CARBON BALANCE OF PGR-IV-TREATED COTTON PLANTS GROWN UNDER TWO IRRIGATION REGIMES

J. Cadena and J.T. Cothren
Department of Soil and Crop Sciences
Texas A&M University
College Station, TX

Abstract

A new plant growth regulator PGR-IV is made of a fermentation broth of soil bacteria, yeast, and fungi that contains gibberellic acid and indolebutyric acid in a nutrient solution blend. This growth regulator has been tested in cotton over the last 10 years and has been reported to enhance the capacity of the plant to sustain growth under suboptimal conditions for growth. Although research has been conducted to evaluate its effects on root growth, nutrient uptake, boll retention, earliness, leaf photosynthesis, and yield, no studies have been reported on the whole-plant carbon balance and transpiration responses of cotton at suboptimal conditions for growth. The objectives of these experiments were to determine the effects of PGR-IV on the carbon and water economies of cotton plants grown in whole-plant test chambers under water stress.

Under water stress conditions the overall carbon fluxes and growth characteristics of cotton plants were severely affected, but applications of PGR-IV caused no effects on the overall carbon and water fluxes of the cotton plant. In a 25-d experimental period without irrigation, cotton plants showed a 71% reduction in the total number of leaves and a 90% reduction in the plant leaf area. The reductions in leaf area caused concomitant reductions in the daily rates of gross carbon uptake by 87%, carbon losses through respiration by 82%, net carbon gains by 92%, and transpiration by 95%. These reductions in the carbon and water fluxes under nonirrigated conditions caused a 60% reduction in the total plant dry weight, most of which was caused by reductions in the dry weight of leaves, petioles, stems, fruits, and branches. Dry matter allocation in roots was not severely affected by the water stress regime.

Application of PGR-IV did not affect the overall carbon and water fluxes of the cotton plant, only numerical tendencies were observed. PGR-IV application caused small reductions in the total plant dry weight (2%), but at the same time induced a greater allocation toward reproductive structures. Application of PGR-IV caused the development of longer fruiting branches and greater number of fruits. Internode length and total plant height were not affected by PGR-IV under either irrigated or nonirrigated conditions. According to these results we conclude that PGR-IV did not alleviate the detrimental effects of water stress on the cotton plant, but may induce the development of more productive plants.

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Introduction

Water stress is one of the most important factors limiting cotton production in most growing areas throughout the world. The plant growth regulator PGR-IV has been reported to partially alleviate the detrimental effects of environmentally stressed cotton plants, including water stress, flooding, and shade (Zhao and Oosterhuis, 1995; 1994). Under controlled environmental conditions, Zhao and Oosterhuis (1994) found that water-stressed cotton plants treated with PGR-IV had lower stomatal conductance and transpiration rates during the early period of water deficit compared with nontreated plants. During the late period of water stress, the same plants showed greater stomatal conductance and photosynthetic rates than control plants, and thus the average photosynthetic rate of plants treated with PGR-IV increased by 13.5% compared with control plants during the water stress treatment. This behavior is similar to the water conservation mechanism shown naturally by sorghum plants (*Sorghum bicolor L. Moench*), which maintains low stomatal conductances, transpiration, and photosynthetic rates at early stages of the water deficit (McCree et al., 1990). Sorghum plants conserve soil water at the start of the stress cycle which make it available at later stages, thus delaying the effects of water stress on leaf senescence and on the internal capacity for photosynthesis (McCree and Fernandez, 1989). As the stress cycle proceeds, sorghum plants show greater photosynthetic rates than plants that do not show this mechanism.

The results reported by Zhao and Oosterhuis (1994, 1995) on photosynthetic rates of water stressed cotton plants are based on measurements made on individual leaves. Little information is available on water stress and PGR-IV treatments at the whole-plant level. Thus, the objective of this experiment was to test the effects of PGR-IV on the whole-plant carbon balance of cotton plants under water stress conditions.

Materials and Methods

Cotton seeds cv "Deltapine 51" were germinated on moistened paper towels in darkness at room temperature (28 °C) and 3 days later uniform seedlings with a tap root length of 2.5 ± 0.5 cm were transplanted to 9.5-L pots containing inert fritted clay (Absorb-N-Dry, Balcones Minerals Co.; Flatonia, Texas). The seedlings were maintained in a nursery room at 28 °C for about 26 days and irrigated daily with a full-strength nutrient solution. When plants developed four fully expanded leaves, the pots were flushed with distilled water to remove any accumulation of nutrients in the soil, the soil surface in the pot was covered with aluminum foil to minimize soil evaporation and then irrigated with 1-L nutrient solution. Two uniform plants with a total leaf area of 0.018 ± 0.08 m^2 were selected for treatment. One plant was sprayed with 146.15 mL of PGR-IV ha^{-1}, using a constant pressure CO_2 sprayer that delivered 187 L ha^{-1} of spray solution at a pressure of 0.18 MPa and speed of 4.8 km h^{-1}. The other plant (nontreated control) was sprayed with distilled water only. Plants were allowed to dry for 5 min and then transferred into whole-plant assimilation chambers. Treated plants received a second application of PGR-IV at the rate of 292.3 mL ha^{-1} at matchhead square stage (34 days after planting and 8 days after the first application of PGR-IV). Treated and nontreated plants were either irrigated with 1-L full strength nutrient solution every day (irrigated treatment) or allowed to deplete the water in the pot for the rest of the experimental period (nonirrigated treatment). Under these conditions, four treatment combinations of the PGR-IV and irrigation treatments were possible (PGR-IV treated irrigated, PGR-IV treated nonirrigated, control irrigated, and control nonirrigated), which were replicated four times. Since only two assimilation chambers were available for this experiment, replications were done in time. Temperature in the test chambers was kept constant at 30 ± 0.5 °C during the daytime and nighttime periods. Other environmental conditions in the test chambers during the experimental period were as follows: wind speed 0.6 m s^{-1}, photosynthetic photon flux density 1500 µmol m^{-2} s^{-1} at the top of the plants supplied with one 400-W Sylvania metalarc lamp, and 12-h photoperiod.

Outdoor air was continuously passed through the chamber at a rate of 20 L min^{-1}, with additional carbon dioxide being injected into the incoming air stream during the daytime to keep a minimum difference between the carbon dioxide concentrations of the air entering and leaving the chambers. The level of CO_2 injection was manually adjusted every day.

Measurements started 24 h after plants were placed in the test chambers. Carbon exchange rates (CER) of the whole plants enclosed in the test chambers were calculated hourly over the experimental period, using the equation described by Fernandez et al., (1992):

$$(Ci - Ce) + Cj + Cn + CER = 0$$

where Ci is the rate of carbon entering the chamber with the incoming flow of outdoor air, Ce is the rate of carbon exiting the chamber with the outgoing air, Cj is the injection rate of carbon into the incoming air stream, and Cn is the rate of release or absorption of carbon by the chamber. The CER is negative for the uptake and positive for the release of carbon by the plant. The rate difference (Ci-Ce) was calculated from the differential of the CO_2 concentration between the incoming and outgoing air flow rate. The CO_2 differential was measured hourly using an infrared gas analyzer (Binos Model 4a.1, Leybold-Heraeus GMBH, Hanau, Germany). The air flow rates were measured with air mass flow meters (Tylan model FM 362-3S, Tylan Corp., Carson, CA). The rates of CO_2 injection were measured with a CO_2 mass flowmeter (Tylan Model FM 360). A complete description of the system used for this experiment can be found in McCree (1986).

The integrated CER values in the daytime (CER_d) and in the nighttime (CER_n,) were used to calculate four carbon balance parameters: (I) daily gross carbon uptake by the plant through photosynthesis, calculated as CER_d minus CER_n; (ii) daily net carbon gain by the plant, calculated as CER_d plus CER_n; (iii) daily carbon loss by the plant through respiration, calculated as daily gross carbon uptake minus daily net carbon gain; and (iv) carbon use efficiency (CUE), defined as the ratio of daily net carbon gain to daily gross carbon uptake.

The daily water loss from each plant was measured from the change in pot mass. The pot mass was measured hourly using a loadcell (Alphatron SL 50 BAA, Division of Alphatron, Manchester, NH), from which the pot was permanently suspended inside the chamber. Hourly water losses were summed over 24 h to obtain the daily water loss. Since soil evaporation was minimized by covering the soil with aluminum foil, the daily water loss was assumed equal to the daily transpiration. Water use efficiency was calculated as the ratio of daily net carbon gain to daily transpiration.

The maximum length and width of each leaf in the plant was measured every 2 days during the experimental period. Leaf area was calculated as length x width x K. The K factor was obtained through regression analysis for each particular plant based on the actual leaf area values of each plant at the end of the experimental period. Actual leaf area was determined with a Li-Cor Model 3100 leaf area meter (Li-Cor Inc., Lincoln, NE). The average K value of all replications and treatments was 0.753. Cumulative leaf are was calculated by adding the areas of all leaves on the plant.

Leaf water potential and osmotic potential were measured daily using a PR-55 psychrometer microvoltmeter (Wescor Inc., Logan, UT). On each day two leaf samples were taken with a paper punch from the same leaf on the main stem at the end of the light period (11:00 h). The leaf samples were immediately placed inside C-52 chambers (Wescor Inc., Logan, UT), and allowed to equilibrate for 2 h before a microvolt reading was taken. The leaf samples were then wrapped in aluminum foil and frozen for 5 min on a block of dry ice. After thawing for 1 min the samples were returned to the sample chambers, and a second microvolt reading was taken after 1 h of equilibration. These microvolt readings were used to calculate the water and osmotic potentials, respectively, using equations obtained during calibration of each sample chamber with NaCl solutions of known potentials. Turgor potential was calculated as the difference between water potential and osmotic potential.

After 25 days in the test chambers (59 days after planting) plants were removed, the number of leaves, leaf area, internode length, number of fruits, fruit branches, vegetative branches, and height were recorded. Subsequently, plants were divided into leaves, petioles, stems, fruits, fruit branches, vegetative branches and roots and oven dried at 70 °C until constant weight. The dry weight of each organ was recorded.

Carbon balance and water potential data were analyzed using PC SAS (SAS Institute, 1987) and analysis of variance procedure for each particular day. Mean separation was accomplished using Duncan's new multiple range test. The experiment was analyzed as a factorial 2 x 2 in a randomized complete block design with four replications (Gomez and Gomez, 1989).

Results and Discussion

Leaf Area

Well irrigated cotton plants showed higher cumulative leaf area than nonirrigated plants throughout the experimental period (Fig. 1). Seven days after the initiation of the water stress treatment, nonirrigated plants showed significantly lower leaf area than well-irrigated plants. The difference between irrigated and nonirrigated plants was 20% less leaf area for nonirrigated plants 7 days after the water stress treatment was imposed. This difference increased throughout the experiment, reaching a 90% difference at the end of the experimental period (25 days). These differences in leaf area were associated with reduced leaf expansion, leaf initiation, and increased leaf senescence as is the case of water-stressed plants.

Application of PGR-IV did not affect the cumulative leaf area of plants under either irrigated or nonirrigated conditions (Fig. 1). These results agree with our previous findings (Cadena et al., 1994) and contrast with reports of other authors (Oosterhuis and Zhao, 1993a; Oosterhuis and Zhao, 1993b; Atkins, 1992), who reported increases in leaf area up to 17% upon application of PGR-IV.

It has been recognized by several authors (Boyer, 1988; Boyer, 1970; Barlow, 1986), that the detrimental effects of water stress on leaf area expansion are induced by reduced turgor potentials available for cell elongation. Under the conditions of this experiment, the turgor potential of non-irrigated plants was lost 16 days after the initiation of the water stress treatment, consequently affecting leaf area expansion (Fig. 2). Irrigated plants were able to maintain turgor throughout the experimental period without limitations for leaf area expansion. For nonirrigated plants, turgor was lost once the leaf water potential became more negative than the osmotic potential, which occurred on day 16 in the experimental period. Both PGR-IV-treated and nontreated cotton plants lost turgor at about the same time. Starting on day 16, the leaf water and osmotic potentials of PGR-IV-treated plants were consistently more negative than in control plants indicating adjustment of the PGR-IV-treated plants to extract more water from an increasingly depleted soil. This difference, however, was not expressed in the maintenance of a better turgor potential, probably due to the fact that the soil in the pot was already depleted of water. Osmotic adjustment is a well established mechanism shown by some plants during periods of water deficits in which turgor potential is maintained by active accumulation of solutes (Morgan, 1984). In cotton, it has been demonstrated to occur in leaves and roots during periods of water deficits (Oosterhuis and Wullschleger, 1987).

The responses of plants to water deficits under controlled environments differ from those grown under field conditions. The difference is primarily attributed to a more rapid onset of water deficits for plants grown in small pots, where size limits root system growth and quantity of water. Under field conditions, gradual onset of water deficits allows time for further root growth and osmotic adjustment to occur (Wilson et al., 1980).

In our experiment, another factor that may have contributed to reductions in leaf area under nonirrigated conditions is a reduction in leaf retention since water stressed plants usually lose most of their leaves.

Carbon Economy

Under nonirrigated conditions, cotton plants showed reduced daily rates of gross carbon uptake 7 days after imposition of the stress treatment (Fig. 3). On day 7, nonirrigated cotton plants showed 9% lower rates of gross carbon uptake than irrigated plants, and at the end of the experimental period, this difference was increased to 87%. Reductions in the rate of photosynthesis caused by water deficits are associated with increased stomatal resistance, increased mesophyll resistance, and decreased leaf expansion (Wilson et al., 1980). This behavior reduces water losses from the plant, but at the same time affects the CO_2 diffusion into the leaf and leads to a decrease in growth due to substrate limitations (Amthor and McCree, 1990). Reductions in leaf growth and initiation under water-stressed plants lead to a reduction in the amount of photosynthetic active radiation absorbed in comparison with non-stressed plants (Amthor and McCree, 1990). The curves for rates of carbon fixation in this experiment closely followed the trends in whole-plant leaf area (average r^2=0.84, $p<0.001$), which indicates that a major factor contributing to the decrease in photosynthesis under nonirrigated conditions was the reduction in leaf area per plant.

Application of PGR-IV did not affect the gross carbon uptake of cotton plants under either irrigated and nonirrigated conditions (Fig. 3). In a previous experiment

(Zhao and Oosterhuis, 1994), reported that application of PGR-IV to water-stressed cotton plants increased the overall leaf photosynthetic rates by 13.5% as a consequence of reduced stomatal conductance at the early stages of the stress cycle, allowing plants to save water and maintain a better water status at later stages in the stress cycle. With these findings, these authors concluded that PGR-IV had the potential to partially alleviate the detrimental effect of water stress on photosynthesis and dry matter accumulation and consequently improve plant growth. In our whole-plant experiment, PGR-IV-treated and nontreated cotton plants showed statistically similar rates of whole-plant gross carbon fixation under both water regimes. The numerical tendency for carbon fixation was rather in the opposite direction as PGR-IV-treated plants showed greater rates of carbon fixation at the start of the stress treatment and lower at the end.

Nonirrigated cotton plants showed reduced rates of carbon loss through respiration 5 days after imposition of the water stress regime (Fig. 3). The differences between irrigated and nonirrigated plants was 12% on day 5 and increased to 82% on day 25. These reductions in the rate of respiration under water stress were associated with reduced availability of substrate, as the gross carbon uptake was reduced concomitant with the reductions in the respiration rates. According to Amthor and McCree (1990), under water limitations, growth and maintenance respiration usually are reduced due to reduced metabolic activity and reduced growth rate. Growth respiration is reduced due to reductions in the total carbon gains of the plants under water stress, which limits the availability of substrate for growth. Maintenance respiration is reduced as well due to reduced metabolic activity of plants under water stress. In an experiment designed to separate the effects of water deficits on the growth and maintenance components of respiration in sorghum plants (*Sorghum bicolor L. Moench*), Wilson et al. (1980), found that under water deficits total plant respiration was reduced by 58%. Of this amount 22% was attributable to decreases in the maintenance component and 36% to a reduction in the growth component.

Application of PGR-IV did not affect the rate of respiration either under irrigated or nonirrigated conditions. The numerical tendency was for PGR-IV to increase respiration of cotton plants, especially under well-irrigated conditions.

Nonirrigated plants showed significantly lower rates of net carbon uptake than irrigated plants (Fig. 4). This corresponds to the substrate carbon available for growth and any factor that depresses carbon availability leads to reduced dry matter accumulated in the plant. In our experiment, the difference between water stressed and nonstressed plants was 13% less net daily rates of carbon gains for nonirrigated plants 8 days after imposition of the water stress regime. On day 25, this difference increased to 92% and nonirrigated plants showed reduced growth.

PGR-IV-treated and nontreated plants showed similar rates of net carbon gains under both water regimes (Fig. 4). The numerical tendency was for PGR-IV to induce initial higher rates of net carbon gains after the first application and lower rates after the second application until the end of the experiment. These increases and reductions in the net carbon gains closely follow the numerical trends shown for the rates of gross carbon uptake in Fig. 3. The reductions in the rates of net carbon gains at the end of the cycle were greater than the increases shown at the beginning, which may lead treated plants to show reduced dry matter accumulation. Under well irrigated conditions the difference between treated and nontreated plants after a second application of PGR-IV was 17.3% lower rates of net carbon gains for the PGR-IV-treated plants on day 13 and 22.9% on day 21. Under nonirrigated conditions, the numerical difference between PGR-IV-treated and nontreated plants on the same days was 6.3% and 71.9% lower rates for the PGR-IV-treated plants.

The carbon use efficiency (CUE) of PGR-IV-treated plants under both water regimes tended to be higher at the initial stages following the first application of PGR-IV (Fig. 5). However, following the second application of PGR-IV, treated plants showed an overall reduction in the CUE. The difference between PGR-IV-treated and nontreated plants was significant on day 13 under irrigated conditions and on day 16 under nonirrigated conditions. These results indicate that cotton plants receiving two applications of PGR-IV were less efficient in converting fixed carbon into biomass than control plants, which may be a consequence of the tendency of PGR-IV to reduce the rates of gross carbon uptake and increase the rates of respiration. This agrees with previous findings (Cadena et al, 1994) in which PGR-IV reduced the CUE of cotton plants, especially when grown at low temperatures.

Water Economy

Under nonirrigated conditions, cotton plants showed significantly lower rates of transpiration than irrigated plants (Fig. 6). The difference between irrigated and nonirrigated plants appeared 2 days after withholding the water supply and was maintained throughout the experimental period. Nonirrigated plants showed 13% lower transpiration rates than irrigated plants 2 d after imposition of the stress treatment, and this difference increased to 94.6% at the end of the experiment. These reductions in the transpiration rates were well correlated with reductions in total-plant leaf area (overall r^2=0.89 $p<0.001$), but the relationship was stronger at later stages of the stress treatment (r^2=0.65 on day 2; r^2=0.97 on day 25). This may indicate that in the earlier stages of water stress, reductions in the whole-plant transpiration rates were associated with leaf area as well as with other factors, such as stomatal movements, and at later stages in the water stress treatment, the reductions in the whole-plant transpiration losses were mostly explained by reductions in the whole-plant leaf area.

Under both water regimes PGR-IV applications tended to increase the rates of transpiration following the first application of PGR-IV (Fig. 6). However, these differences were non significant and did not appear 11 days after the first application, and PGR-IV-treated and nontreated plants exhibited similar rates of transpiration at the end of the experimental period.

Under nonirrigated conditions, there was a numerical tendency for the PGR-IV-treated plants to show greater rates of transpiration initially and reduced rates at later stages in the stress cycle, which may be a consequence of a rapid depletion of soil water in the pot. This behavior is inadequate under water stress conditions as soil water is not conserved and plants experience water deficits at the end of the stress cycle. Concomitant with this, PGR-IV plants were unable to maintain the rates of transpiration and gross carbon uptake at later stages in the stress cycle. These results do not agree with findings of Zhao and Oosterhuis (1994) who reported that water stressed cotton plants treated with PGR-IV had lower stomatal conductance and transpiration rates than control plants during the early stages of the water stress cycle, and greater stomatal conductances and photosynthesis rates at later stages. Our results suggest that cotton plants treated with PGR-IV were not able to control stomata movements to save water during the early stages of water stress and were subjected to water limitations at later stages which in turn affected the rates of gross carbon uptake.

Due to the tendency of nonirrigated plants to conserve water through stomatal closure and reductions in leaf area, water-stressed cotton plants showed higher water use efficiency than unstressed plants (Fig. 7).

Application of PGR-IV did not affect the water use efficiency of cotton plants, but had the tendency to increase it after the first application under both water regimes. However, following the second application, PGR-IV-treated plants had lower WUE, especially under irrigated conditions. Under nonirrigated conditions, the WUE of PGR-IV treated plants was similar to control plants.

Plant Growth

The total plant dry weight of nonirrigated cotton plants was significantly lower (60%) than that of well irrigated plants (Fig. 8). Most of the effects of water stress on dry matter accumulation were detected on leaves, petioles, stems, fruits, and branches. No differences were detected on the dry matter accumulation on roots of irrigated and nonirrigated cotton plants, which indicates that under nonirrigated conditions dry matter allocation was mostly directed toward root growth. As a consequence, the overall root to shoot ratio was greater for nonirrigated plants (0.86) compared with irrigated plants (0.24) (Table 1).

Application of PGR-IV caused small reductions (2%) in the overall dry matter accumulated in the cotton plant (Fig. 9). However, dry matter partitioning in PGR-IV treated plants was favored toward a greater allocation in reproductive structures (fruits and fruiting branches) under both irrigated and nonirrigated conditions (Table 1). Even though at the end of the experimental period the cotton plants used in this experiment were at early stages in the reproductive period (59 days after planting), these differences, if maintained, may impact cotton lint yields. These results are consistent with earlier reports in which application of PGR-IV have resulted in increased number of squares (Oosterhuis and Zhao, 1993b), increased boll retention (Locke et al., 1994; Oosterhuis and Zhao, 1993a; Atkins, 1992; Hickey and Atkins, 1992), greater number of bolls per plant (Urwiler and Stutte, 1988; Weir et al., 1994), and increased earliness (Robertson and Cothren, 1993).

Application of PGR-IV did not increase the total dry matter partitioned toward roots in either irrigation condition, but under nonirrigated conditions the shoot to root ratio was greater for the PGR-IV-treated plants (Table 1). In an earlier experiment, Oosterhuis and Zhao (1994) have reported dramatic increases in root dry weight (29%) and total number of lateral roots (75%) after an in-furrow application of PGR-IV. However, in the present experiment we used foliar instead of in-furrow applications of PGR-IV.

Well-irrigated plants were taller, had greater number of leaves, fruits, fruit branches, vegetative branches, internodes, and leaf area than were nonirrigated plants (Table 2). The dramatic reductions in leaf number (71%) and leaf area (90%) observed in this experiment for water stressed plants were associated with observed reductions in the carbon fluxes described before, which in turn affected the carbon available for growth and thus the overall number of structures developed by the plants. PGR-IV-treated and nontreated cotton plants showed similar values for the above variables under both water stressed and nonstressed conditions (Table 2); however, the tendency was for the PGR-IV treatment to induce a greater number of fruits and fruit branches per plant ($p<0.06$).

PGR-IV-treated and nontreated plants showed similar internode length under both water regimes (Table 3), which indicates little effect of this growth regulator on stem elongation and total plant height under these conditions.

Under well irrigated conditions, longer fruiting branches were detected on the PGR-IV-treated plants at nodes 8 through 11 (Table 4). Other fruiting branches on the main stem had statistically similar lengths, but the tendency was for longer branches on PGR-IV-treated plants. Under nonirrigated conditions, there were no statistical differences, but the tendency was similar to well irrigated conditions. These results indicate that PGR-IV may favor the reproductive growth of cotton plants, probably by diverting more carbon toward the production of more fruits and fruiting branches. This has been the case in field experiments under non stressed conditions (Locke et al., 1994; Weir et al., 1994; Oosterhuis and Zhao, 1993a; Robertson and Cothren, 1993; Atkins, 1992; Hickey and Atkins, 1992; Urwiler and Stutte, 1988).

Conclusions

The carbon fluxes and growth characteristics of cotton plants were severely affected under nonirrigated conditions. In a 25-d experimental period without irrigation, cotton plants showed a 71% reduction in the total number of leaves and a 90% reduction in the plant leaf area. The reductions in leaf area caused concomitant reductions in the daily rates of gross carbon uptake by 87%, carbon losses through respiration by 82%, net carbon gains by 92%, and transpiration by 95%. These reductions in the carbon and water fluxes under nonirrigated conditions caused a 60% reduction in the total plant dry weight, most of which was caused by reductions in the dry weight of leaves, petioles, stems, fruits, and branches. Dry matter allocation in roots was not severely affected by the water stress regime.

Application of PGR-IV did not affect the overall carbon and water fluxes of the cotton plant, but several numerical tendencies were observed. Under PGR-IV application, plants showed initial higher rates of gross carbon uptake following the first application of PGR-IV, but then lower rates were detected once a second application was made. The overall rates of respiration were numerically greater for the PGR-IV-treated plants, and thus net carbon gains and CUE were reduced. Applications of PGR-IV also caused a numerical increase in the rate of transpiration at the start of the water stress cycle causing depletion of soil water and lower transpiration rates toward the end of the experimental period. These results contrasted with those obtained by other authors in which lower stomatal conductance and transpiration losses were reported for the PGR-IV-treated cotton plants at the start of a stress cycle, thus delaying the onset of the stress symptoms. PGR-IV application also caused small reductions in the total plant dry weight (2%), but at the same time caused a greater allocation toward reproductive structures. Application of PGR-IV caused the development of longer fruiting branches and greater number of fruits. Internode length and total plant height were not affected by PGR-IV under either irrigated or nonirrigated conditions.

According to these results we conclude that PGR-IV did not alleviate the detrimental effects of water stress on the cotton plant, but may induce the development of more productive plants.

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Table 1. Dry matter accumulation in PGR-IV-treated cotton plants grown under two irrigation regimes (g plant^{-1}).

Organ	Irrigated PGR-IV†	Irrigated Control	Mean Irrigated	Nonirrigated PGR-IV	Nonirrigated Control	Mean Non-irrigated
Leaves	21.96‡	23.12	22.54	5.52	5.46	5.49
Petioles	4.34	4.60	4.47	0.77	0.64	0.71
Stem	6.26	6.30	6.28	2.82	2.72	2.77
Sympodia.	3.81	2.70	3.26	0.31	0.28	0.29
Fruits	2.05	1.58	1.81	1.74	1.19	1.46
Roots	8.34	11.71	10.02	10.47	8.25	9.35
Monopodia	2.31	3.42	2.86	0.17	0.06	0.12
Total plant	49.00	53.43	51.24	21.80	18.60	20.19
Root/shoot	0.20	0.28	0.24	0.92	0.80	0.86

†PGR-IV treated plants received two applications at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage and matchhead square, respectively.
‡Mean of four replications.

Table 2 Vegetative and reproductive growth of PGR-IV-treated cotton plants under two irrigation regimes.

Variable	Irrigated PGR-IV†	Irrigated Control	Mean Irrigated	Nonirrigated PGR-IV	Nonirrigated Control	Mean Non-irrigated
Height (cm)	55.25‡	54.50	54.88	19.87	19.38	19.63
Fruits (no.)	39.25	36.25	37.75	10.00	8.75	9.38
Sympodia (no.)	12.50	11.50	12.00	5.75	6.50	6.13
Monopodia (no.)	3.00	3.75	3.38	1.75	1.00	1.38
Internodes (no.)	17.25	17.25	17.25	10.75	10.00	10.38
Leaves (no.)	90.50	85.50	88.00	27.75	24.75	26.25
Leaf area (cm^2)	5771.10	5754.58	5762.80	578.50	501.70	540.10

†PGR-IV treated plants received two applications at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage and matchhead square, respectively.
‡Mean of four replications.

Table 3. Internode length of PGR-IV-treated cotton plants grown under two irrigation regimes.

Internode	Irrigated PGR-IV†	Irrigated Control	Mean Irrigated	Nonirrigated PGR-IV	Nonirrigated Control	Mean Non-irrigated
1	3.00‡	3.12	3.06	3.00	3.88	3.43
2	1.70	1.38	1.54	1.75	1.38	1.56
3	1.88	1.75	1.81	2.50	2.20	2.35
4	2.15	1.75	1.95	1.50	1.25	1.38
5	1.87	2.25	2.06	2.70	2.87	2.79
6	2.33	1.50	1.91	1.10	1.50	1.30
7	2.22	2.88	2.56	2.50	2.38	2.44
8	3.00	2.87	2.94	1.95	1.58	1.76
9	2.68	3.63	3.15	1.68	1.00	1.34
10	4.43	3.75	4.08	0.75	0.42	0.59
11	4.23	5.25	4.74	0.40	-	0.40
12	5.43	5.63	5.53	-	-	-
13	5.89	6.38	6.13	-	-	-
14	5.25	4.38	4.81	-	-	-
15	3.63	3.88	3.75	-	-	-
16	2.251	2.75	2.50	-	-	-
17	1.67	1.43	1.53	-	-	-
18	1.00	0.60	0.73	-	-	-
19	0.50	-	0.50	-	-	-

†PGR-IV treated plants received two applications at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage and matchhead square, respectively.
‡Mean of four replications.

Table 4. Fruit branch length (cm) of PGR-IV-treated cotton plants grown under two irrigation regimes.

Main stem node	Irrigated PGR-IV†	Irrigated Control	Mean Irrigated	Nonirrigated PGR-IV	Nonirrigated Control	Mean Non-irrigated
4	-	-	-	5.00	-	5.00
5	23.50‡	18.00	20.75	3.00	4.50	3.75
6	23.88	19.00	21.79	3.88	4.13	4.00
7	22.38	27.38	24.88	3.13	2.88	3.00
8	29.00	24.50	26.75	2.43	2.38	2.40
9	26.75	23.38	25.06	1.63	1.00	1.31
10	27.63	21.38	24.50	1.33	0.55	0.89
11	24.50	14.25	19.38	1.00	0.50	0.75
12	17.88	9.75	13.81	-	0.20	0.20
13	13.25	9.38	11.31	-	-	-
14	7.75	2.88	5.31	-	-	-
15	4.00	1.63	2.81	-	-	-
16	1.87	1.07	1.53	-	-	-
17	1.25	0.55	0.90	-	-	-
18	0.35	-	0.35	-	-	-

†PGR-IV treated plants received two applications at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage and matchhead square, respectively.
‡Mean of four replications.

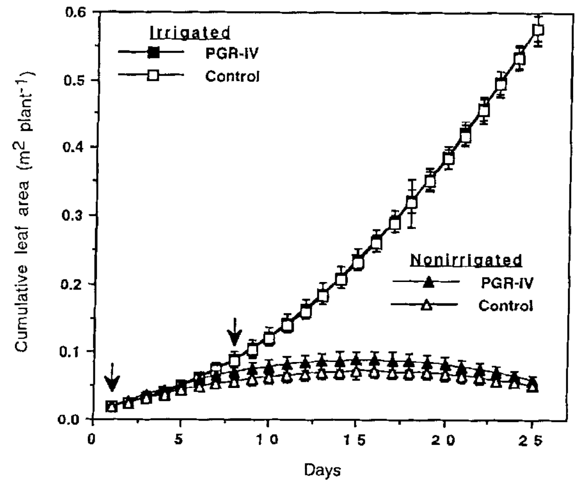

Fig. 1. Cumulative leaf area of PGR-IV-treated cotton plants grown under two irrigation regimes (m^2 $plant^{-1}$). Arrows indicate PGR-IV applications to treated plants at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each point represents the mean of four replications. Vertical bars represent the standard error of the mean.

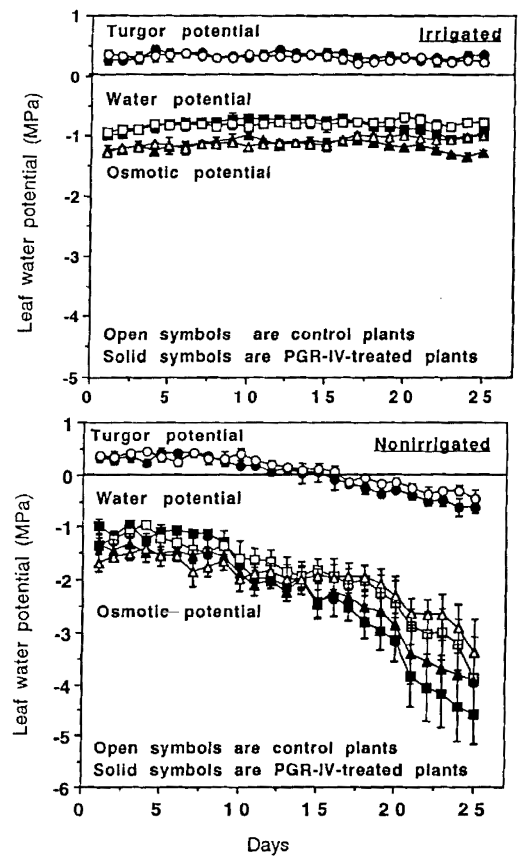

Fig. 2. Leaf water potential, leaf osmotic potential, and leaf turgor potentials of PGR-IV-treated cotton plants grown under two irrigation regimes (MPa). Arrows indicate PGR-IV applications to treated plants at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each point represents the mean of four replications. Vertical bars represent the standard error of the mean.

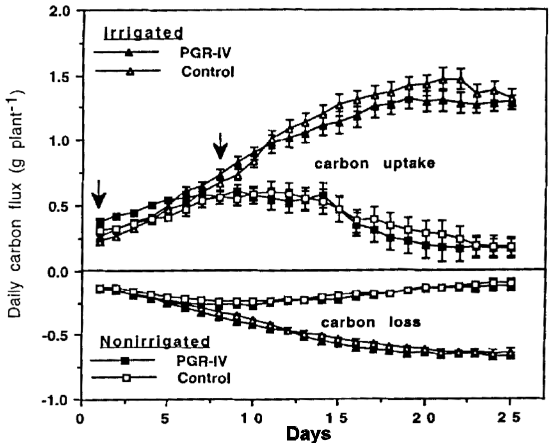

Fig. 3. Daily gross input of carbon and daily respiration of PGR-IV-treated cotton plants grown under two irrigation regimes (g plant^{-1}). Arrows indicate PGR-IV applications to treated plants at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each point represents the mean of four replications. Vertical bars represent the standard error of the mean.

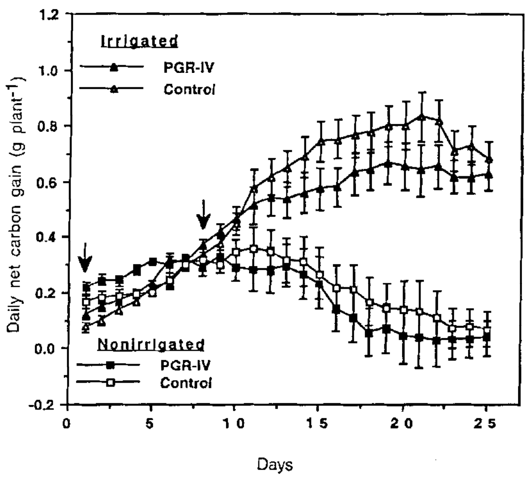

Fig. 4. Daily net carbon gain of PGR-IV-treated cotton plants grown under two irrigation regimes (g plant^{-1}). Arrows indicate PGR-IV applications to treated plants at the rates of 146.15 + 292.3 mL ha $^{-1}$ at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each point represents the mean of four replications. Vertical bars represent the standard error of the mean.

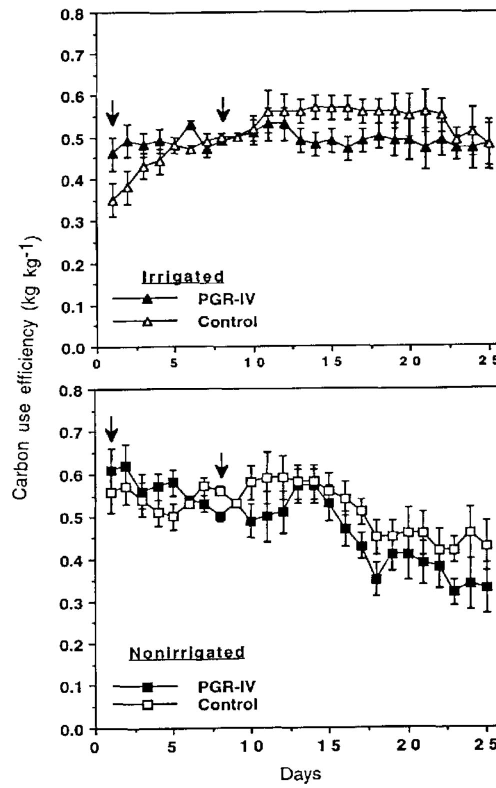

Fig. 5. Carbon use efficiency of PGR-IV-treated cotton plants grown under two irrigation regimes (kg kg^{-1}). Arrows indicate PGR-IV applications to treated plants at the rates of 146.15 + 292.3 mL ha $^{-1}$ at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each point represents the mean of four replications. Vertical bars represent the standard error of the mean.

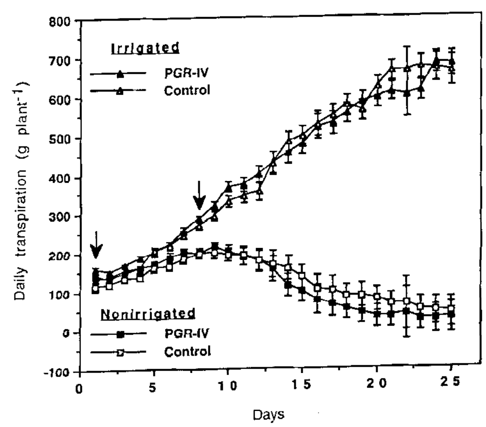

Fig. 6. Daily transpiration of PGR-IV-treated cotton plants grown under two irrigation regimes (g plant^{-1}). Arrows indicate PGR-IV applications to treated plants at the rates of 146.15 + 292.3 mL ha $^{-1}$ at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each point represents the mean of four replications. Vertical bars represent the standard error of the mean.

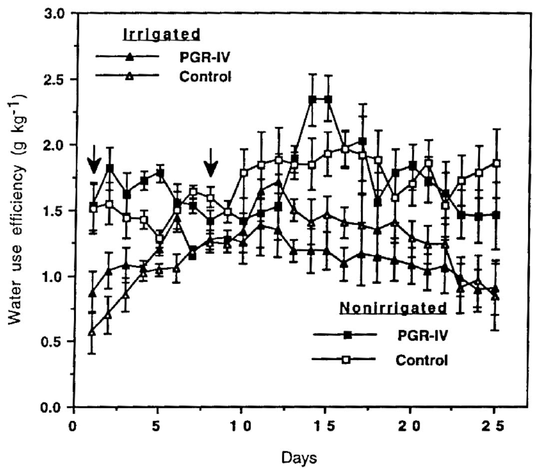

Fig. 7. Water use efficiency of PGR-IV-treated cotton plants grown under two irrigation regimes (g kg^{-1}). Arrows indicate PGR-IV applications to treated plants at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each point represents the mean of four replications. Vertical bars represent the standard error of the mean.

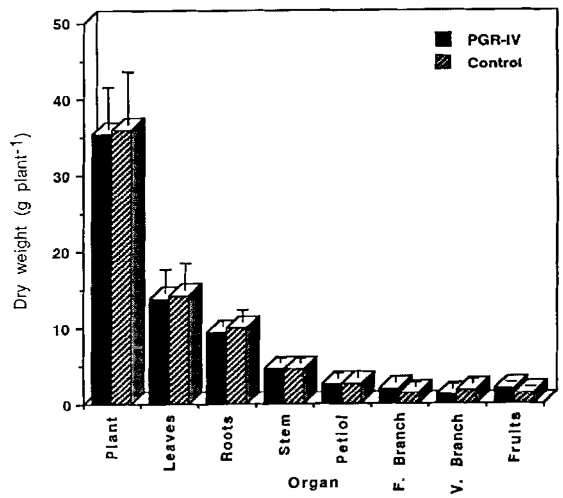

Fig. 9. Dry matter partitioning of cotton plants treated with PGR-IV (g $plant^{-1}$). Treated plants received two applications of PGR-IV at the rates of 146.15 + 292.3 mL ha^{-1} at the four-leaf stage (day 1) and matchhead square (day 8), respectively. Each column represents the mean of three replications. Vertical bars represent the standard error of the mean.

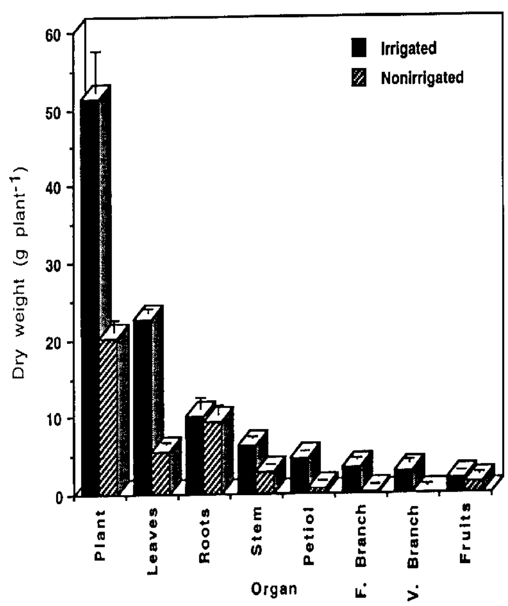

Fig. 8. Dry matter partitioning in cotton plants under irrigated and non-irrigated regimes (g $plant^{-1}$). Each column represents the mean of four replications. Vertical bars represent the standard error of the mean.