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Photosynthetic capacity and carbon contribution of leaves and bracts to developing floral buds in cotton

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Abstract

During ontogeny of *Gossypium hirsutum* L. floral buds (squares), increases in area and dry mass (DM) of floral bracts and the subtending sympodial leaf followed a sigmoid growth curve with increasing square age. The maximum growth rates of the bract area and bract DM occurred between 15 and 20 d after square first appearance (3 mm in diameter). Net photosynthetic rate (P_N) of the sympodial leaf at first fruiting branch position of main-stem node 10 reached a maximum when the subtended square developed into a white flower. Floral bracts had much lower P_N and higher dark respiration than the subtending leaf. The amount of $^{14}CO_2$ fixation by the bracts of a 20-d-old square was only 22 % of the subtending leaf, but 56 % of ^{14}C-assimilate in the floral bud was accumulated from the bracts, 27 % from the subtending leaf, and only 17 % from the main-stem leaf at 6 h after ^{14}C feeding these sources. Hence floral bracts play an important role in the carbon supply of developing cotton squares.

Additional key words: boll; bract removal; ^{14}C-assimilate translocation; dark respiration rate; dry matter accumulation; *Gossypium hirsutum* L.; lint; net photosynthetic rate; seed; sympodial and main-stem leaves.

Introduction

A cotton square consists of a floral bud and three bracts (Fig. 1). Development of cotton squares is fundamental for yield since it is the first step in the cotton fruiting cycle. However, squares often fail to form flowers (Guinn 1982). If failure occurs with too many squares abscised, maturity can be delayed and lint yield and fiber

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Abbreviations: C_i, intercellular CO_2 concentration; DM, dry mass; E, transpiration rate; g_s, stomatal conductance; MSN, main-stem node; LA, leaf area; P_N, net photosynthetic rate; PAR, photosynthetically active radiation, R_D, dark respiration rate.
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quality can be reduced. Therefore, a better understanding of initiation, differentiation, and development of squares, and the characteristics of their physiology and biochemistry during development is important for improving cotton production (Zhao 1997).

Insufficient assimilate supply is one of the major factors causing abscission of squares and bolls (Guinn 1982). An adequate supply of photosynthate for boll development in the cotton plant canopy requires the contribution of assimilate from several sources (Ashley 1972, Benedict *et al.* 1973, Peoples and Matthews 1981). The major sources of carbon for boll development are the leaf subtending the boll, the sympodial leaf at the adjacent fruiting position, and the main-stem leaf subtending the sympodial fruit branch (Horrocks *et al.* 1978). Bracts are also minor suppliers of saccharides for developing bolls, and are approximately 5-15 % as efficient as leaves in the ability of $^{14}CO_2$ fixation during boll development (Elmore 1973, Benedict and Kohel 1975, Wullschleger and Oosterhuis 1990*a*).

All previous studies on the photosynthesis of leaves and bracts related to cotton fruit development only focused on developing bolls after flowering. Carbon contribution of different source tissues to developing squares has not been reported. Our hypothesis was that bracts may be more important in providing assimilate for square development than for boll development, because the subtending sympodial leaf only unfolded 7 to 10 d after the square first appeared (Zhao 1997). The objectives of the present studies were (*1*) to quantify the changes in area and DM of the subtending leaf and bracts, bud DM, and P_N of the leaves and floral bracts during square development, and (*2*) to determine the carbon contribution of leaves and bracts to square growth.

Materials and methods

Field studies: The cotton (*Gossipium hirsutum* L.) cultivar Deltapine 20 was machine-planted in the field on a moderately well-drained Captina (Typic Fragiudults) silt loam at the Arkansas Agricultural Research and Extension Center, University of Arkansas in Fayetteville, AR, USA on 4 June 1993, 17 May 1994, and 19 May 1997. Rows were spaced 1 m apart and oriented in a north-south direction. Plants were hand-thinned to a density of 9 plants per 1 m row when the seedlings had approximately three true leaves. Preplant fertilizer was applied at a rate of 4.5-3.0-7.5 g(N-P-K) m^{-2} and an additional side-dressing of 5.6 g(N) m^{-2} as ammonium nitrate was given on 13 July 1993, 28 June 1994, and 14 June 1997 (early square stage). Control of weeds and insects, and furrow irrigation were applied as needed during the growing seasons according to Arkansas cotton extension recommendations (Bonner 1993). The field was divided into two blocks for sampling and for determining final boll economical properties and lint yield. Each block consisted of three plots (replications). The plot size was 10×15 m (1993 and 1994) or 5×5 m (1997).

When the squares at the fruiting position 1 of main-stem node (MSN) 10 (Fig. 1) first became visible (about 3 mm in diameter), they were individually labeled by

tagging main-stem leaves at the respective node with dated jeweler's tags. Approximately 900 (1993 and 1994) or 100 (1997) squares similar in size at this position from three replications were tagged in a day (23 July 1993, 6 July 1994, 4 July 1997). Squares at this date were considered day zero in age. During development of the tagged squares in 1993 and 1994, samples of the squares and the sympodial leaves subtending the squares were taken at 5, 10, 15, 20, and 25 d after the tagging date until the squares developed into white flowers (anthesis). Up to 30 tagged squares and subtending sympodial leaves in each plot of three replications were randomly collected starting at 09:00 h Central Daylight Savings Time (CDST) at each sampling date. The tissues were immediately transported to the laboratory. Squares were separated into floral buds and bracts. Areas of leaves and bracts were measured individually with a *CI-251* area meter (*CID*, Moscow, ID, USA). Thereafter, tissues were dried at 70 °C for 72 h in a forced draft oven, and weighed.

During the development of tagged squares in 1993, transpiration rate (E), stomatal conductance (g_s), intercellular CO_2 concentration (c_i), P_N, and incident photosynthetically active radiation (PAR) for the main-stem leaf and sympodial leaf at fruiting position 1 of MSN 10 were determined with a portable photosynthesis system (*LI-COR 6200*, Lincoln, NE, USA), between 11:30 and 13:00 h (CDST) on cloudless days. After measuring P_N, these leaves were immediately collected and leaf area (LA) was measured with a *CI-251* area meter.

In the 1993 and 1994 growing seasons, bracts of approximately 100 tagged young squares from 3 replications were removed by hand when they were 5 d old to investigate the effect of bract removal on the development of squares and bolls. When most bolls at the tagged positions opened, 60 mature tagged bolls were harvested from bract removal and control treatments, ginned, and the following parameters determined: average seed cotton mass per boll (boll mass), lint %, 100-seed mass (seed index), lint mass from 100 seeds (lint index), and the number of seeds per boll.

Greenhouse study: Cotton (cv. Deltapine 20) seeds were planted in four polyvinylchloride pots (45 cm diameter, 67 cm deep) filled with Captina silt loam from a cotton field on 21 April 1995. After emergence, seedlings were thinned to two plants per pot.

Water and fertilizer were supplied as needed and the greenhouse temperature during growth ranged between 30 (day) and 20 (night) °C. Supplementary irradiation was provided by two 1000-W *Sylvania* lights (*Underwriters Lab.*, York, PA, USA). The photosynthetically active radiance (PAR) at the top of plants at noon of sunny days was about 1300 $\mu mol\ s^{-1}\ m^{-2}$. From the day of first square appearance, all visible squares at all fruiting positions were labeled daily with dated jeweler's tags. When the first square on the plant became a white flower, the P_N and dark respiration rates (R_D) of all tagged squares, which included the bracts and floral bud, and sympodial leaves subtending the squares in the plant canopy were individually determined with the *LI-6200* photosynthesis system and a custom built cylindrical cuvette with a volume of 325 cm^3. Thereafter, the bud was removed from the square with a razor blade, and the cut was immediately sealed with vaseline. R_D of bracts

alone was then measured. When we were measuring the R_D, the cuvette was covered with a double-layer of aluminum foil painted inside with black paint. Bud R_D and bract P_N were calculated by subtracting bract R_D from R_D of a square (bud + bracts), and subtracting bud R_D from square P_N, respectively.

$^{14}CO_2$ fixation and ^{14}C-assimilate translocation study: In 1997, when tagged squares at the fruiting position 1 of MSN 10 were 20 d in age (24 July, sunny day), carbon fixation and translocation of the main-stem leaf, the sympodial leaf at fruiting position 1, and bracts of tagged squares at MSN 10 were measured by monitoring the ^{14}C radioactivity in various plant organs following exposure of selected leaves or bracts to $^{14}CO_2$. The three $^{14}CO_2$-feeding treatments were (*1*) the main-stem leaf at MSN 10, (*2*) the sympodial leaf at fruiting position 1 of MSN 10, and (*3*) the bracts of the square at fruiting position 1 of MSN 10. Each treatment included 6 plants from 3 replications. The structures and relative sizes of a sympodial fruiting branch from MSN 10 and a 20-d-old square from fruiting position 1 when the $^{14}CO_2$-feeding treatments commenced are given in Fig. 1.

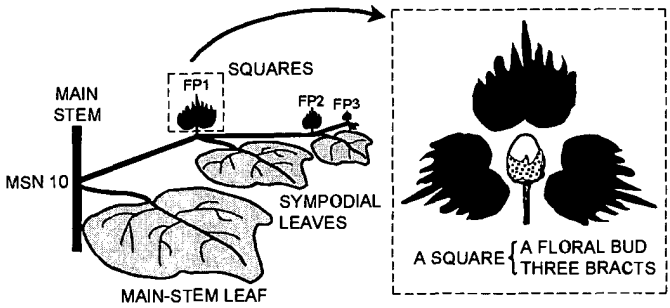

Fig. 1. Diagrammatic representation of a cotton sympodial branch from main-stem node (MSN) 10 and a 20-d-old square. The sympodial branch (*left*) shows the relative size and positions of the main-stem leaf, three squares at fruiting positions 1, 2, and 3 (FP1, FP2, and FP3), and three sympodial leaves subtending the squares. The square (*right*), which is separated into a floral bud and three bracts, shows the relative size of the floral bud and the bracts surrounding the bud.

The ^{14}C-labeling technique utilized was similar to that of Wullschleger and Oosterhuis (1990*b*). Approximately 1.85×10^5 Bq of $^{14}CO_2$ was released into a 3 500 cm^3 polyethylene bag (*Ziploc, Dow Chemical*, Indianapolis, IN, USA) that enclosed the photosynthetic organ and had been tightly sealed around the petiole of the source leaf or the peduncle of the square (for investigating bract carbon fixation). Evolution of $^{14}CO_2$ was initiated by injecting 4 cm^3 of 2.5 M lactic acid into a scintillation vial which was attached to the inside of the bag and contained 1.5 cm^3 of $NaH^{14}CO_3$ (specific activity $>1.85 \times 10^8$ Bq $mmol^{-1}$). The main-stem leaf, sympodial leaf, and floral bracts at fruiting position 1 of MSN 10 were individually exposed to $^{14}CO_2$ for 15 min starting at 11:30 h CDST. Tissues of the petiole and blade of the source leaf, and the peduncle, bracts, and floral bud of the tagged square were harvested 6 h after $^{14}CO_2$-feeding. Samples were dried at 70 °C for 72 h in a forced draft oven, and weighed. Individual samples were subsequently combusted in a sample oxidizer, and

the ^{14}C radioactivity counted in a *Packard Tri-Carb 4530* liquid scintillation spectrometer (*Packard Instrument*, Downers Grove, IL, USA).

Values analysis: The patterns of LA, bract area, and DM of leaf, bracts, and floral bud *versus* square age were fitted with nonlinear regression. The remaining values were analyzed statistically using variance analysis and least significant difference (LSD) tests according to the general linear model (GLM) procedure of a statistical analysis system (*SAS Institute*, Cary, NC, USA). Differences of means were considered significant when $p<0.05$.

Results

Growth of a square and subtending sympodial leaf: During square development, the increases in the area and DM of bracts of a square exhibited a typical sigmoid growth curve with increasing square age, and reached near maximum values when the square became a white flower (Fig. 2). The period of maximum growth rates of bract area enlargement and DM accumulation was between 14 and 18 d after a square was first visible (about 3 mm in diameter).

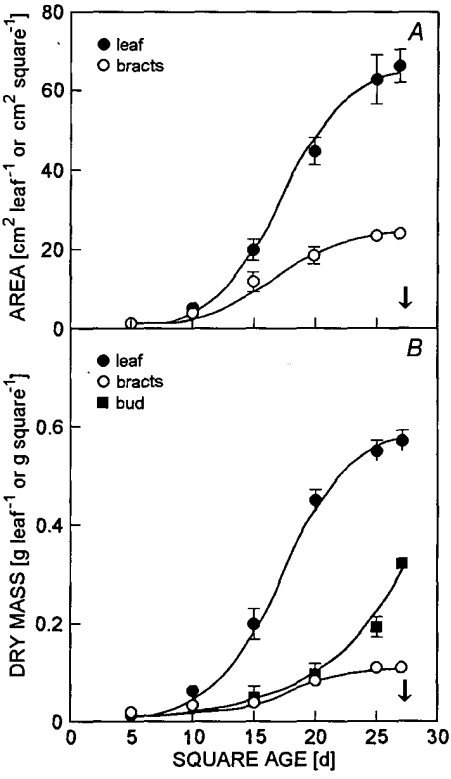

Fig. 2. Changes in (*A*) the areas of the sympodial leaf and floral bracts subtending a square at sympodial fruiting position 1, and (*B*) dry mass accumulations of the sympodial leaf, the bracts, and the floral bud during the square development. Values are means ± SD of 1993 and 1994. *Arrows* indicate flowering.

The increase in DM of a floral bud with increasing square age exhibited a typically exponential growth curve (Fig. 2*B*). Bud DM increased slowly during the first 15 d of square development. Thereafter, the DM increased rapidly, and 1 d before anthesis was triple that at 15 d.

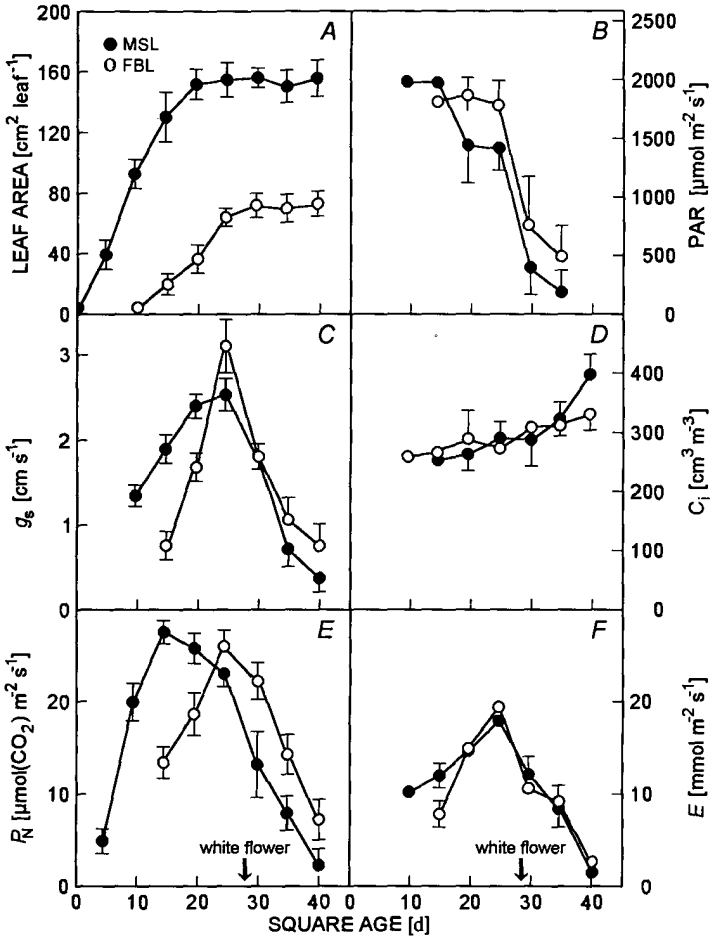

Fig. 3. Patterns of (*A*) leaf area, (*B*) photosynthetically active radiation (PAR), (*C*) stomatal conductance, g_s, (*D*) intercellular CO_2 concentration, C_i, (*E*) net photosynthetic rate, P_N, and (*F*) transpiration rate of main-stem leaf (MSL) and sympodial fruiting branch leaf (FBL) at the fruiting position 1 of main-stem node 10 during the development of the square in 1993. Each point shows the mean ± SD of the nine leaves.

Patterns of LA and DM of the sympodial leaf subtending a square with square age were similar to those of the floral bud bracts (Fig. 2). The sympodial leaf and floral bracts at a specific fruiting position had similar area and DM within the first 10 d of the square development. Thereafter, the subtending sympodial leaf exhibited significantly greater LA and DM than bracts of the square. The LA and DM of the

sympodial leaf were 3- and 5-fold greater than those of floral bracts, respectively, when the square became a white flower.

Gas exchange characteristics of leaves and bracts: Under field conditions, LA, P_N, g_s, C_i, E, and PAR for an undisturbed main-stem leaf at MSN 10 and a sympodial leaf subtending a tagged square at fruiting position 1 of the same main-stem node were measured during the subtended square developmental period in 1993 (Fig. 3). The main-stem leaf had just unfolded (about 3 cm^2 in size) when the square at fruiting position 1 of this sympodial branch first appeared. The sympodial leaf unfolded in 5 to 10 d after the appearance of the subtended square. Thereafter, the main-stem and sympodial leaves grew rapidly, and their LA and P_N peaked at 15 and 25 d after appearance of the square at fruiting position 1, respectively. The maximum P_N of the subtending sympodial leaf occurred at the time the subtended square developed into a white flower, after which leaf P_N declined rapidly as the young boll developed. During square development, the subtending leaf also had the greatest g_s and the highest E (Fig. 3*C,F*) when their P_N reached maximum. The leaf exhibited less change in C_i with square age compared to other leaf parameters (Fig. 3*D*).

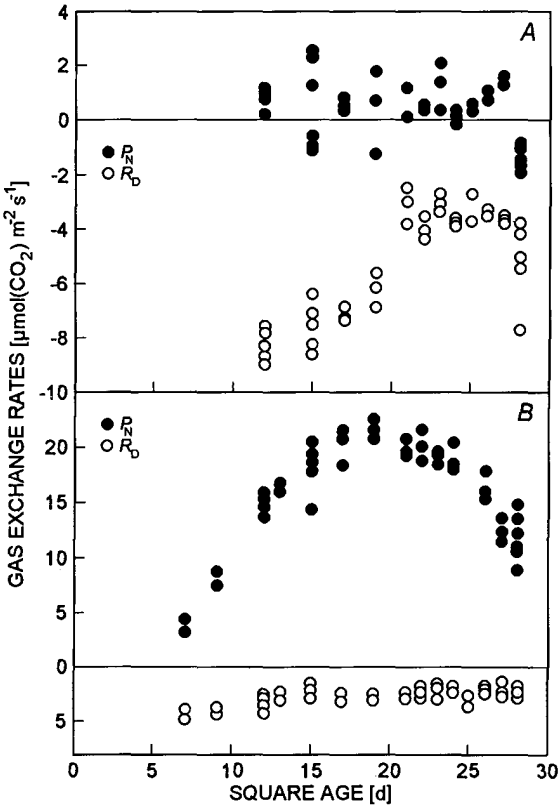

Fig. 4. The net photosynthetic rate (P_N) and dark respiration rate (R_D) of (*A*) square bracts and (*B*) sympodial leaves subtending the squares with increasing square ages for greenhouse-grown cotton plants.

Under greenhouse conditions, P_N of bracts ranged between -2.0 and 2.0 μmol m^{-2} s^{-1} during square ontogeny, and showed no clear pattern of change with square age (Fig. 4*A*). Compared to leaf photosynthetic properties, bract P_N was very low, and the change in bract P_N with square age was less than that in leaf P_N. During square development, R_D of bracts for 10- to 15-d-old squares was highest, and then decreased with increasing square age. In contrast, the R_D of the sympodial leaf subtending a square was much lower than that of the bracts, and showed much less change with square age (Fig. 4*B*).

Under field conditions, removing bracts of 5-d-old squares did not significantly affect the square developmental phase (days from first visible square through white flower) and floral bud DM (values not presented). However, the squares with bract removed had about a 20 % ($p<0.05$) decrease in the final average boll mass compared with squares with bracts intact (Table 1). Bolls with bracts removed tended to increase lint percentage, with no effect on the number of seeds per boll.

Table 1. Effect of removing bracts of young squares at fruiting position 1 of main-stem node 10 on boll mass [g per boll], lint percentage [%], seed index and lint index [g per 100 seeds], and the number of seeds [number per boll] of field-grown cotton. * significant difference between bract intact and bract removal treatments ($p<0.05$). +Bracts removed at 5 d after the first appearance.

Year	Treatment	Boll mass	Lint %	Seed index	Lint index	Seeds
1993	control	4.83	40.9	9.64	6.67	29.6
	removal+	3.87*	41.3	7.91*	5.57*	28.7
1994	control	6.41	38.7	10.72	6.77	36.7
	removal	5.16*	39.9	8.78*	5.83	35.3

Carbon contribution of main-stem leaf, sympodial leaf, and bracts to the floral bud: Main-stem and sympodial leaves at fruiting position 1 of MSN 10 had similar abilities for total carbon fixation on a tissue basis, whereas total $^{14}CO_2$ fixation of bracts was only 21 % of the leaf (Table 2). However, when the ^{14}C radioactivities per dry mass were compared for the three $^{14}CO_2$-labeled tissues, the main-stem leaf had significantly lower radioactivity ($p<0.05$), while the bracts and subtending sympodial leaf had similar ^{14}C-fixing abilities. The low radioactivity per unit LA or per unit DM for the main-stem leaf was possibly due to shade from upper leaves in the plant canopy (Oosterhuis and Urwiler 1988). It is possible that some ^{14}C-assimilate produced by the main-stem leaf was exported into other tissues, such as the main stem and adjacent fruiting branches (Brown 1968).

Although the bracts had lowest total $^{14}CO_2$ fixation of the three organs labeled, the floral bud of $^{14}CO_2$-labeled bracts had significantly higher ^{14}C radioactivity than those of $^{14}CO_2$-labeled main-stem or sympodial leaves at 6 h after $^{14}CO_2$-labeling treatments. In a 6-h translocation period, the bracts supplied about 18 % of the ^{14}C-assimilate fixed to the floral bud, whereas the main-stem leaf and subtending sympodial leaf exported only 1 and 2 % of their fixing ^{14}C-assimilate, respectively.

Table 2. Total $^{14}CO_2$ fixation [dps per tissue or per unit DM] of main-stem leaf, sympodial leaf, and floral bracts, and floral bud radioactivities [dps bud^{-1}] and % of ^{14}C-assimilate translocated into the bud of a square at fruiting position 1 of main-stem node 10 at 6 h after $^{14}CO_2$-labeling in 1997. Each value is mean ± SD of 3 replications. Total $^{14}CO_2$ fixation is the sum of radioactivities in the tissues of the petiole and blade of source leaf, and the peduncle, bracts, and floral bud of the subtended square for labeled leaves, and the sum of radioactivities in the bud and subtending bracts for labeled bracts. % transported to floral bud = [floral bud radioactivities : total ^{14}C fixation] × 100. Means followed by the same letter within a column are not significantly different ($p > 0.05$).

Source tissue	Total $^{14}CO_2$ fixation [dps]		Floral bud radioactivity [dps bud^{-1}]	% transported to floral bud
	per leaf or square	per mg DM		
Main-stem leaf	12 558 ± 330^a	10.2 ± 0.5^b	139.8 ± 18.0^b	1.10 ± 0.11^b
Sympodial leaf	11 682 ± 669^a	27.6 ± 1.8^a	220.8 ± 43.9^b	1.90 ± 0.31^b
Bracts	2 626 ± 13^b	32.5 ± 1.5^a	465.9 ± 35.3^a	17.70 ± 1.27^a

The carbon contributions of these three source tissues to a 20-d-old floral bud at fruiting position 1 were estimated according to the bud radioactivity (Table 2). The bracts subtending a floral bud were the major carbon supplier for the bud, providing about 56 % of ^{14}C-assimilate imported into the bud. The main-stem leaf and subtending sympodial leaf provided only 17 and 27 % of the ^{14}C-assimilate, respectively, for the floral bud at fruiting position 1.

Discussion

In this study, patterns of LA and P_N for an individual leaf with square age during square development were similar to the reports of Constable and Rawson (1980*a*), Wullschleger and Oosterhuis (1990*a*), and Bondada and Oosterhuis (1998a,b), who found that maximum P_N of a leaf for both greenhouse- and field-grown cotton was between 14 and 20 d after the leaf unfolded, and thereafter declined steadily as the leaf aged. Decreased leaf P_N is related to both leaf senescence and shade from leaves at higher canopy positions (*i.e.*, low PAR, Fig. 3). Sassenrath-Cole and Heitholt (1996) reported that the environmental alterations resulting in low incident photon flux during leaf senescence presented a much more substantial limitation to leaf carbon uptake than the physiological loss of photosynthetic activity due to increasing leaf age.

Bracts of cotton fruits not only protect fruit growth during the development of squares and bolls, but also provide assimilate for boll development (Brown 1968, Elmore 1973, Benedict *et al.* 1973, Elmore and McMichael 1975). Elmore and McMichael (1975) reported that bract area and bract DM were only about two thirds of their maximum values by the time squares became white flowers, and peak bract area and bract DM were reached at about 14 d after flowering. However, in our study, the area and DM of bracts reached the maximum values at approximately

white flower, and the final area of bracts of a square at anthesis was much smaller than that of the subtending sympodial leaf (Fig. 2).

The P_N of bracts during cotton boll development has been studied by several researchers using different methods (Morris 1965, Ashley 1972, Benedict *et al.* 1973, Elmore and McMichael 1975, Constable and Rawson 1980*b*, Wullschleger and Oosterhuis 1990*b*, Bondada *et al.* 1993). All these researchers found that the contribution of bract photosynthesis to boll development was much smaller than the leaves. During square development, however, bract photosynthetic properties and bract carbon contribution to floral buds are not clear. Our greenhouse study indicated that P_N of bracts during square ontogeny was only 10 to 15 % of the subtending leaf P_N (Fig. 4). Bondada *et al.* (1993) pointed out that low P_N of bracts was probably associated with a poor anatomical structure and low irradiance because bracts had significantly lower stomatal density and lower chlorophyll concentration than leaves. However, in our $^{14}CO_2$ fixation study, ^{14}C radioactivity per unit DM was similar between bracts of 20-d-old squares and the subtending leaf (Table 2). During square development, the bract DM:bract area ratio (52 g m^{-2}) averaged by cross sampling dates and years was much smaller than the ratio of the subtending leaf (99 g m^{-2}). Since the P_N is usually expressed on a LA basis or on bract area basis, lower bract P_N was also related to a smaller bract DM:area ratio compared to the leaf. Generally, carbon contribution of bracts to fruit was smaller than the subtending leaf because the area and DM of the bracts of a square were only about 36 and 19 % of the subtending leaf, respectively, at flowering (Fig. 2).

Constable and Rawson (1980*b*) measured the P_N, R_D, and E of cotton fruit (including bracts) during square and boll development of greenhouse grown cotton plants, and reported that radiant energy-saturated P_N and R_D were greatest for young squares and then decreased linearly up to 10 d after anthesis. In our greenhouse study, however, the P_N of bracts showed little change during the square development, and was much lower than the P_N of the subtending leaves. In contrast, floral bracts showed higher R_D than the subtending leaf (Fig. 4). Therefore, low bract P_N was also associated with higher bract R_D compared to the leaf.

Although bracts had lower P_N than the leaves during cotton boll development, Wullschleger and Oosterhuis (1990*b*) pointed out the function of bracts in carbon assimilation may increase under water stress and shade. Our study of $^{14}CO_2$ fixation and ^{14}C-assimilate translocation from sources (leaves and bracts) to the sink (floral buds) revealed that the floral bracts were very important for the carbon supply of square development. In the floral bud of a 20-d-old square at fruiting position 1 of MSN 10, about 56 % of ^{14}C-assimilate came from subtending bracts, only 17 % from the main-stem leaf, and 27 % from subtending sympodial leaf (Table 2). Bract assimilate was apparently easier to move into the floral bud compared to the leaf assimilate. This may be related to a shorter pathway between bracts and the floral bud. Additionally, more rapid translocation of assimilate from bracts to the floral bud is also associated with nonstructural saccharide composition in bracts. In the other studies, we found that the portion of sucrose and total nonstructural saccharide (hexose + sucrose + starch) concentrations in floral bracts was much greater than the portion in the leaves (Zhao and Oosterhuis 1998*a*,*b*). Therefore, a greater sucrose

fraction in the bracts may be one of the causes leading to faster translocation of bract photosynthate into the fruits because the sucrose is a major form in which carbon is translocated in this plant (Kruger 1990).

In conclusion, results of our study indicated that although the P_N of the bracts was lower than that of leaves during cotton square development, the change in bract P_N with square age and boll age (Wullschleger *et al.* 1990*b*) was much smaller compared to their subtending leaves. The ^{14}C-assimilate translocation studies indicated that bracts play an important role in floral bud growth during square development. The bracts exported assimilate to the floral bud much more rapidly than the associated leaves did. Therefore, bract removal of young squares would lead to a significant decrease in final boll mass.

References

Ashley, D.A.: ^{14}C-labelled photosynthate translocation and utilization in cotton plants. - Crop Sci. **12**: 69-74, 1972.

Benedict, C.R., Kohel, R.J.: Export of ^{14}C-assimilates in cotton leaves. - Crop Sci. **15**: 367-372, 1975.

Benedict, C.R., Smith, R.H., Kohel, R.J.: Incorporation of ^{14}C-photosynthate into developing cotton bolls, *Gossypium hirsutum* L. - Crop Sci. **13**: 88-91, 1973.

Bondada, B.R., Oosterhuis, D.M.: Decline in photosynthesis as related to alterations in chloroplast ultrastructure of a cotton leaf during ontogeny. - Photosynthetica **35**: 467-471, 1998a.

Bondada, B.R., Oosterhuis, D.M.: Relationships between nitrogen content and net gas exchange components of a cotton leaf during ontogeny. - Photosynthetica **35**: 631-635, 1998b.

Bondada, B.R., Oosterhuis, D.M., Wullschleger, S.D., Kim, K.S., Harris, W.M.: Anatomical considerations related to photosynthesis in cotton (*Gossypium hirsutum* L.) leaves, bracts, and the capsule wall. - J. exp. Bot. **45**: 111-118, 1993.

Bonner, C.M.: Cotton production recommendations. - Misc. Publ. **AG 310-03-93**. University of Arkansas. Cooperative Extension Service, Fayetteville 1993.

Brown, K.J.: Translocation of carbohydrate in cotton: movement to the fruiting bodies. - Ann. Bot. **32**: 703-713, 1968.

Constable, G.A., Rawson, H.M.: Effect of leaf position, expansion and age on photosynthesis, transpiration and water use efficiency of cotton. - Aust. J. Plant Physiol. **7**: 89-100, 1980*a*.

Constable, G.A., Rawson, H.M.: Photosynthesis, respiration and transpiration of cotton fruit. - Photosynthetica **14**: 557-563, 1980*b*.

Elmore, C.D.: Contributions of the capsule wall and bracts to the developing cotton fruit. - Crop Sci. **13**: 751-752, 1973.

Elmore, C.D., McMichael, B.L.: Growth, $^{14}CO_2$ uptake and translocation. - In: 1975 Proceedings of Beltwide Cotton Production and Research Conference. Pp. 54-56. National Cotton Council of America, Memphis 1975.

Guinn, G.: Cause of square and boll shedding in cotton. - USDA tech. Bull. **1672**. US Government Print Office, Washington 1982.

Horrocks, R.D., Kerby, T.A., Buxton, D.R.: Carbon source for developing bolls in normal and superokra leaf cotton. - New Phytol. **80**: 335-340, 1978.

Kruger, N.J.: Carbohydrate synthesis and degradation. - In: Dennis, D.T., Turpin, D.H. (ed.): Plant Physiology, Biochemistry and Molecular Biology. Pp. 59-76. Longman, New York 1990.

Morris, D.A.: Photosynthesis by the capsule wall and bracteoles of the cotton plant. - Cotton Growing Rev. **42**: 49-51, 1965.

Oosterhuis, D.M., Urwiler, M.J.: Cotton main-stem leaves in relation to vegetative development and yield. - Agron. J. **80**: 65-67, 1988.

Peoples, T.R., Matthews, M.A.: Influence of boll removal on assimilate partitioning in cotton. - Crop Sci. **21**: 283-286, 1981.

Sassenrath-Cole, G.F., Heitholt, J.J.: Limitations to optimal carbon uptake within a cotton canopy. - In: Dugger, P., Richter, D. (ed.): 1996 Proceedings of Beltwide Cotton Conference. Pp. 1239-1240. National Cotton Council, Memphis 1996.

Wullschleger, S.D., Oosterhuis, D.M.: Photosynthetic carbon production and use by developing cotton leaves and bolls. - Crop Sci. **30**: 1259-1264, 1990*a*.

Wullschleger, S.D., Oosterhuis, D.M.: Photosynthetic and respiratory activity of fruiting forms within the cotton canopy. - Plant Physiol. **94**: 463-469, 1990*b*.

Zhao, D.: Cotton Floral Bud Development and Responses to Shade and Application of PGR-IV. - Ph.D. Thesis. University of Arkansas, Fayetteville 1997.

Zhao, D., Oosterhuis, D.M.: Physiologic and yield responses of shaded cotton to the plant growth regulator PGR-IV. - J. Plant Growth Regul. **17**: 47-52, 1998*a*.

Zhao, D., Oosterhuis, D.M.: Cotton responses to shade at different growth stages: nonstructural carbohydrate composition. - Crop Sci. **38**: 1196-1203, 1998*b*.