

Heterosis in Upland Cotton. II. Relationship of Leaf Area to Plant Photosynthesis

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ABSTRACT

Heterosis results in a generalized increase in plant growth, yet the involvement of photosynthesis in this response is not well understood. We examined the relationship between leaf area (LA) and canopy photosynthesis of F₁ cotton (*Gossypium hirsutum* L.) hybrids and their parents. The effect of heterosis on leaf apparent photosynthesis (AP) was also studied. Three established cultivars and three F₁ hybrid progeny were examined in two field environments. Hybrid progeny had significantly greater leaf area index and canopy photosynthesis rates in both environments during the earliest plant growth stages studied. At the same time, the hybrids and their parent showed no differences in single leaf AP efficiency. Total dry matter was significantly correlated with LA ($r = 0.85^{**}$, significant at the 0.01 probability level). All measurements during early growth found AP per plant to be significantly associated to LA per plant. Later in growth, the association between AP per plant and LA per plant weakened after mutual shading of leaves had developed. The data indicate that hybrids produced generally bigger plants that intercepted more light than their parents, and hence had increased photosynthesis rates on a per plant basis. Factors that affect early plant growth can result in associated changes in AP per plant and accentuate the need for prudent crop management during early development.

Additional Index Words: *Gossypium hirsutum* L., F₁ hybrids, Leaf photosynthesis, Seedling growth, Leaf area index.

BLACKMAN (3) theorized that plants grow in a manner analogous to the compound interest law of monetary growth. In other words, early growth is the foundation upon which further development is based. This concept is important to understanding crop growth because it emphasizes the full-season nature of crop development and the many controllable and uncontrollable factors (e.g., management, genotype, environment) that can affect it.

Production of leaf area is very important in determining early season growth (7,8,12). Both interspecific (5,7) and intraspecific (12) cotton hybrids have greater growth rates and produce greater leaf area (LA) than their parents. Greater plant leaf area during seedling growth should theoretically increase photosynthesis per plant, since the plants can intercept more light prior to significant interplant competition for space (4).

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Published in Crop Sci. 28:522-525 (1988).

While heterosis would appear to affect canopy photosynthesis indirectly by leaf area changes, there have been conflicting reports about whether heterosis affects cotton leaf photosynthetic efficiency per se. While Bhatt and Rao (2) found considerable increases in hybrid leaf photosynthesis when hybrids were compared to their parents, Muramoto et al. (7) found no increases due to heterosis.

This study examined the relationship between plant leaf area and seedling photosynthetic rates among intraspecific cotton hybrids and their parents. In addition, the effect of heterosis on leaf photosynthetic efficiency was also examined.

MATERIALS AND METHODS

Three established upland cotton cultivars and three F_1 hybrid combinations were grown in two field environments (ENV). The hybrids represent bulked progeny of reciprocal crosses. No attempt was made to identify maternal or paternal effects in any ENV, since the overall effect of heterosis was of interest.

Environments 1 and 2 were planted at the same location on 16 Apr. and 20 May 1985, respectively. The soil type was a Dundee silty clay (fine-silty, mixed, thermic Aeric Ochraqualls). Prior to planting, 90 g N m^{-2} was applied as urea and incorporated. Trifluralin (α, α, α -trifluoro-2,6-dinitro- N, N -dipropyl- p -toluidine) was applied preplant at a rate of 1.1 g m^{-2} . The plots consisted of five, 7.5 m long rows at a width of 1 m. At approximately 3 wk after planting, the plots were thinned to 10 plants m^{-1} of row. Irrigation was not applied to the plots during the study. Photosynthesis measurements were made shortly (1 to 3 d) after rainfall of at least 2.5 cm.

Seedling photosynthesis measurements were made at 41 days after planting (DAP) for ENV 1, and at 31 and 36 DAP for ENV 2. Measurements were made using an aluminum-framed chamber covered with 0.7-mm thick Mylar¹. The chamber consisted of a lower body 1 m long \times 0.25 m wide \times 0.30 m high and a removable lid of the same dimensions. The bottom of the chamber body was pressed into the soil, forming an air-tight seal when the lid was closed. A fan was located at one end of the chamber to facilitate air movement within the chamber. With the fan, the effective chamber length became approximately 0.8 m. The change in CO_2 concentration of the air was monitored and photosynthetic rates were computed using a LI-COR (Lincoln, NE) Model LI-6000 Portable Photosynthesis System. The sensor head, consisting of air ports (sampling and return) and a thermocouple, was attached to a plastic plate (21 \times 36 cm) fastened to the chamber on a side opposite the fan. Measurements were made over a 30-s period at the ambient environmental conditions (e.g., CO_2 concentration, relative humidity, temperature). Plants from the earliest sampling of both ENV showed similar changes within the chamber since the plants were of similar size. During the measurement period, the following changes were typical: CO_2 would decline 15 to 30 $\mu L L^{-1}$, relative humidity would increase 5 to 15%, and the temperature in the chamber would increase 0.5 to 2.0 $^{\circ}C$. At the later measurement in ENV 2, larger plants than those mentioned above were measured, and the changes in CO_2 concentration and relative humidity reflected those plant size differences yet remained within the ranges given. All mea-

surements were made when the light intensity was at least 1000 $\mu mol m^{-2} s^{-1}$.

At 72 DAP and ENV 1, photosynthesis was determined with a larger chamber (1 m long \times 1 m wide \times 1 m high) with a flat lid. All conditions were as above.

Single-leaf measurements were made in ENV 1 at 45 DAP as described above except a 4-L hand-held chamber was used. The environmental changes within the chamber during the measurement period was similar to those mentioned above. A leaf about three nodes down from the top of the plant was used in the measurement. The light intensity requirement described above also pertained to single leaf measurements.

The plants in the seedling chamber were harvested following measurements of apparent photosynthesis (AP). They were separated into leaves and stems (petioles included). The leaf area was determined with a LI-COR Model LI-3000 area meter. The leaves and stems were dried at 70 $^{\circ}C$ and then weighed. At 72 DAP (ENV 1), the large leaf area required a sub-sample to be taken. Three adjacent plants were harvested within the chamber area. From one plant, 20 leaves of representative area and position were harvested and leaf areas were determined. The specific leaf weight (SLW) of these leaves was calculated by dividing dry weight by area. The total leaf area of the three harvested plants was then determined by dividing the total dry weight of leaves by the SLW.

The experimental design was a randomized complete block. The two samples in ENV 2 were considered a split of the whole plot. The data were analyzed using analysis of variance. Error variances of the two early samplings from both ENV were found to be heterogeneous from the error variance of the second sampling in ENV 2. The data from these growth stages were analyzed separately. The data collected during the early growth stage of both ENV were of similar magnitude and expressed no significant generation \times ENV or genotype \times ENV interactions. These data are therefore presented as averages across ENV. The probability of significance ($P(\bar{X})$) in Table 1 is for the generation (F_1 vs. parents) main effects since genotype \times generation interactions were nonsignificant. Data represent six replications.

The relationship between LA per plant and AP per plant was analyzed by subclass regression, where nonsignificant model parameters were pooled with error and continued until only significant parameters remained. Plotted points represent the predicted values plus the residual error. The distance the points lie from the predicted regression line represents error not explained by the model.

RESULTS AND DISCUSSION

The F_1 hybrids had greater leaf area index (LAI) than did their parents during the earliest stage of growth (Table 1). In addition, the canopy photosynthesis and total dry weight (DW) were different at the 0.06 and 0.08 levels of probability, respectively. There were no significant generation (F_1 , parents) \times cultivar interactions, indicating that the heterosis observed was expressed within all parental combinations. Later in development, the parent and hybrid LAIs were different at the 0.09 level of probability. The total dry weight of the plants was highly correlated to the LAI ($r > 0.85$; $P = 0.01$) in both ENV during the early stages of growth. The greater LAI of hybrids as compared with their parents and the close association between LAI and dry matter production was described earlier in cotton by both Muramoto et al. (7) and Wells and Meredith (12). Similarly, Potter and Jones (8) found

¹ Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the USDA and does not imply its approval to the exclusion of other products that may be suitable.

that leaf area production was extremely important in determining growth during early development in a number of crop and weed species. When plants are small and LAI is low, factors that maximize light interception (e.g., genotypic variation in leaf area) are important for increased growth potential (4). Increased leaf area during early growth would theoretically result in heightened light interception prior to significant interplant competition for space, and would increase the plant's assimilatory capacity.

There were highly significant relationships between AP per plant and LA per plant in ENV 1 (Fig. 1). The slope was significantly different from zero, and the R^2 indicates a strong association between AP per plant and LA per plant. A similar relationship between AP per plant and LA per plant was evident in ENV 2 despite the larger plant size at that time (Fig. 2). The LA per plant was much larger at an earlier time in growth in ENV 2 than ENV 1 and reflects the greater growth response to a later planting date. This response by cotton to a later planting date has been described in earlier reports (9,11).

The relationship between AP per plant and LA per plant early in growth of the plant confirms the importance of large LAI during seedling establishment. Hybrids produce plants with increased plant size and have leaf area ratios that are similar to their parents (12). Since these large plants can intercept more light prior to significant interplant competition for space, they possess increased growth potential. This situation is somewhat analogous to the linear relationship between net assimilation rate and light intensity in a number of species (10).

An obvious question is whether the enhanced can-

Table 1. Canopy apparent photosynthesis (CAP), leaf area index (LAI), and dry weight (DW) of F_1 hybrids and their parents at two stages of vegetative development.

Cross	CAP	LAI	Total DW
	mg CO ₂ m ⁻² s ⁻¹		g m ⁻²
Growth Stage 1†			
Coker 3114 × MD 82ne	0.137	0.24	25.7
Coker 3114 × PD 9241	0.124	0.24	24.9
PD 9241 × MD 82ne	0.115	0.24	27.2
Coker 3114	0.116	0.22	24.6
PD 9241	0.109	0.22	25.5
MD 82ne	0.101	0.19	21.4
Hybrid \bar{X}	0.125	0.24	25.9
Parent \bar{X}	0.109	0.21	23.8
P (\bar{X})‡	0.06	0.006	0.08
CV, %	25.4	17.7	19.8
Growth Stage 2			
Coker 3114 × MD 82ne	0.269	0.50	49.3
Coker 3114 × PD 9241	0.261	0.54	51.7
PD 9241 × MD 82ne	0.258	0.45	46.5
Coker 3114	0.254	0.48	49.1
PD 9241	0.249	0.46	47.9
MD 82ne	0.246	0.42	40.3
Hybrid \bar{X}	0.263	0.50	49.2
Parent \bar{X}	0.250	0.45	45.8
P (\bar{X})	0.29	0.09	0.24
CV, %	14.4	16.3	18.2

† Growth Stage 1 represents similar plant sizes averaged across ENV 1 and ENV 2 at 41 and 31 days after planting (DAP), respectively; Growth Stage 2 represents plants in ENV 2 at 36 DAP.

‡ Probability of significance for difference between the overall means of the hybrids and their parents. The generation × genotype interaction was not significant.

opy photosynthesis of the hybrids is related to the photosynthetic efficiency of the leaves. Neither AP per unit LA nor AP per leaf was significantly different between the hybrids and their parents in ENV 1 (data not shown). Similarly, Muramoto et al. (7) found no difference in AP among an interspecific hybrid and its parents, although the F_1 progeny expressed increased LA growth rates. The AP per unit LA was negatively correlated with LA per leaf ($r = -0.76^{**}$). Kaplan and Koller (6) found similarly negative relationships between leaf size and AP rate among soybean [*Glycine*

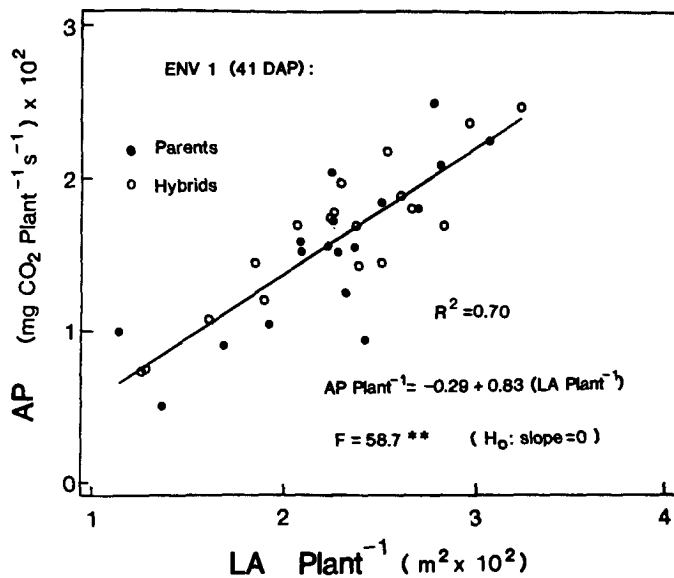


Fig. 1. Relationship of LA per plant to AP per plant during early growth in ENV 1 (41 DAP). The F values are based on a null hypothesis that the slope equals zero. Symbols represent the predicted values plus the residual error. The distance of a point from the predicted regression line represents variability not explained by the model.

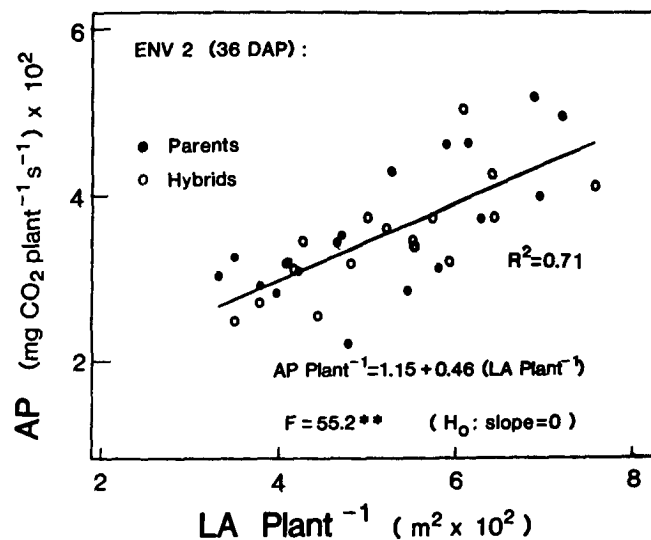


Fig. 2. Relationship of LA per plant to AP per plant in ENV 2 (36 DAP). The F values are based on a null hypothesis that the slope equals zero. Symbols represent the predicted values plus the residual error. The distance of a point from the predicted regression line represents variability not explained by the model.

max (L.) Merr.] cultivars that exhibited a positive association between relative leaf area growth rate and plant growth rate. The negative association between LA per leaf and AP has been found in many species and may contribute to the poor relationship between leaf AP and yield (1).

The relationship between AP per plant and LA per plant weakened as the plants' LA approached maximum values in ENV 1 (Fig. 3). The R^2 declined to 0.49 and the slope was no longer significantly different from zero. By this time, parent LA per plant values were similar to those of the progeny (0.39 vs. 0.34 $\text{m}^2 \text{ plant}^{-1}$). The diminished relationship between AP per plant and LA per plant is an indication of increased mutual shading of leaves within the canopy profile as suggested by Watson (10) in regard to declining net assimilation rates during the season.

In summary, the hybrids had increased growth during seedling development, which produced greater LAI. At early dates of measurement, the LA per plant was significantly related to AP per plant in both environments. Increased early development of the hybrids enhanced the capacity for further growth by increasing

photosynthate production through heightened light intercepting capacity. These changes in hybrid growth were not causes for the vigor noted, but are really consequences of heterosis. The true causes of hybrid vigor remain unidentified and are involved in earlier growth events than investigated in this study. The increased canopy photosynthesis of the hybrids is an indirect effect of the heterosis and further enhances the potential for growth.

Further, these data imply that all factors that affect seedling growth and early leaf area development (e.g., genotype, seed quality, weather, pests) can influence the magnitude of AP per plant, and emphasize the importance of early season crop management. Relatively small variations in early development, although seemingly innocuous at the time, can result in considerable differences later in growth. After critical leaf area indices are attained, the importance of LAI is reduced and other physical limitations associated with canopy architecture prevail.

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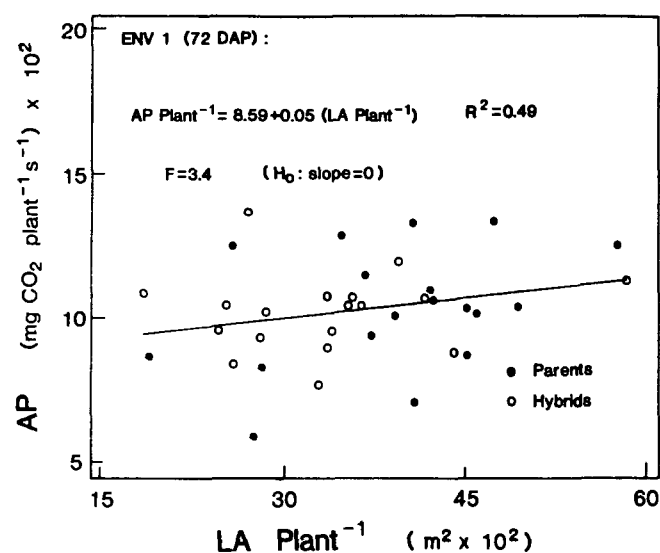


Fig. 3. Relationship of LA per plant to AP per plant during early reproductive growth in ENV 1 (71 DAP). The F values are based on a null hypothesis that the slope equals zero. Symbols represent the predicted values plus the residual error. The distance of a point from the regression line represents variability not explained by the model.