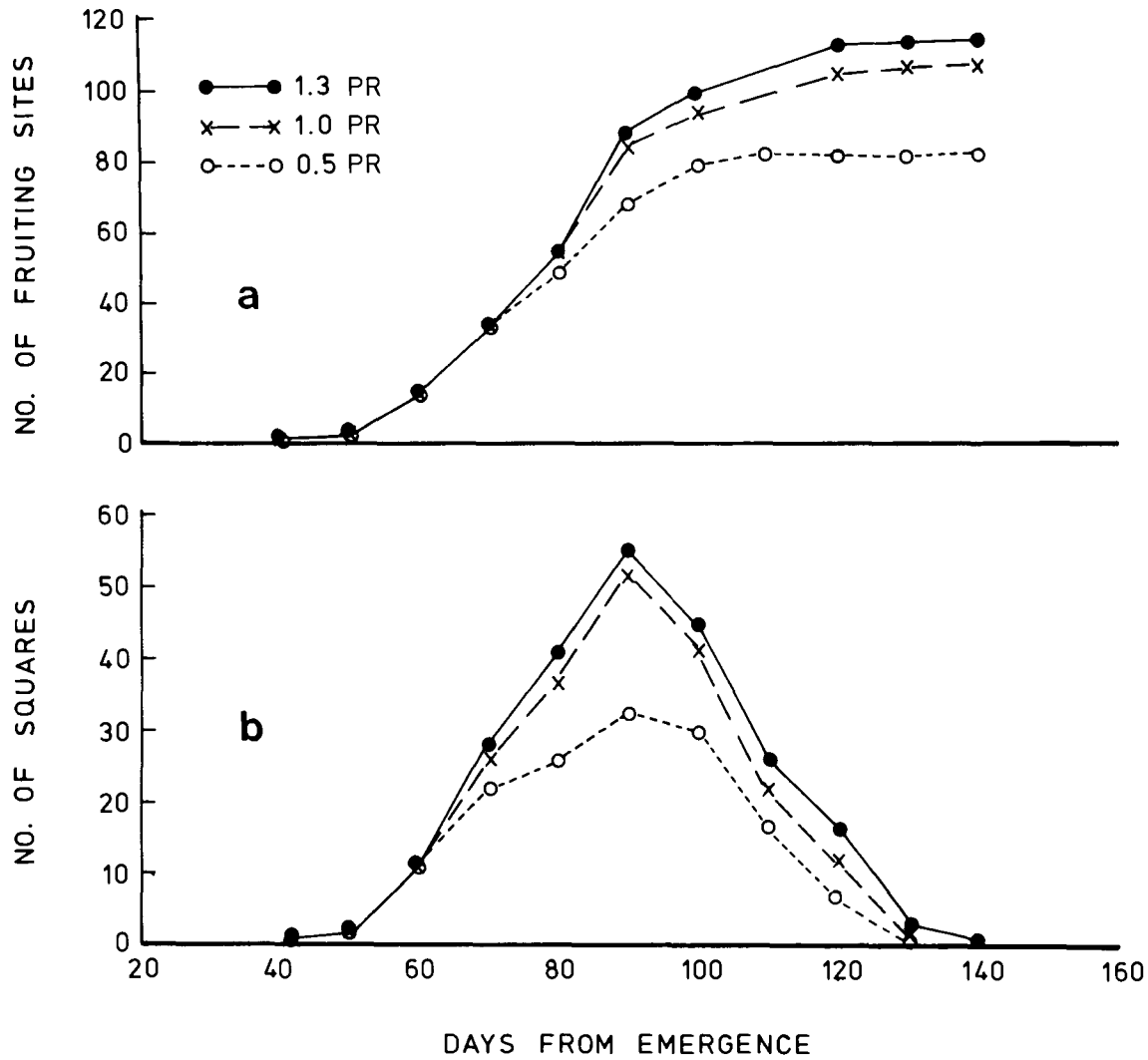


Fig. 4. The simulated seasonal development of the number of fruiting sites (a) and squares (b) as influenced by photosynthetic rate (PR). (336 kg N/ha and 375 mm of water.)

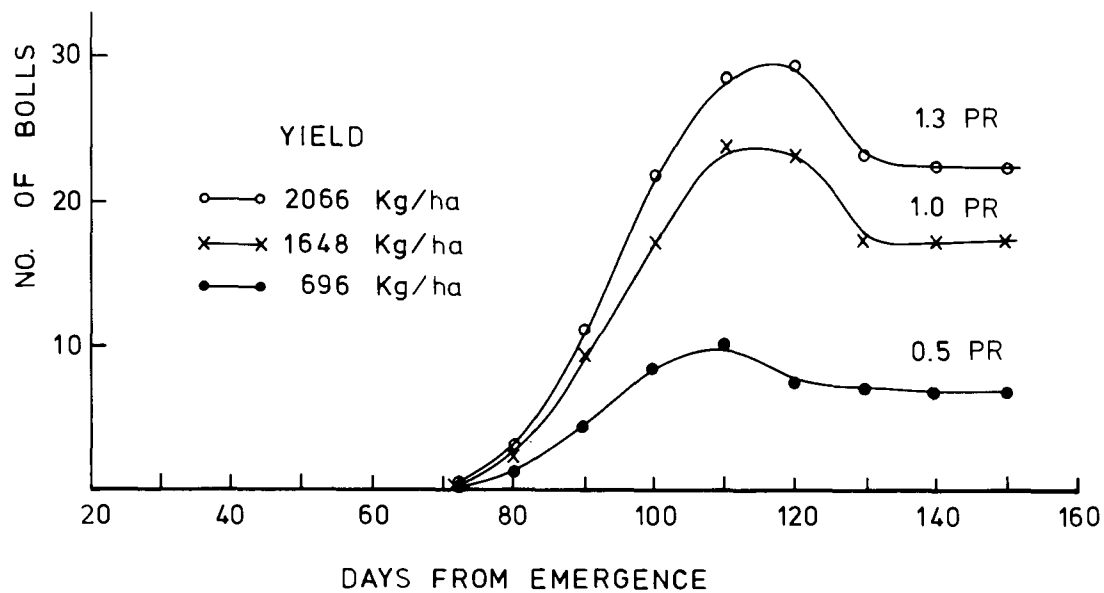


Fig. 5. The simulated seasonal development of the number of bolls and lint yield as influenced by photosynthetic rate (PR). (336 kg N/ha and 375 mm of water.)

produced somewhat more fruiting sites, but the difference was not very large.

The time course of square (floral bud) development is shown in Fig. 4b. The 0.5 PR crop produced considerably fewer squares than the 1.0 PR crop. Again the number of squares produced in the 1.3 PR was not much larger than the 1.0 PR crop. The benefit of increasing the photosynthetic efficiency was in increasing the percentage of fruit retention. Similar results were reported by Mauney et al. (26), however they obtained larger percent of fruit retention than our simulated results. Figure 5 shows the time course of boll load development at the various photosynthetic efficiency levels. Although the difference in the number of squares produced was not very large between the 1.0 PR and the 1.3 PR, the difference in the number of green bolls retained was higher as shown in Fig. 5. This resulted in a difference of 416 kg of cotton lint per ha at the end of the season.

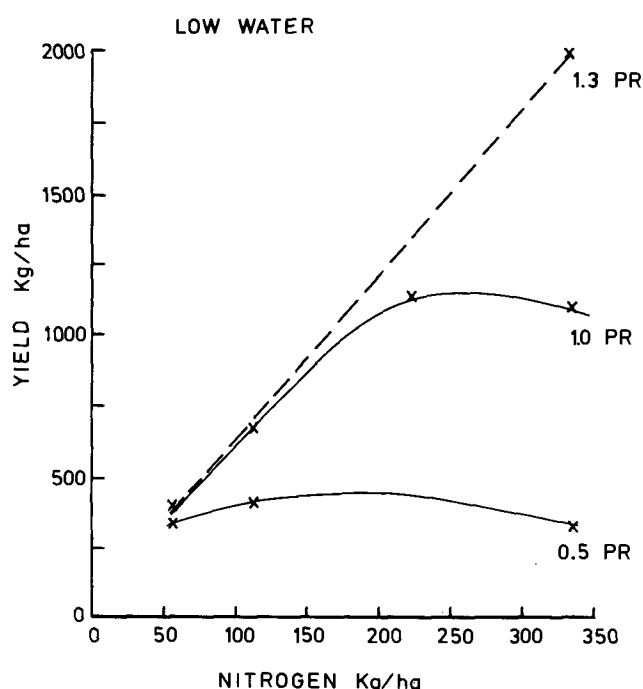


Fig. 6. The simulated influence of nitrogen application rate of crops with three levels of photosynthetic rate (PR) on cotton lint yield. (186 mm of water.)

The N response curve at the various PR levels is shown in Fig. 6. At 0.5 PR, no benefit was obtained from N application rates. The average crop (1.0 PR) shows a typical N response curve for cotton, reaching a point of diminishing return at around 200 kg/ha of N. The nitrogen requirement to produce maximum yield was considerably increased when the photosynthetic rate was increased to 1.3, suggesting that higher than normal amounts of nitrogen will be required to obtain maximum yield of a crop with higher photosynthetic efficiency. This result agrees with the observations of Mauney and his coworkers (26) that CO<sub>2</sub> enrichment increased boll set 51% with normal nutrients, and 116% with two times the concentration of the normal nutrient solution used in their atmospheric CO<sub>2</sub> enrichment experiment.

The model predicted that increased photosynthetic efficiency will increase lint yield considerably, assuming adequate mineral nutrition is available. As the photosynthetic efficiency increased, maturity was delayed, especially in the high water and high N treatments. In the field this may create insect problems at the end of the season. Therefore earliness should be considered along with breeding for higher photosynthetic rates.

Several simulation runs were made to study the effects of specific leaf weight on final lint yield. Figure 7 shows the results in terms of organ weights. Crop B and C with higher rates of photosynthesis produced a higher total plant dry weight than crop A. However, crop B had thicker leaves, the plant invested a larger fraction of its available carbohydrate in the production of leaves, rather than in fruit. The thicker leaves of crop B caused an increase in the sink strength of the leaves, leading to carbohydrate stresses. The plant compensated for these stresses by aborting more fruit. This eventually relaxed the stresses. Fruiting in crop B was then reinitiated, but maturity was delayed and final yield was similar to the crop with normal photosynthetic efficiency. The yield of crop C was about 90 kg/ha of lint higher than B. Crop C represents a crop in which the photosynthetic rate has been enhanced by CO<sub>2</sub> fertilization such as in the experiments of Baker (2) and Mauney et al. (26). This analysis suggests caution toward using specific leaf weight as a criterion for selecting for higher yields in fruiting crops; it also suggests that if one selects for higher leaf photosynthesis rates, partitioning of the extra carbohydrate into the economic crop components should be considered in the breeding program.

Several reports have demonstrated the yield benefits of

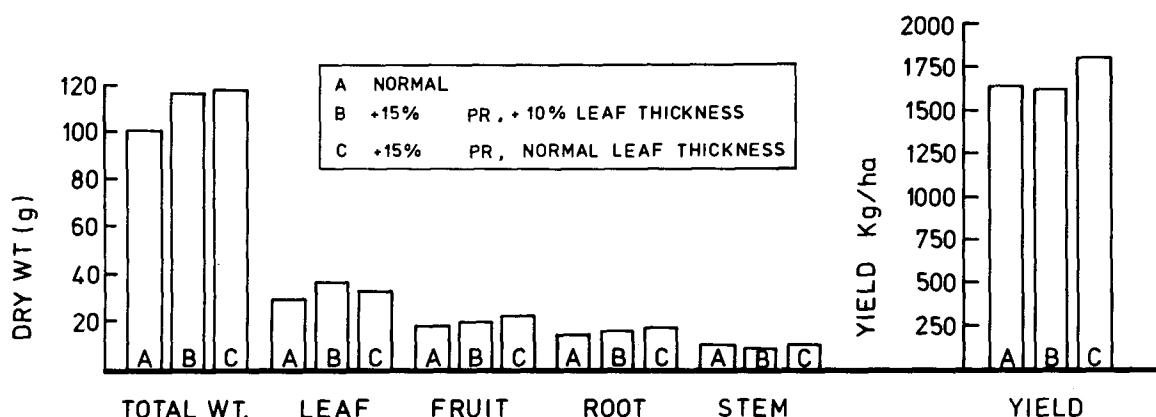


Fig. 7. Plant weights 140 days after emergence, resulting from simulating a normal crop (bars A), a crop with 15% increase in photosynthetic rate (PR) with a 10% higher leaf specific weight (bars B), and a crop with 15% increase in PR but normal specific leaf weight (bars C). (336 kg N/ha and 375 mm of water.)

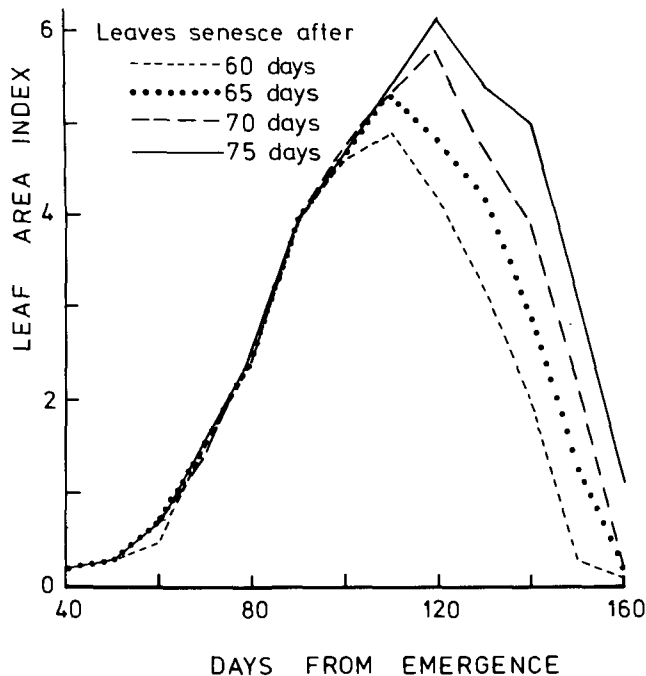


Fig. 8. The simulated influence of delaying leaf senescence on the seasonal development of the leaf area index. (336 kg N/ha and 375 mm of water.)



Fig. 9. The simulated influence of delaying leaf senescence on cotton lint yield. (336 kg N/ha and 375 mm of water.)

higher rates of photosynthesis during the post-anthesis period (15, 16, 23). In cotton, an indeterminate species, higher rates of crop photosynthesis may be obtained during the time of heavy boll load by delaying leaf senescence, i.e. keeping the leaves photosynthetically active for a few more days. In order to test this hypothesis a series of simulation runs were made in which the leaves were dropped 60, 65, 70, and 75 days after being initiated. Delaying leaf senescence helped to maintain a higher LAI (Fig. 8). As leaf senescence was delayed the crops intercepted a higher frac-

tion of the incoming solar radiation,<sup>4</sup> resulting in higher photosynthate production. The simulated results indicated that maintaining a higher canopy cover during the boll filling period should result in important increases in lint yield (Fig. 9). It also points out that premature leaf senescence can reduce yield potentials considerably.

The data of Elmore et al. (12) emphasizes the significance of maintaining the leaves photosynthetically active longer. They showed that the leaves of field grown cotton became photosynthetically inactive after 35 to 40 days. If the potential longevity of cotton leaves is 70 days as shown by D. N. Baker (unpublished data) and the data of Elmore et al. (12) represents the typical longevity of cotton leaves in the field, then considerable yield increases can be made by increasing the potential longevity of cotton leaves, so that they can remain photosynthetically active up to 70 days under typical field conditions. The simulation indicates that this mean of increasing photosynthesis is superior to selection based on specific leaf weight. This seems to agree with the failure of many researchers to increase yield when specific leaf weight was used as a criterion and suggest that increasing photosynthesis by maintaining the leaves photosynthetically active up to 70 days should prove successful in increasing yields.

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<sup>4</sup> GOSSYM contains logic based on observations of Ludwig et al. (25) that when LAI of the crops falls below 2.9, a significant fraction of light will penetrate through the canopy to the soil surface.

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