# Normal vs. Okra Leaf Yield Interactions in Cotton.
# II. Analysis of Vegetative and Reproductive Growth[1]

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## ABSTRACT

Past studies on differences in growth between Okra ($L_2°,L_2°$) and normal (broad-leaved, $l_2l_2$) cottons (*Gossypium hirsutum* L.) have routinely used Okra lines derived from backcrossing the Okra leaf trait into established cultivars. In the current study, we compared plant growth and fiber yield among near-isogenic lines of Okra and normal selected from bulked heterozygous populations derived from two sets of contrasting crosses. Four paired near-isogenic Okra leaf and normal leaf lines were planted in replicated trials on two planting dates in 1983 at Stoneville, MS. Two strains had superior lint yield by the normal leaf sib while two others had superior lint yield by the Okra sib. 'Stoneville 213' (STV 213), the Okra leaf cultivar produced by conventional backcrossing, served as the control wherein the normal leaf has been superior in yield compared to the Okra leaf. Except for plant height, the parameters of vegetative and reproductive growth showed no significant leaf type × strain, or leaf type × strain × harvest date interactions. The Okra leaf entries produced maximal leaf area indices that were 26 and 49% smaller than those produced by the normal leaf entries for the April and May plantings, respectively. This disparity was partially offset by the production of more leaves by the Okra entries in the early planting, but not in the late planting. The number of squares and flowers produced by the Okra leaf entries indicates a greater fruiting potential than was realized. The percentage of bolls that was shed was closely associated with the maximal number of immature bolls produced. We concluded that the Okra leaf cottons can produce plant canopies competitive in yield with those of broad-leaved cottons. The maximum potential of cottons with Okra leaves remains unclear, because of the large leaf type × environment interactions.

*Additional index words:* Gossypium hirsutum L., Vegetative growth, Reproductive growth, Yield components, Light penetration, Leaf area, Genotype × environment interaction.

THE Okra leaf trait ($L_2°,L_2°$) in cotton (*Gossypium hirsutum* L.) determines a leaf shape that is deeply cleft with narrow lobes, in contrast with normal (broad) leaf ($l_2,l_2$). In addition to a radically different leaf shape, the Okra leaf trait exhibits a large change in growth characteristics. When compared with normal types, plants homozygous for Okra have decreased total leaf area (11, 13), fewer vegetative branches (13), fewer nodes on the main plant axis with resulting shorter plant height (13), and greater production of floral buds (squares) and flowers (1, 13, 14) which, in turn, suggests the possibility of increased yield potential. However, Okra-leaved plants shed a higher proportion of fruits (bolls) than normal-leaved plants, probably because of increased competition for available photosynthate (14), and therefore a shift in the supply-demand ratio for carbohydrates (15). Okra-leaved cottons have photosynthetic rates that are similar to those of normal-leaved cultivars (3, 19), so lowered photosynthate production does not appear to be the cause of increased fruit loss. The above physiological differences result in a noticeable contrast between Okra and normal-leaved cottons that is especially evident in plant canopy architecture, light penetration characteristics, and reproductive growth patterns associated with altered carbohydrate source-demand ratios. Information about these differences may suggest growth alterations which can increase cotton plant productivity.

Okra-leaved stocks have generally yielded less fiber than normal-leaved isolines (4, 15, 17). Simulation studies suggest that the lower yielding potential is a result of insufficient leaf area to intercept solar radiation during sub-optimal growing conditions (15). Examples where Okra cottons produced greater lint yields than normal cottons were usually due to reduced boll rot, since the more open canopy of the Okra leaf produces a less humid environment (1, 12, 13).

Previous studies of Okra vs. normal cottons have usually included lines of Okra from backcrossing the Okra trait into cultivars with no accompanying selection for agronomic traits (1, 11, 12, 19). This procedure does not appear effective for developing agronomically competitive Okra-leaved lines. Meredith and Wells (18) developed high-yielding Okra and normal near-isolines by pedigree selection from two heterozygous bulked populations and selecting for performance. Such a procedure allowed for new, apparently more favorable gene combinations to enhance the performance of Okra trait lines. In the study reported herein, we determined the growth characteristics of Okra and normal near-isolines developed by the techniques outlined above.

## MATERIALS AND METHODS

Near-isogenic sibling lines with homozygous normal and homozygous Okra leaf shapes were selected by methods outlined in a previous report (18). Two pairs, Strain 1 from the 'Deltapine' (DPL) cross and Strain 146 from the 'Carolina Queen' (CQ) cross, were selected because the normal isoline produced more lint than the Okra sibline. Two additional pairs, Strain 28 from the DPL cross and Strain 138 from the CQ cross, were selected because the Okra sib produced more lint than the normal counterpart. 'Stoneville 213' (STV 213) normal and Okra-leaf near-isolines represent cotton where the Okra sib was produced by continual backcrossing to the cultivar. Normal STV 213, a broadly adapted cultivar with a long history of use, produces greater fiber yields than its Okra sibline.

The six entries were planted in randomized complete blocks with four replications per entry at Stoneville, MS in 1983 with the sibline pairs grown as paired comparisons. Sampling through the season could thus be regarded as the splitting of whole plots.

Experiments were planted on two dates, 27 April and 27 May. The two planting dates were expected to provide opportunities for the phenotypes to interact (16, 21). A main plot consisted of five rows with three borders and one row each for destructive and nondestructive sampling. Rows were 7.5 m in length and were spaced 1 m apart. The soil type was a Dundee silty clay (fine-silty, mixed, thermic Aeric

Ochraqualfs). Prior to planting, 101 kg N/ha and trifluralin herbicide ($\alpha,\alpha,\alpha$-Trifluoro-2,6-dinitro-$N$-$N$-dipropyl-$p$-toluidine) at the rate of 1.1 kg/ha were incorporated in the seedbed. Both test plots were furrow-irrigated on 26 July. Plants were thinned to 10/m at 31 and 21 days after planting (DAP) for the early and late planting, respectively. Insects were controlled with a full season insecticide applications program.

Parameters of growth were determined at 47, 54, 70, 90, and 119 DAP for the 27 April planting, and at 46, 55, 75, 97, and 123 DAP for the 27 May planting. Only complete replications were harvested on any day, and the data presented are based on mean DAP values for each harvest. A row section of 0.3 m was used for all destructive harvests. Harvested plants were separated into stems (including petioles and branches), leaves, floral buds (squares), immature bolls (closed), and mature bolls (boll walls open 1 cm). Leaf area was estimated from leaves of one of the harvested plants. Twenty leaves, which were representative sub-samples of the various leaf ages and positions on one plant, were removed for leaf area determination with a Li-Cor Model LI-3000[3] area meter. All samples were dried at 70° C for 72 h and the dry weights recorded. From the area and dry weight of the leaf sub-sample, the specific leaf weight (SLW) of the leaves was calculated. The SLW was in turn used to calculate the total leaf area index (LAI) by division into the total leaf dry weight (sub-sample dry weight + remaining plot leaf dry weight). Plant heights and the number of main stem nodes were recorded at all harvests.

The parameters for both vegetative and reproductive growth were determined for the top 30 cm, the next 30 cm, and the remaining plant section between the top 60 cm and the ground at the last two harvests for the 27 April, and the last three harvests for the 27 May plantings. Since there were no significant leaf type × canopy position, or leaf type × strain × canopy position interactions, only the whole plant parameters of vegetative and reproductive growth will be presented.

The photosynthetic photon flux density (PPFD) was determined at 91 DAP for the April planting and 73 DAP for the May planting, at 30 cm and 60 cm below the canopy apex and at ground level, utilizing a Li-Cor Model LI-1915B[3] line quantum sensor. By dividing the recorded value by the PPFD measured above the canopy, the percent light penetration was calculated for each point in the canopy.

Once every week, starting at 70 DAP for the April planting and at 53 DAP for the May planting, the number of flowers that opened on a given day were counted in the nondestructive sampling row. These values were used to estimate flowering activity.

Modified growing degree days were calculated after the methods of Gilmore and Rogers (7) by summing the value calculated for each day after planting as: $D = [(T_{max} + T_{min})/2] - T_B$, where the degree days for a given day was $D$, $T_{max}$ was the maximum air temperature (upper limit of 30° C), $T_{min}$ was the minimum air temperature (lower limit of 10° C), and $T_B$ was equal to 10° C.

The data were analyzed by analysis of variance with planting date as whole plot, strain as sub-plot, and leaf type as sub-sub-plot. Since harvest error variances were heterogeneous, the data were analyzed for each harvest separately. Except for plant height, no significant strain × leaf type interactions were evident in the data representing growth prior to seed cotton harvest, and the data are presented ac-

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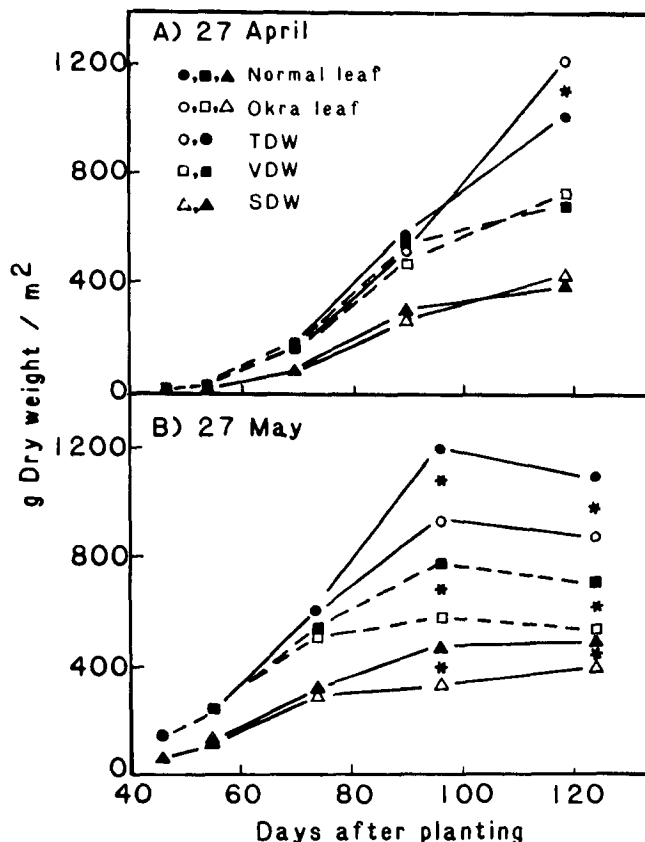


Fig. 1. Total dry weight (TDW), vegetative dry weight (VDW), and stem dry weight (SDW), measured at various dates, of the normal and Okra leaf cottons planted on (A) 27 April and (B) 27 May 1983. * indicates a significant difference between leaf types at the 0.05 level of probability.

cordingly.

The relationships between maximum observed immature boll number (IBN), and both the maximum observed LAI and the percentage of bolls shed prior to seed cotton harvest were analyzed by sub-unit regression. Non-significant model parameters were pooled with the appropriate error and analyses were continued until only significant model parameters remained. The dependent variables (IBN/$m^2$ and percentage of bolls shed) are presented as adjusted values, which are the predicted values plus the residual.

## RESULTS AND DISCUSSION

Plants of the two leaf types exhibited very little difference in either total dry weight (TDW), vegetative dry weight (VDW), or stem dry weight (SDW) for the 27 April planting (Fig. 1A). The only significant difference was at 119 DAP when Okra leaf plants had 11% greater TDW than normal leaf ones. The differences in TDW, VDW, and SDW between the leaf types were much more pronounced for the May planting (Fig. 1B). Normal leaf lines were consistently greater and had about 25% greater TDW than Okra leaf lines at 97 and 123 DAP. The trends and differences in VDW were similar. Generally, plants from the May planting had grown faster than those from the April planting at similar DAP dates. Lines planted in late May had TDW approaching 600 g/$m^2$ at 74 DAP, while lines planted in late April had TDW less than 200 g/$m^2$ at 70 DAP. Much of this difference is attributable

Table 1. Leaf area index (LAI), leaf dry weight (LDW), leaf number, specific leaf weight (SLW), and leaf size, measured at various dates, of the normal and Okra leaf cottons planted on 27 Apr. and 27 May 1983.

| | 27 April | | | 27 May | |
| | Leaf type | | | Leaf type | |
| Days after planting | Normal | Okra | Days after planting | Normal | Okra |
|---|---|---|---|---|---|
| | | LAI (m²/m²) | | | |
| 47 | 0.1 | 0.1 | 46 | 1.5 | 1.4 |
| 54 | 0.4 | 0.3 | 55 | 2.5 | 2.2 |
| 70 | 2.2 | 2.0 | 74 | 4.7* | 3.7 |
| 90 | 4.8* | 3.7 | 96 | 5.5* | 3.7 |
| 119 | 4.9* | 3.8 | 123 | 3.5* | 2.0 |
| | | LDW (g/m²) | | | |
| 47 | 9* | 8 | 46 | 85 | 81 |
| 54 | 19 | 19 | 55 | 126 | 124 |
| 70 | 95 | 89 | 74 | 233 | 211 |
| 90 | 234 | 205 | 96 | 301* | 224 |
| 119 | 287 | 288 | 123 | 215* | 132 |
| | | Leaf no./m² | | | |
| 70 | 222 | 230 | 74 | 493 | 573 |
| 90 | 538 | 606 | 96 | 654 | 635 |
| 119 | 592* | 755 | 123 | 542 | 470 |
| | | SLW (g/m²) | | | |
| 47 | 64* | 68 | 47 | 57* | 60 |
| 54 | 54* | 58 | 54 | 52* | 57 |
| 70 | 42* | 44 | 74 | 50* | 57 |
| 90 | 50* | 58 | 96 | 55 | 61 |
| 119 | 59* | 78 | 123 | 63* | 69 |
| | | Leaf size (cm²) | | | |
| 70 | 102* | 88 | 74 | 95* | 71 |
| 90 | 89* | 62 | 96 | 84* | 60 |
| 119 | 84* | 51 | 123 | 64* | 41 |

* Difference between the two leaf types, on the same date, is significant at the 0.05 level of probability, according to an LSD test.

Table 2. Percent light penetration at different distances below the canopy apex of normal and Okra leaf cottons at 91 and 73 days after planting on 27 Apr. and 27 May 1983, respectively.

| | Light penetration | | | |
| | 27 April | | 27 May | |
| | Leaf type | | Leaf type | |
| Distance from canopy apex | Normal | Okra | Normal | Okra |
|---|---|---|---|---|
| cm | | % | | |
| 30 | 63 | 68 | 52 | 62* |
| 60 | 29 | 35* | 21 | 28* |
| Ground | 7 | 10 | 7 | 8 |

* Difference significant at the 0.05 level of probability according to an LSD test.

The large LAI of the normal leaf isolines resulted in less light penetration into normal leaf canopies than in Okra leaf canopies (Table 2). At 60 cm below the canopy apex, the Okra leaf cottons allowed 6 and 7% more penetration of available light (PPFD) than did the normal leaf cottons. This difference was less noticeable at ground level as critical LAI values were approached by both leaf types. In both environments, the Okra leaf lines intercepted comparable amounts of light at ground level, yet had considerably lower LAI values. These data indicate that the Okra leaf lines had a larger energy return per unit of energy expended for growth. Furthermore, greater amounts of light penetrated to lower portions of the Okra leaf canopies, and could theoretically increase the photosynthetic contribution of individual leaves at lower canopy strata. The net result would be increased photosynthetic efficiency per unit LAI by Okra leaf canopies due to greater accessibility to light by leaves at positions that are commonly shaded, or partially so, in normal leaf canopies. In corroboration, there are reports that Okra leaf types, having greatly reduced leaf areas, do not have reduced canopy photosynthetic rates when expressed on a ground area basis (3, 19). As suggested by Landivar et al. (15), the underlying factor affecting the potential assimilatory capacity of Okra leaf canopies would be the ability to produce and maintain sufficient LAI to intercept the available solar radiation.

Plant height displayed the only significant strain × leaf type interactions. The normal leaf types of Strain 1 were significantly taller than their Okra leaf counterparts. For the remaining strains, Okra leaf plants were as tall as or taller than their normal leaf alternatives for both planting dates. The plant height differences do not appear to be associated with the fiber yields (18).

There were no significant differences in the number of nodes produced per plant between the leaf types, regardless of the date of harvest or the date of planting (Table 3). There were more squares/main stem node produced by the Okra leaf types from both planting dates than by the normal leaf cottons at certain DAP. The greater number of squares/main stem node of the Okra leaf lines significantly increased the number of squares/m² at 70 and 90 DAP for the first planting and at 55 DAP for the second planting.

As expected, the Okra leaf isolines also produced more flowers than the normal leaf lines (Fig. 2). The time interval prior to onset of flowering was shorter for plants from the May planting than for those from

to the greater cumulative heat units during early growth of the May planting compared to those of the April planting at similar DAP values. Increased temperature regimes in past studies have increased the growth of seedlings (6, 20) and have decreased the time between early reproductive events (10).

Normal leaf lines had significantly greater LAI values at the last two and three measurement dates of the April and May plantings, respectively (Table 1). Maximum LAI values for normal leaf lines were 29 and 65% greater than for the Okra leaf lines for the two planting dates. The larger leaf areas of the normal leaf types are reflected by the dry weights of leaves from the May planting but not by those from the April planting. This result is attributable partly to the number of leaves produced by the two leaf types. At 90 and 119 DAP of the April planting, Okra leaf lines produced 13 and 28% more leaves, respectively, than did the normal leaf lines. This result was not evident for plants from the May planting, however, because the normal leaf types had produced more leaves at both 90 and 119 DAP.

The intra-leaf dry matter partitioning was different as expected for the two leaf types. Leaf size of the Okra leaf type isolines was considerably smaller than that of the normal leaf counterparts at all dates measured, and for both plantings. An alternative to smaller leaves is development of thicker leaves, which appeared to be true for the Okra leaf isolines because their leaves exhibited consistently greater values of SLW.

the April planting. The greater square and current day (white) flower production by Okra leaf lines has been observed in other studies (1, 14). Kerby and Buxton (14) found that Okra leaf types produced more fruiting positions than did normal leaf types. They theorized that the Okra leaf types grew more slowly due to their lower LAI. Therefore, a suppression of apical dominance would increase reproductive proliferation. This theory is not a likely explanation of the greater Okra leaf square and flower production that we observed, however, since there were no significant leaf type differences in either early VDW or node number. The larger square-to-node ratios of the Okra leaf types suggests that differences exist between leaf types either for sympodial development or for square shedding. It has been reported that increased LAI results in increased *Lygus* spp. populations, which have been implicated as causal agents of square shedding (8); however, insects were controlled in our experiments.

The number of immature bolls (IBN) on plants from the April planting corresponded generally to the number of white flowers (Table 3). The Okra leaf cottons averaged 32 more immature bolls than the normal leaf cottons at 119 DAP of the April planting; no bolls had matured prior to the last harvest. Similarly, the Okra leaf cottons from the May planting had 20 more immature bolls than did the normal leaf ones at 74 DAP. The Okra lines, however, had matured 42% more bolls/ $m^2$ than the normal lines by 123 DAP.

The sub-class regression data for the relationship between the maximum measured IBN and the maximum measured LAI averaged over strains from each planting date are shown in Fig. 3. The Okra leaf cottons showed a significant positive association between maximum IBN and maximum LAI, adding over 40 immature bolls per unit increase in LAI, regardless of planting date. The normal leaf plants, however, showed a significant positive association between IBN and LAI only for the May planting. The slopes of the Okra and normal leaf regression lines were not significantly different for the later planting.

The data suggest that boll initiation is associated with the amount of leaf area present. The fact that the normal leaf cottons also had a positive relationship between LAI and IBN for the May planting suggests that greater leaf area is advantageous with later planting dates. Similarly, Ashley et al. (2) found that boll set was positively associated with leaf area, but they also found a positive relationship between lint yield

**Table 3. Node number, floral buds per main stem node, total floral buds, and immature boll number (IBN), measured at various dates, of the normal and Okra leaf cottons planted on 27 Apr. and 27 May 1983.**

| Days after planting | 27 April | | Days after planting | 27 May | |
| | Leaf type | | | Leaf type | |
| | Normal | Okra | | Normal | Okra |
| --- | --- | --- | --- | --- | --- |
| | Nodes/plant | | | | |
| 47 | 6 | 6 | 46 | 11 | 11 |
| 54 | 8 | 8 | 55 | 14 | 15 |
| 70 | 12 | 12 | 74 | 18 | 19 |
| 90 | 19 | 20 | 96 | 22 | 21 |
| 119 | 22 | 23 | 123 | 24 | 24 |
| | Floral buds/main stem node | | | | |
| 47 | 0.0 | 0.0 | 46 | 0.6 | 0.7 |
| 54 | 0.2 | 0.1 | 55 | 1.0* | 1.2 |
| 70 | 0.7* | 0.9 | 74 | 1.0 | 1.2 |
| 90 | 1.5* | 1.9 | 96 | 0.3 | 0.2 |
| 119 | 0.2 | 0.2 | 123 | 0.1 | 0.0 |
| | Floral buds/m² | | | | |
| 47 | 0 | 0 | 46 | 70 | 79 |
| 54 | 12 | 10 | 55 | 134* | 181 |
| 70 | 86* | 101 | 74 | 189 | 221 |
| 90 | 294* | 366 | 96 | 57 | 50 |
| 119 | 36 | 37 | 123 | 2 | 1 |
| | IBN/m² | | | | |
| 70 | 0 | 0 | 74 | 59*(100) | 79 (100) |
| 90 | 36 (100)† | 39 (100) | 96 | 148 (100) | 127 (100) |
| 119 | 123*(100) | 155 (100) | 123 | 85 (72) | 88 (65) |

* Difference between the two leaf types, occurring on the same date, is significant at the 0.05 level of probability according to a LSD test.
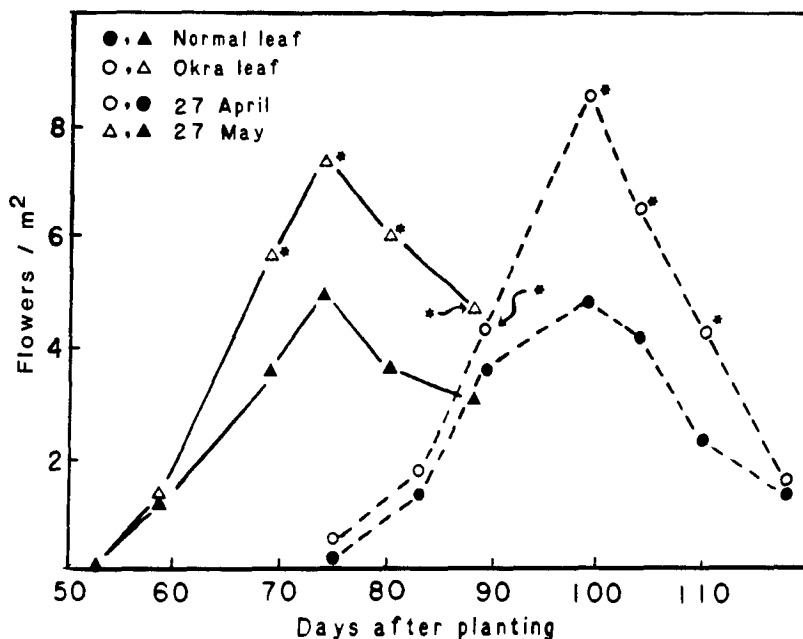† Percentage IBN of the number of total bolls (immature + mature).



Fig. 2. Flowers, counted at various dates, of the normal and Okra leaf cottons planted on (A) 27 April and (B) 27 May. * indicates a significant difference between leaf types at the 0.05 level of probability.
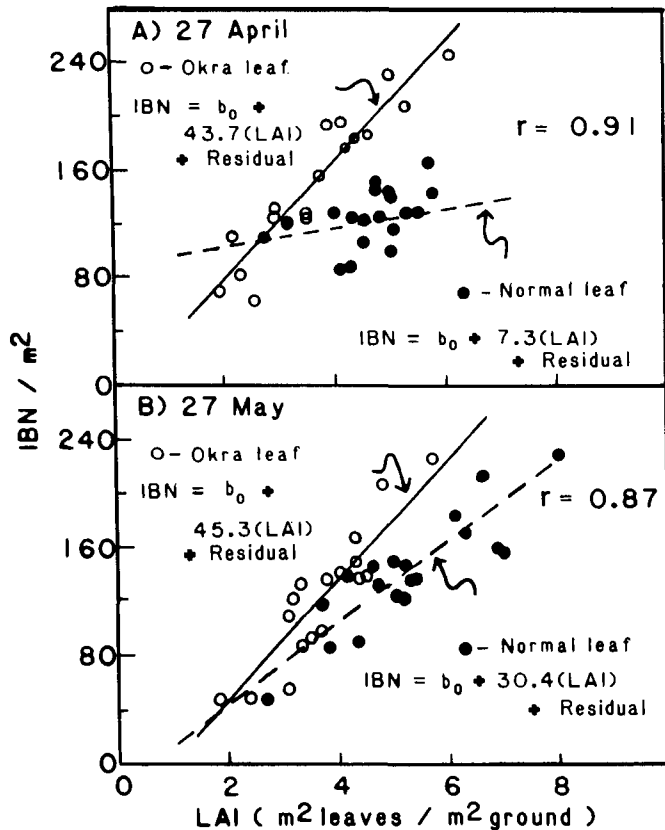
Fig. 3. Relationships between adjusted values (predicted + residual) of immature boll number (IBN) and leaf area index (LAI) for Okra leaf and normal leaf cottons planted on (A) 27 April and (B) 27 May.

and LAI that was not evident in our study (18).

The percentage of immature bolls that were shed prior to maturation was estimated by the relationship: % bolls shed = [(maximum observed IBN − total harvested bolls)/maximum observed IBN] × 100. Meredith and Wells (18) previously presented the data on total harvested bolls. The maximum observed IBN occurred at 119 and 96 DAP for the April and May plantings, respectively. The sub-class regression analysis between IBN and boll shed showed significant linear and quadratic associations at both dates (Fig. 4). No significant differences in the relationship were attributable to leaf type for either planting. Kerby and Buxton (14) reported that the number of bolls and squares shed were dependent on the number of fruiting positions produced. Similarly, other studies have found that fruit load was the major reason for low boll retention and early cessation of flowering (5, 9).

The negative values for percent boll shed were from plots that had more open bolls in the sample harvested at the end of the study than found as immature bolls counted earlier in the season. These observations are indicative of the plant-to-plant variability found at common plant populations. The constancy of the pattern was unaffected, however, between the percentage of boll shed and the maximum IBN.

Landivar et al. (15) proposed that Okra leaf cottons perform in an inconsistent manner in the field because they do not produce and maintain sufficient LAI during adverse conditions, specifically when N and water are limiting. In this study, the difference between the leaf type LAI was increased in response to the May
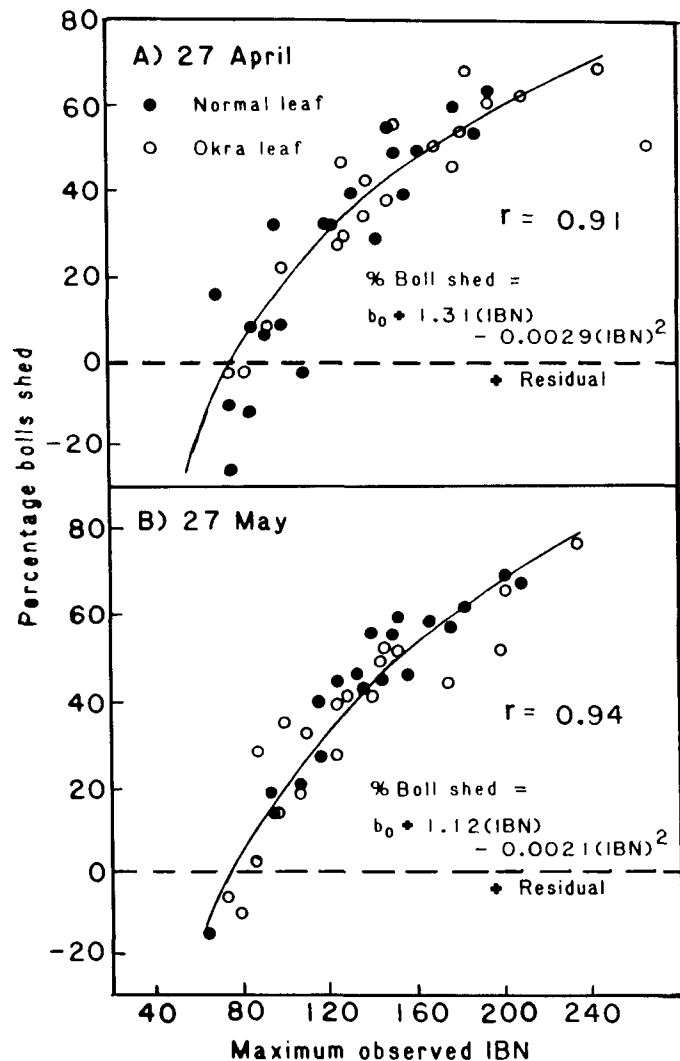


Fig. 4. Relationships betweeen adjusted values (predicted + residual) of percent boll shed and immature boll number (IBN) for the (A) 27 April and (B) 27 May planting dates.

planting date. For example, LAI of Okra leaf was 78% as high as that of normal leaf in the April planted plots but only 57% as high in the May planted plots at a comparable DAP (119 vs. 123 days). Nevertheless, yields from the late May planting did not indicate clearly that Okra leaf isolines yielded less than the normal leaf ones (18). Our results show that there is a high degree of genotype × environment interaction related to gene substitution at the $L_2^o$ locus (16, 18). The nature of this interaction with regard to vegetative growth and its relationship to yield remains unclear. The data, however, indicate that Okra leaf cottons can yield as well as normal leaf cottons in the Mississippi environment (18). Investigations into the effect of varying leaf type on full season canopy photosynthesis and its relationship to crop maturity may give solutions to yet unanswered questions.

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