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Influence of Boll Removal on Assimilate Partitioning in Cotton[1]

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ABSTRACT

Field experiments with Upland cotton (*Gossypium hirsutum* L.) were initiated to determine the effect of boll removal on the distribution of ^{14}C-assimilates 24 hours following removal. The mainstem leaf subtending the sympodium supplied the first and second boll positions with assimilates. In the absence of bolls, assimilates in the mainstem leaf moved basipetally from the leaf subtending the first position. The majority of assimilates were translocated to the first position boll. Removal of the first position boll resulted in assimilate movement to the second position parts of the plant when the second position was 10 days old. The majority of the assimilates from the second position leaf, being further out on the sympodium, remained in the sympodium, as long as at least one fruiting body was present. Removal of all the bolls from the sympodium resulted in translocation primarily in a basipetal direction.

Additional index words: Photosynthate translocations, Photosynthate allocation, Asbcission, Shedding.

COTTON (*Gossypium* spp.) shed up to 70% of all initiated fruiting structures from sympodial branches during various times in the reproductive stage of development. Although research has been devoted to the causes of the shedding, little research has been reported in the literature indicating the effect of the boll shedding on the subsequent redistribution of the photosynthetic assimilates originally destined for the shed fruiting structures. The developing cotton boll receives photosynthetic assimilates from the bracts (Brown, 1968), the leaves subtending the boll and sympodium (Brown, 1968; Horrocks et al., 1978), the leaves above the sympodium on the same side of the main stem (Brown, 1978) and the boll wall (Elmore, 1973). The major sources of assimilates are the leaves subtending the boll, the leaf subtending adjacent fruiting positions (in the absence of a developing boll), and the leaf subtending the sympodium (Horrocks et al., 1978). As fruiting structures (squares or bolls) are shed from the sympodium, a redistribution of the assimilates destined for this structure must occur.

Matthews (1979) indicated that natural shedding of Upland cotton bolls had a significant effect on adjacent bolls. The shedding of the boll at the first fruiting position increased the tendency for the boll at the second fruiting position to be retained and produce significantly more seed cotton than the no-shed control. This research suggested that assimilates destined for the first position boll were reallocated to the second position boll, resulting in a larger fruiting structure. The objective of this research was to determine the influence of artificial boll removal on the redistribution of ^{14}C-assimilates in Upland cotton.

MATERIALS AND METHODS

'Deltapine-61' Upland cotton was planted at the Univ. of Arizona Agricultural Experiment Farm at Marana, Ariz. on 22 Apr. 1978, in a fine-silty, mixed, thermic family of Typic Tor-

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Table 1. Distribution of ^{14}C-assimilates from the leaves subtending the sympodium (SYM), first position boll (FPBL), or second position boll (SPBL) at two stages of development.

Plant part	Boll removal treatments					
	SYM		FPBL		SPBL	
	1-10DO†	2-10DO	1-10DO	2-10DO	1-10DO	2-10DO
	% of total ^{14}C exported					
B1‡	24.5	46.5	61.5	40.1	31.8	36.1
B2	2.3	3.1	29.4	43.2	24.2	29.5
LB	12.1	4.2	3.7	5.0	42.3	4.5
VA	6.8	2.4	0.9	1.8	0.6	0.3
VB	32.1	38.4	4.6	0.2	0.4	19.0
RT	22.6	6.7	1.8	9.6	0.4	10.6

† First position boll 10 days old: 1-10DO; second position boll 10 days old: 2-10DO. 1-10DO and 2-10DO were approximately 6 days apart, see text.
‡ First position boll: B1; second position boll: B2; labeled branch: LB; vegetation above the labeled branch: VA; vegetation below the labeled branch: VB; roots: RT.

Table 2. Effect of selective boll removal on the distribution of ^{14}C-assimilates from the leaf subtending the sympodium.

Plant part	Boll removal treatments							
	First position boll 10 days old				Second position boll 10 days old			
	NR†	1R	2R	BR	NR	1R	2R	BR
	% of total ^{14}C exported							
B1‡	24.5	-§	22.6	-	46.5	-	44.3	-
B2	2.3	0.9	-	-	3.1b	44.1a	-	-
LB	12.1a	0.2b	0.9b	1.6b	4.2	0.5	4.7	0.4
VA	6.8b	5.9b	1.9b	20.4a	2.4	0.3	9.8	4.2
VB	32.1bc	60.1a	37.0b	22.4c	38.4	53.8	39.8	47.2
RT	22.6c	33.0b	37.0b	55.5a	6.7b	2.3b	5.8b	48.1a

* Means within a row and age treatment followed by different letters are significantly different ($P < 0.05$) according to Duncan's Multiple Test.
† No bolls removed: NR; first position boll removed: 1R; second position boll removed: 2R; and both first and second position bolls removed: BR.
‡ First position boll: B1; second position boll: B2; labeled branch: LB; vegetation above labeled branch: VA; vegetation below labeled branch: VB; roots: RT. § - Indicates the boll was removed.

rifluvents (Pima clay loam) after a pre-plant irrigation. Plants were established on 102 cm beds and, on 26 July 1978, thinned to 100 cm between plants within a row. At anthesis, flowers at the first and second fruiting position on sympodia at nodes 10 to 15 were tagged with the date of anthesis. Two groups of plants were selected for 10-day-old (10 DO) bolls on the sympodium at the first or second nodes. Flowers on a sympodium occur at approximately 6-day intervals, so bolls at the other nodes were approximately 4 or 16 DO. Ten-day-old bolls were used, because such bolls are at their peak strength as a photosynthetic sink (Benedict et al., 1973). Within each group, four removal treatments were imposed: no bolls removed (NR), the first position boll removed (1R), the second position boll removed (2R), and both positions removed (BR). The shedding treatments were initiated during maximum fruit load (approximately 110 days post-planting). Bolls were severed at the pedicel or the sympodium 24 hours prior to administration of $^{14}CO_2$. All other fruiting bodies on the sympodium were also removed to eliminate further sink demands on the sympodium. The remaining sympodial branches received no treatments.

Three labeling treatments were imposed over the four shedding and two boll age treatments. Either the mainstem leaf subtending the sympodium, the leaf subtending the first boll position or the leaf subtending the second boll position was pulse-labeled with 15 Ci $^{14}CO_2$ with 5 min in a Plexiglas leaf chamber (Horrocks et al., 1978) with continuous circulation of the air. The $^{14}CO_2$ was released into the chamber by the addition of 1 ml 0.2 *N* $HClO_4$ to a basic solution containing 15μCi $NaH^{14}CO_3$ (spec. act. 51 mCi/m*M*, ICN, 2727 Campus Drive, Irvine, CA 92715) in water. After 5 min, the reaction was terminated by the addition of 1.0 ml 1 *N* NaOH to the reaction vessel and the leaf removed from the chamber. Labeling occurred between 1100 and 1400 hours, during which the chamber temperature ranged between 30 and 35 C. Twenty-four hours following the pulse-labeling, the labeled leaf, first position boll, second position boll, sympodium with leaves including the leaf subtending the sympodium, vegetation below the labeled sympodium, vegetation above the labeled sympodium, and roots were separated from each plant. Each plant part was dried at 65 C in a forced-air oven, weighed, and ground in a Wiley mill to pass a 40-mesh sieve. The total dpm per plant part and percent of total exported ^{14}C was determined by liquid scintillation spectrophotometry, as previously described (Peoples and Koch, 1978). Counting efficiency was determined by internal standardization using z14C-toluene. Each treatment was replicated four times and arranged in a completely randomized design. The subsamples were analyzed as a nesting design and the means of each removal treatment with an age *X* labeled leaf treatment compared according to Duncan's Multiple Range Test.

RESULTS AND DISCUSSION

^{14}C-assimilate Distribution. Labeling of leaves subtending the sympodium (SYM), the first position boll (FPBL), or the second position boll (SPBL) at two stages of development [first position boll 10 days old (10 DO), or 6 days later when the second position boll was 10 days old (10 DO)] resulted in distinctly different patterns of ^{14}C-assimilate distribution (Table 1). Labeled ^{14}C in *the main stem leaf subtending the sympodium* was distributed to three major sinks when the first position boll was 10 DO; the first position boll, the vegetation below the labeled leaf, and the roots. The labeled branch retained more than 10% of the ^{14}C-assimilate. Six days later, when the second position boll was 10 days old (10 DO), the major sinks were again the first position boll and the vegetation below the labeled leaf, with the roots not serving as a major sink. The sink strength of the first position boll doubled during this time (24.5 to 46.5%) indicating that at 16 DO the boll has a greater sink strength than at 10 DO for the main stem leaf, contrary to the reported data of Benedict et al. (1973). At 16 days, the increase in ^{14}C in the first position boll (+22%) was associated with a decrease in that found in roots and the labeled branch (−23.8%).

At the first labeling date, the first position boll (10 DO) and the second position boll (4 DO) served as the major sinks for the labeled ^{14}C in *the leaf subtending the first position boll* (FPBL). The first position boll was twice as strong a sink for the ^{14}C-assimilate as the second position boll. On the second labeling date, when the second position boll was 10 DO, its sink strength was similar to that of the first position boll (43.2 vs. 40.1, Table 1) with little change observed in other plant parts.

The first and second position bolls (10 DO and 4 DO, respectively) also served as major sinks of equal strength for labeled ^{14}C in *the leaf subtending the second position boll* (SPBL) at both sampling dates.

The data present in Table 1 provide the control values to examine the effect of boll removal on the redistribution of ^{14}C-assimilates. In addition, these data indicate two interesting points. Firstly, the ^{14}C-assimilates distribution patterns from various leaves on a sympodial branch are distinctly different. The main stem leaf serves

Table 3. Effect of selective boll removal on the distribution of ^{14}C-assimilates from the leaf subtending the first node on the sympodium.

Plant part	Boll removal treatments							
	First position boll 10 days old				Second position boll 10 days old			
	NR†	1R	2R	BR	NR	1R	2R	BR
	% of total ^{14}C exported							
B1‡	61.5b	–§	92.5a	–	40.1	–	32.0	–
B2	29.4b	77.0a	–	–	43.2	45.6	–	–
LB	3.7	5.0	2.6	0.0	5.0b	20.3a	5.1b	6.9b
VA	0.9b	4.6b	1.1b	78.6a	1.8b	1.7b	0.5b	37.4a
VB	4.6	10.1	2.9	11.3	0.2c	25.2b	39.1a	38.0a
RT	1.8	3.2	1.9	10.2	9.6bc	0.8c	23.5a	17.7ab

* Means with a row and age treatment following by different letters are significantly different ($P < 0.05$) according to Duncan's Multiple Range Test. † No bolls removed: NR; first position boll removed: 1R; second position boll removed: 2R; and both first and second position bolls removed: BR. ‡ First position boll: B1; second position boll: B2; labeled branch: LB; vegetation above labeled branch: VA; vegetation below labeled branch: VB; roots: RT. § – Indicates the boll was shed.

Table 4. Effect of selective boll removal on the distribution of ^{14}C-assimilates from the leaf subtending the second node on the sympodium.

Plant part	Boll removal treatments							
	First position boll 10 days old				Second position boll 10 days old			
	NR†	1R	2R	BR	NR	1R	2R	BR
	% of total ^{14}C exported							
B1‡	31.8b	–§	81.7a	–	36.1b	–	50.7a	–
B2	24.2b	83.8a	–	–	29.5b	66.4a	–	–
LB	42.3a	10.1b	13.5b	9.8b	4.5b	4.5b	10.4ab	18.0a
VA	0.6b	0.7b	0.5b	21.4b	0.3b	7.3b	7.7b	35.8a
VB	0.4b	4.3b	0.0b	52.3a	19.0	19.2	18.0	26.3
RT	0.4b	1.3b	4.2b	16.5a	10.6ab	2.6b	13.5a	14.2a

* Means within a row and age treatment followed by different letters are significantly different ($P < 0.05$) according to Duncan's Multiple Range Test. † No bolls removed: NR; first position boll removed: 1R; second position boll removed: 2R; both first and second position bolls removed: BR. ‡ First position boll: B1; second position boll: B2; labeled branch: LB; vegetation above labeled branch: VA, vegetation below labeled branch: VB; roots: RT. § – Indicates the boll was removed.

as a ^{14}C-assimilate source for the first position boll, the vegetation below the labeled branch, and the roots; while the leaves subtending fruiting position on the sympodium divert the majority of their exported ^{14}C-assimilates to the first position fruiting bodies. These data are consistent with those of Horrocks et al., (1978), which indicate that the leaves subtending fruiting positions are primarily responsible for the production of assimilates for these developing fruits. Ashley (1972) and Benedict and Kohel (1975) have also shown the importance of the leaves subtending the developing boll as a source of assimilates. Secondly, sink strength of the two bolls appeared to be affected not only by the age of the boll, but also by which leaf was labeled as the source leaf. For the main stem leaf, the sink strength doubled from 10 DO to 16 DO for the first position boll; while it decreased one-third during the same period for the leaf subtending the first position boll as the source. Sink strength of the first position boll did not change with time, for the leaf subtending the second position boll as the source. The second position boll did not change in sink strength with time, for the main stem leaf and the leaf subtending it; however, sink strength did increase one and one-half times from 3 DO to 10 DO for the leaf subtending the first position boll.

Boll Removal and ^{14}C-Assimilate Distribution. Table 2 indicates the effect of selective boll removal on the distribution of ^{14}C-assimilates from the leaf subtending the sympodium at two stages of development. Removal of the first position boll at 10 DO, the major sink on the sympodium, increased the partitioning of ^{14}C-assimilates to the vegetation below the labeled branch and roots. These two plant parts served as major ^{14}C-assimilate sinks in the control plants and would be expect to receive the additional assimilates. The second position boll was not a major sink for the main stem leaf and its removal had no effect on the partitioning of the ^{14}C-assimilates. In the absence of both bolls, an increased basipetal partitioning occurred, with a significant increase in (acropetal) partitioning to the vegetation above the labeled branch.

When the first position boll was 16 DO, control plants demonstrated a similar allocation pattern as the 10 DO control plants; primarily a basipetal distribution, with the first position boll a major sink. Removal of this sink resulted in an increased allocation to the second position boll in addition to the basipetal distribution. This was not observed when the second position boll was 4 DO and did not represent a major sink. At 10 DO, however, it was a major sink for the main stem leaf, in the absence of the first position boll. Removal of the second position boll had no effect on ^{14}C-allocation and removal of both bolls increased the allocation to the roots, similar to the 10 DO plants, but did not increase acropetal allocation.

When the leaf subtending the first position boll was labeled, a different allocation pattern from the main stem leaf pattern was observed (Table 3). At 10 DO, the major sinks were the first position boll and second position boll in control plants, with little basipetal or acropetal allocation occurring. The first position boll was the major sink and received twice as much ^{14}C as the second position boll, with 90.9% of the total exported ^{14}C in the two bolls. Removal of the first position boll resulted in an allocation of the ^{14}C-assimilates to the second position boll, with the reverse occurring when the second position boll was removed. A significant increase in acropetal distribution from the leaf subtending the first position boll occurred with the removal of both bolls (0.9 to 78.6%).

The second position boll at 10 DO increased in sink strength equal to that of the first position boll at 16 DO for the leaf subtending the first position as source. Unlike the case when the first position boll was 10 DO, removal of either position boll resulted in (basipetal) allocation to the vegetation below the labeled leaf. Removal of both position bolls not only resulted in basipetal allocation, but also in an increased allocation to the vegetation above the labeled leaf.

The leaf subtending the second position boll maintained almost 99% of the exported ^{14}C-assimilates within the sympodium when the first position boll was 10 DO (Table 4). While 4 days later, second position boll 10 DO, a significant basipetal translocation occurred (>20%). At

this time, the first and second position boll served as the major sinks of approximately equal strength. Even with the maturation of the second position boll to 10 DO, it still remained at equal sink strength to the first position boll. In both cases, first position boll 10 DO and second position boll 10 DO, removal of either boll resulted in allocation of the remaining boll with no changes in allocation to the remainder of the plant.

In the absence of reproductive sinks, significant redistribution of the ^{14}C-assimilates was observed. The mainstem leaf served as a source leaf to the lower portion of the plant. The leaf subtending the first position supplied ^{14}C-assimilates to the vegetation above and below the labeled leaf in the absence of reproductive sinks on the sympodial branch and retained less than 10% of the ^{14}C-assimilates within the sympodium. Translocation in a basipetal direction was evident from the leaf subtending the second position, however, the total amount exported from the sympodium was reduced, compared to the leaf subtending the sympodium and first position.

While shedding of fruiting structures in cotton leads to reductions in total yield, more assimilates become available to other fruit structures on a sympodial branch, which can lead to increased seed cotton at that fruiting position.

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