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PHYSIOLOGY

Carbon Dioxide Exchange Rate of Cotton After Complete Boll Removal

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INTERPRETIVE SUMMARY

Cotton plants must take up a sufficient amount of CO_2 to allow for plant growth maintenance and production of leaves, stems, roots, branches, and reproductive structures. Taking up insufficient CO_2 will reduce plant growth and development and could decrease yield.

Carbon dioxide assimilation in cotton is influenced by many factors, including the loss of bolls, which not only has the potential to decrease yield, but also reduces the amount of CO_2 taken up by the plant, and, subsequently, the amount of CO_2 available for other plant growth and development activities.

The objective of this study was to establish the effect of total boll removal on the CO_2 exchange rate of whole cotton plants grown in a controlled environment.

Many biotic and abiotic stresses contribute to boll loss in cotton. The effect of this loss on the whole-plant CO_2 uptake of cotton is unclear, but literature reports on other crop species indicate that, when fruit is lost or removed from the plant, the resulting changes in source/sink relationships alter CO_2 uptake. These changes in CO_2 uptake vary among crop species, some crops showing an increase in CO_2 uptake while others show a decrease or no change in CO_2 uptake. Changes in plant hormone concentrations have been implicated as the cause for some of the observed differences in CO_2 uptake. For example, increased abscisic acid levels in response to boll loss have been associated with decreased CO_2 uptake. Presumably, an increase in abscisic acid causes stomatal closure, which leads to a reduction in CO_2 uptake.

The results of the current study indicate that complete cotton boll removal affects the daytime and nighttime CO_2 exchange rates. The reduction was transient, however. Even after complete boll removal, plant CO_2 exchange rates returned to near those observed prior to boll removal. It took about 3 d for the plant to recover its former daytime CO_2 exchange rate. The nighttime CO_2 exchange rate also displayed a recovery, but had not returned to pre-boll removal levels by 7 d after complete boll removal.

The indeterminate nature of cotton growth offers one possible explanation for this recovery in CO_2 exchange rate. In contrast to determinate plants, the indeterminate growth characteristic of cotton allows the plants to produce vegetative and reproductive structures simultaneously. After all of the bolls were removed from the cotton plant, its indeterminate growth nature allowed it to commence production of new leaves, stems, roots, and bolls. This increase in biomass production resulted in a recovery in the CO_2 exchange rate due to the increased demand for CO_2.

What is the relationship between complete boll removal and the CO_2 uptake rate of cotton? It is well established that there is a strong relationship between CO_2 source and sink in cotton, and photosynthetic productivity of plants has been related to sink strength. But the dynamics of source/sink relationships in cotton are not well established, although some strong relationships between cotton sinks and sources have been demonstrated.

Our study shows that complete boll removal alters the CO_2 exchange rate of cotton plants and that the amount of CO_2 taken up and released by the plant is reduced temporarily. The mechanism behind this observation has not been determined.

Observations in this study, combined with the results from other reports, indicate that boll removal has a number of effects on CO_2 assimilation, the most significant being that the plant can recover from the negative effects of boll loss. This recovery

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capacity may have significant implications for cotton growers, especially when large numbers of bolls are lost from the plant. When sufficient time remains in the growing season, it appears that the plant has the ability to recover from the fruit loss through the adjustment in CO_2 assimilation in support of production of new bolls.

ABSTRACT

Environmental and physiological factors can lead to boll loss in cotton (*Gossypium hirsutum* L.). Boll loss, in turn, may limit the rate of CO_2 assimilation. The effects of complete boll removal on the daytime and the nighttime CO_2 exchange rates of cotton were investigated in a 10-d study conducted in a controlled environment whole-plant assimilation chamber. All bolls were removed from the cotton cultivar DPL50 when it reached an average hourly daytime CO_2 exchange rate of 150 mg C h^{-1}, a growth stage occurring approximately 95 d after planting. Only the bolls were removed, the squares and flowers were retained. The daytime CO_2 exchange rate decreased on the day immediately following boll removal (day 4 of the 10-d study). A marked recovery period for daytime CO_2 exchange rate occurred from day 8 to 10. Nighttime CO_2 exchange rate displayed a decreased loss of CO_2 (values became more positive) immediately following complete boll removal and continuing for 2 d (days 4 and 5), after which the nighttime CO_2 exchange rate entered a recovery period from day 6 to 10 (when this study terminated). The results indicate that complete boll removal alters CO_2 exchange rates during both day and night periods, and that cotton plants can recover from these changes in CO_2 exchange rates. This recovery may be important in field situations where boll loss is higher than normal. Plants that lose large numbers of bolls may be only temporarily affected by the loss.

Developing bolls can be lost from cotton as a result of insect damage, nutrient deficiencies, water stress, cloudy weather, and physiological factors. Boll loss not only reduces the number of bolls available for harvest at the end of the season but also may affect CO_2 assimilation. Some studies on single-leaf CO_2 assimilation measurements have determined that sink removal does not affect the CO_2 assimilation rate (Geiger, 1976; von Caemmerer and Farquhar, 1984), but others have reported that sink removal enhanced CO_2 assimilation (Maggs, 1964).

Most research on C balance and allocation in cotton has depended on measurements of only a single leaf or boll (Ashley, 1972; Benedict and Kohel, 1975; Wullschleger and Oosterhuis, 1990). Few studies have investigated whole-plant C balances, although these are better indicators of plant responses to specific environmental and metabolic conditions. It is possible that whole-plant responses differ from single-leaf responses because the CO_2 exchange rate is measured on the entire plant, rather than a single leaf.

In addition, few studies have investigated the effect of complete fruit removal on the CO_2 exchange rate (Austin and Edrich, 1975; Setter and Brun, 1980; Hein et al., 1984). To our knowledge, no studies have investigated the effect of complete boll removal on the whole-plant CO_2 exchange rate of cotton. Although complete boll loss is unlikely to occur in the field, we chose to perform complete boll removal as a means of understanding more fully the relationship between cotton bolls and the whole-plant CO_2 exchange rate.

MATERIALS AND METHODS

Plant Culture and Assimilation Chamber Conditions

The CO_2 exchange rates of DPL50 cotton plants were studied using the whole-plant method described by McCree (1986). That cultivar was selected for this study because it is a cotton variety commonly grown in central Texas. Seeds were planted at a 2.5-cm depth in 10-L black plastic pots containing a fritted clay growth medium that was previously rinsed thoroughly with distilled water to remove contaminants. Holes in the bottom of the pots were plugged with non-absorbent air-conditioner filter strips. After seedling emergence, the soil surface was covered with aluminum foil to minimize water evaporation. A few small holes were punched in the aluminum foil to allow gas exchange and passage of nutrient solution.

Plants initially were grown in a growth room under the following cultural conditions: air temperature, 30°C; photosynthetic photon flux density (PPFD), 800 to 900 mol m^{-2} s^{-1} supplied for 12 h by six 400-W Sylvania Metalarc lamps contained in pyramidal aluminum reflectors; and

wind speed of 0.7 m s^{-1}. Neither humidity nor CO_2 concentration were controlled in the growth room. Plants were irrigated to excess daily (1 L d^{-1}) with full-strength nutrient solution having the following composition: 2 m*M* $NH_4H_2PO_4$, 6 mM KNO_3, 4 mM $Ca(NO_3)_2 \cdot 4H_2O$, 2 mM $MgSO_4 \cdot 7H_2O$, 50 μM H_3BO_3, 10 μM $MnCl_2 \cdot 4H_2O$, 0.76 μM $ZnSO_4 \cdot 7H_2O$, 0.8 μM $CuSO_4 \cdot 5H_2O$, 0.4 μM $Na_2MoO_4 \cdot 2H_2O$, 100 μM NaCl, and 90 μM $FeSO_4 \cdot 7H_2O$ in 90 μM Na-EDTA.

When plants reached the 12-leaf stage, they were moved into a 1500-L controlled environment chamber where they remained until the plants had 8 to 10 bolls each (approximately 95 d after planting). Cultural conditions in the 1500-L chamber were as follows: air temperature, 30 °C; PPFD, 900 to 1000 mol m^{-2} s^{-1} supplied for 12 h by a 1000-W Sylvania super Metalarc lamp; and wind speed of 0.7 m s^{-1}. Neither humidity nor CO_2 concentration was controlled in the chamber. Plants were irrigated daily (1 L d^{-1}) with the full-strength nutrient solution previously described.

Once the plants had developed 8 to 10 bolls, they were transferred to 400-L controlled environment assimilation chambers for testing. These chambers were similar to those described by McCree (1986). Environmental conditions were: air temperature, 30 °C; humidity, near saturation; wind speed, 0.6 m s^{-1}; and PPFD, 1200 μmol m^{-2} s^{-1} (at the top of the plant) supplied for 12 h by a 400-W Sylvania super Metalarc lamp.

Each chamber was operated as an open gas exchange system. Outdoor air was pumped through continuously at a rate of 50 L min^{-1}, and a low positive pressure (0.15 m water) above atmospheric pressure inside was maintained constantly to avoid contamination with room air. Air entering and exiting the chamber was sampled hourly, and differences in CO_2 concentrations were measured using infrared gas analysis (Binos, Leybold-Heraeus GMBH, Hanau, Germany). Carbon dioxide gas was injected into the chamber to minimize this concentration differential. Air samples were passed over saturated NaCl solutions before measurements were taken in order to eliminate differences in water vapor concentration. Air sampling and data acquisition and analysis were controlled by a computerized system (Hewlett Packard 9826 and 9497A).

Table 1. Average dry weight of leaves, stems, and roots for cotton plants with complete boll removal and no boll removal at the end of the 10-d test period.

	Average Dry Weight	
Plant Structure	**Complete Boll Removal**	**No Boll Removal**
	----------g ----------	
Leaves	**41.57 a†**	**44.88 a**
Stems	**48.61 a**	**51.32 a**
Roots	**31.13 a**	**26.86 a**
Total	**121.38 a**	**123.06 a**

† Means between treatments with like letters are not significantly different at a 0.05 probability level.

Plants in the assimilation chambers were irrigated to excess daily with the full-strength nutrient solution (1 L d^{-1}) previously described. Each replicate was initiated when the plant reached an average C exchange rate of 150 mg C h^{-1} (approximately 95 d after planting). A base C exchange rate of 150 mg h^{-1} was chosen arbitrarily to ensure a uniform initial whole-plant C exchange rate, thus reducing the experimental error component of data when different test replications were compared. Plants at the stage of 150 mg C h^{-1} had 8 to 10 bolls.

After the plants were first placed into a test chamber they were allowed to acclimate until a base average hourly C exchange rate of 150 mg C h^{-1} was reached. The plants were monitored for 3 d more, after which, all the bolls were removed. A port on the front of the assimilation chamber was opened and the bolls were removed by a scalpel cut at the junction of the peduncle and stem. Leaf area measurements were not possible inside assimilation chambers due to the construction of the chambers.

Dry weights of leaves, stems, and roots were recorded at the end of the 10-d test period for both the plants that had undergone complete boll removal and the control plants with no boll removal (Table 1).

Carbon Exchange Rate Calculations

The whole-plant C exchange rate (CER) inside the test chamber was calculated hourly using the following equation:

$$(C_i - C_e) + C_j + C_n + CER = 0,$$

where C_i is the net rate of C entering the chamber with the incoming flow of outdoor air, C_e is the rate of C exiting the chamber with the outgoing air, C_j is

the injection rate of CO_2 into the incoming air stream, and C_n is the rate of release or absorption of C by the test chamber. The C exchange rate is negative for C uptake and positive for release of C by the plant. The rate difference (C_i - C_e) was calculated from the differential CO_2 concentration between incoming and exiting air and air flow rate. The CO_2 differential was measured hourly using an infrared gas analyzer (Leybold-Heraeus, Binos Model 4a.). The airflow rate was measured with a mass flowmeter (FM 362, Tylan Corp., Carson, CA). The rate of CO_2 injection was measured with a CO_2 mass flowmeter (Tylan model FM 360). The rate of release or absorption of C by the empty test chamber was determined by running a 48-h blank test with no plant and no CO_2 injection and averaging the resulting balance of C. The average C balance of the blank test was <1% of the C exchange rate of plants at the start of the experiment.

The integrated C exchange rate values in the daytime (CER_d) and the nighttime (CER_n, a negative number) were used to calculate four 24-h C balance parameters: (i) daily gross C uptake by the plant through photosynthesis, calculated as CER_d minus CER_n; (ii) daily net C gain by the plant, calculated as CER_d plus CER_n; (iii) daily C loss by the plant through respiration, calculated as daily gross C uptake minus daily net C gain; and (iv) C use efficiency, defined as the ratio of daily net C gain to daily gross C uptake.

The design of the experiment was a randomized complete block in which all treatments were replicated three times. Data for average dry weight were analyzed for significance using the general linear model (GLM) procedure in the SAS statistical program. Treatment differences were separated using Tukey's multiple range testing.

RESULTS AND DISCUSSION

Daytime CO_2 exchange rates of intact plants were typical of growing plants during the leaf expansion stage (Fig. 1). Uptake of CO_2 increased steadily before boll removal. Daytime CO_2 exchange rate decreased the day immediately following boll removal (day 4). After this initial decrease, CO_2 uptake showed a recovery period for days 8 to 10. On day 10 (the last day of the study), the CO_2 exchange rate was near, but still less than, pre-boll removal levels.

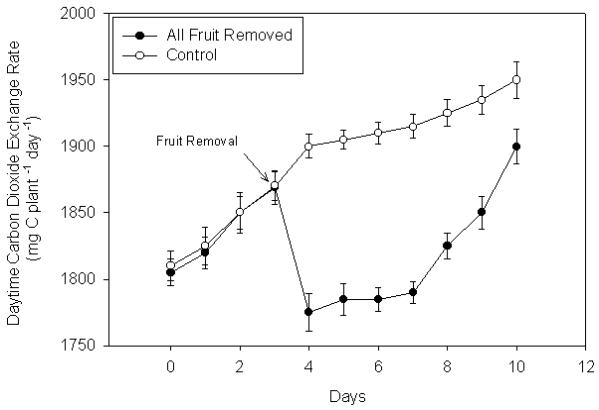

Fig. 1. Progression of daytime CO_2 exchange rate of cotton plants grown in controlled environment assimilation chambers with complete boll removal or no boll removal. Each data point represents the mean of 24 individual observations replicated three times. Results are means ± SE.

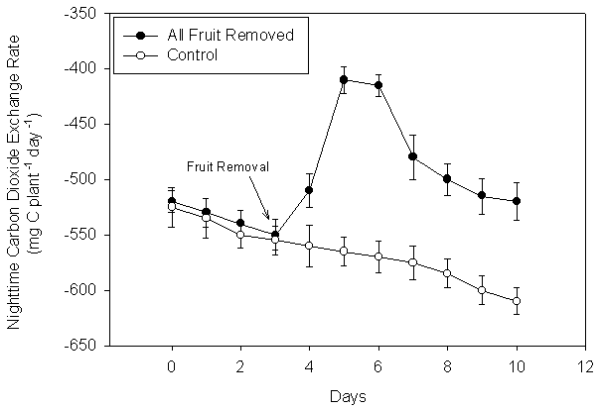

Fig. 2. Progression of nighttime CO_2 exchange rate of cotton plants grown in controlled environment assimilation chambers with complete boll removal or no boll removal. Each data point represents the mean of 24 individual observations replicated three times. Results are means ± SE.

The day immediately after boll removal (day 4), night respiration declined (increasingly less CO_2 loss) (Fig. 2). This trend continued for 2 d following boll removal. There was a recovery period between days 7 to 10, but the nighttime CO_2 exchange rate did not return to pre-boll removal levels by the end of the study (day 10).

Average dry weight of leaves, stems and roots at the end of the study for both treatments was not significantly different ($P < 0.05$) (Table 1). Boll dry weights for both treatments also were not significantly different ($P < 0.05$). Bolls that were

removed on day 4 of the 10-d complete boll removal treatment study had an average dry weight of 45.49 g. The average dry weight of the bolls on the control plants, which were removed at the end of the study, was 47.56 g. This comparison indicates that the plants used in both treatments were similar in biomass distribution.

Complete boll removal decreases the CO_2 exchange rate of whole cotton plants grown in assimilation chambers. The decrease in assimilation rate indicates that there is a relationship between the presence of cotton bolls and the rate of CO_2 assimilation. It is unclear whether the bolls are the main regulators of CO_2 assimilation. However, this study shows that cotton bolls (as sinks) play a role in the whole-plant CO_2 assimilation of cotton plants. Although hormone levels were not measured in this study, it is possible that hormone levels (most likely ethylene and/or abscisic acid) were altered due to injury caused by boll removal. Ethylene, abscisic acid, or both, may have at least in part affected CO_2 assimilation by inducing a stress or wounding response in the plant after fruit removal.

In a study by Burt (1964), net CO_2 assimilation decreased when growing potato (*Solanum tuberosum* L.) tubers were removed from the plants. King and coauthors (1967) found that net CO_2 assimilation decreased 50% within 3 to 15 h after wheat (*Triticum aestivum* L. em. Thell.) inflorescence removal. In addition, other studies on changes in sink strength have shown decreases in assimilation rates (Birecka and Dakic-Wlodkowska, 1963; Humphries and Thorne, 1964; Maggs, 1964; Thorne and Evans, 1964; Sweet and Wareing, 1966). The results of our study are consistent with the findings of these previous studies.

A significant result of the current study is that cotton can recover from the changes in CO_2 exchange rate associated with complete boll removal. Recovery was shown for both daytime and nighttime C exchange rates. The daytime recovery appeared to occur more rapidly than did the nighttime recovery. By the end of the study (day 10), the daytime CO_2 exchange rate had returned to a level similar to that of pre-boll removal, but the nighttime values did not approach pre-boll removal levels by the end of the study. Nonetheless, the nighttime CO_2 exchange rate did show a recovery trend.

The results of this study indicate that even after severe boll removal (loss), the CO_2 exchange rate during the daytime and nighttime can recover to levels near those found prior to boll removal (loss). This implies that, under field conditions when boll loss is not usually so severe, the plants can recover relatively quickly without significant impact on plant productivity. Although the possibility was not investigated in this study, the less extensive boll loss normally experienced by a cotton plant in the field may have little or no effect on the CO_2 exchange rate. It may be that CO_2 exchange rate is affected only after severe boll losses from which the cotton plant may recover within a few days. The results presented here indicate that boll loss has a large effect (at least temporarily) on the CO_2 exchange rate of cotton plants, but the long-term effects may be minimized when the crop has sufficient growing time to compensate for the boll loss by producing additional bolls.

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