

## Physiological effects of plant hormones in cotton under drought

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### Abstract

Effects of plant hormones indole-3-yl-acetic acid (IAA), gibberellic acid (GA), benzylaminopurine (BAP), abscisic acid (ABA) and ethrel (ETH) in 5  $\mu$ M concentration on gas exchange, ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO, EC 4.1.1.39) activity, pigment content and yield in cotton (*Gossypium hirsutum* L. cv. H-777) under drought were studied. At reproductive stage (55 - 60 d after sowing) these hormones were sprayed on shoots one day prior to stress imposition by withholding irrigation. The soil moisture of control plants was kept at field capacity. Net photosynthetic rate ( $P_N$ ), stomatal conductance ( $g_s$ ), transpiration rate (E), carboxylation efficiency (CE), water use efficiency (WUE), RuBPCO activity, boll number per plant, seed number per plant and lint mass per plant significantly decreased at drought while chlorophyll (Chl) *b* content and flower number per plant increased. ABA and ETH significantly reduced gas exchange parameters, Chl *a* and Chl *b* content. Detrimental drought effect on  $P_N$ ,  $g_s$ , E, CE, RuBPCO and lint mass per plant was significantly alleviated by BAP and also its effect on seed number and lint mass per plant was significantly alleviated with the ABA treatment.

*Additional key words:* abscisic acid, benzylaminopurine, chlorophyll, ethrel, gas exchange, gibberellic acid, *Gossypium hirsutum*, indole-3-yl-acetic acid, ribulose-1,5-bisphosphate carboxylase/oxygenase, water use efficiency, yield.

### Introduction

Cotton is one of the important commercial crop grown throughout world. Both stomatal and non-stomatal factors contributes to the effects of water deficit on photosynthesis and water use efficiency (Matthews and Boyer 1984). Drought causes reduction in net photosynthetic rate ( $P_N$ ) (Cadena and Cothren 1996, Faver *et al.* 1996, Kumar *et al.* 2001), transpiration rate (E), stomatal conductance ( $g_s$ ) (Iersel *et al.* 1996, Kumar *et al.* 2001), carboxylation efficiency (CE) (Leidi *et al.* 1999, Kumar *et al.* 2001), and water use efficiency (WUE) (Van Rensburg and Krüger 1993). According to Kumar *et al.* (2001) under drought WUE was not affected. With drought ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity decreased (Berkowitz and Wahlen 1985, Pandey *et al.* 2000). Chlorophyll (Chl) *a* and Chl *b*

content decreased with increasing severity of water stress (Gadallah 1995). During drought quality of chloroplast proteins decreased and electrophoretic spectrum of proteins changed in the test plants (Samlev and Martin 1982). Drought reduced seed yield of mungbean, soybean and cowpea (Pandey *et al.* 1984).

Under drought endogenous contents of auxins, gibberellins and cytokinin usually decrease while contents of abscisic acid and ethylene increase (Nilsen and Orcutte 1996). At drought exogenous application of indole-3-yl-acetic acid (IAA), gibberellic acid (GA), benzylaminopurine (BAP) resulted an increase in  $P_N$ , E and  $g_s$  (Kumar *et al.* 2001). BAP increased RuBPCO activity under drought (Pandey *et al.* 2000). Leaves of droughted cotton plants treated with PGR-IV (GA,

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*Abbreviations:* ABA - abscisic acid; BAP - benzylaminopurine; CE - carboxylation efficiency; Chl - chlorophyll;  $c_i$  - internal carbon dioxide; DTT - dithiothreitol; E - transpiration rate; EDTA - ethylenediamine tetraacetic acid; ETH - ethrel; GA - gibberellic acid;  $g_s$  - stomatal conductance; IAA - indole-3-yl-acetic acid; MCE - mercaptoethanol;  $P_N$  - net photosynthetic rate; PVP - polyvinyl-pyrrolidone; RuBPCO - ribulose-1,5-bisphosphate carboxylase/oxygenase; WUE - water use efficiency.

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indole-butyric acid and proprietary fermentation broth) had significant higher  $g_s$ ,  $P_N$  (Zhao *et al.* 1997) and lint yield (Livingston *et al.* 1993).

However, there is lack of more detailed information of hormonal effects on gas exchange, enzymes, pigment

## Materials and methods

**Plant and stress treatment:** Acid delinted seeds of cotton (*Gossypium hirsutum* L. cv H-777) were sown in polythene bags filled with 10 kg thoroughly washed dune sand. Ten days after sowing 100 cm<sup>3</sup> of complete Hoagland solution was added to each bag and plants were thinned. Further 150 cm<sup>3</sup> Hoagland's solution supplemented with 40 mM KNO<sub>3</sub> was applied to each bag at 10-d intervals.

The plants were subjected to drought at reproductive stage (55 - 60 d after sowing, DAS) by withholding irrigation in order to induce permanent wilting point (PWP) in young leaves (soil moisture content of dune sand, SMC = 5 ± 0.5 %). The control plants were kept at field capacity (SMC = 10 ± 0.5 %). The shoots were sprayed by IAA, GA, BAP, ABA and ETH at 5 µM concentration or by distilled water, one day prior to drought treatment. The control plants were also sprayed similarly.

**Gas exchange:** Gas exchange parameters were measured on fully expanded leaf from 10:00 to 11:30 using infrared gas analyzer (*Ciras-1*, P.P. Systems Inc., Hitchin, UK) under natural day-light (1000 - 1100 µmol m<sup>-2</sup> s<sup>-1</sup>), temperature (32 ± 1.5 °C), air humidity (60 ± 5 %) and CO<sub>2</sub> concentration (360 ± 5 µmol mol<sup>-1</sup>). CE and WUE were calculated according to Van Rensburg and Krüger (1993): CE =  $P_N/c_i$  and WUE =  $P_N/E$ , respectively.

**Enzyme extraction and assay:** At the end of stress treatment, fully expanded leaf was frozen in liquid nitrogen and kept at -80 °C. The leaf tissue was extracted by grinding in chilled mortar and pestle with 2.5 cm<sup>3</sup> of Tris-HCl buffer (0.05 M, pH 7.4) containing 0.4 µM PVP,

contents and yield parameters in cotton under drought. Therefore, present study was conducted to understand the mode of action and complex physiological responses of plant hormones in cotton under drought condition.

1 mM DTT, 2 mM EDTA, 5 mM MCE, 0.01 % Triton-100X, 20 mM MgCl<sub>2</sub> and 5 mM NaHCO<sub>3</sub>. The extract was centrifuged at 12 000 g for 30 min at 0 - 4 °C. The supernatant was collected and volume made 3.0 cm<sup>3</sup> with extraction buffer. This is referred as enzyme extract and was used for RuBPCO activity.

RuBPCO (EC 4.1.1.39) activity was estimated by radiochemical method of Björkman (1968). To 0.1 cm<sup>3</sup> of enzyme extract in a scintillation vial 1.0 cm<sup>3</sup> of reaction mixture containing CO<sub>2</sub>-free 0.05 mM Tris-HCl buffer, pH 8.2, 40 mM MgCl<sub>2</sub> and 0.1 M NaHCO<sub>3</sub>, 0.37 MBq NaH<sup>14</sup>CO<sub>3</sub> (specific activity 1.89 kBq mol<sup>-1</sup>), and 81 mM DTT was added. Then 0.25 cm<sup>3</sup> of RuBP (0.4 mM) was added to vial. The reaction was allowed to proceed at 30 ± 2 °C for 1 min and terminated by the addition of 0.2 cm<sup>3</sup> of 2 M HCl. The sample was heat dried and reconstituted with 0.2 cm<sup>3</sup> of 2 M HCl, again heat dried and redissolved in 0.5 cm<sup>3</sup> of distilled water. Then 4.5 cm<sup>3</sup> of liquid scintillation fluid (Brey 1960) was added to each scintillation vial and radioactivity counted with a LKB WALLAC, 1209 RACKBETA liquid scintillation counter.

**Pigments:** Chlorophyll *a*, chlorophyll *b* and carotenoids in fully expanded leaf were extracted and measured by dimethylsulphoxide (DMSO) (Hiscox and Israelstam 1979).

**Yield parameters:** At final harvest flower number, boll number, seed number and lint mass per plant were determined.

**Statistics:** The data of three replications were statistically analyzed by factorial completely randomized design.

## Results

**Gas exchange studies:** In control plants foliar application of IAA, GA and BAP significantly increased  $P_N$  while ABA and ETH reduced it.  $P_N$  significantly reduced under drought. Exogenous application of GA and BAP significantly alleviated the deleterious effect of drought while ABA and ETH reduced it further (Fig. 1A). Under drought internal concentration of carbon dioxide ( $c_i$ ) increased. Except IAA, all hormones reduced  $c_i$  under drought and significantly lowest  $c_i$  was after BAP treatment (Fig. 1B). Stomatal conductance in control

plants was enhanced with foliar application of IAA, GA and BAP while it was reduced by ABA and ETH. At drought  $g_s$  decreased significantly. Alleviation of drought effects on  $g_s$  with GA and BAP was nonsignificant. However, ABA and ETH further decreased  $g_s$  at drought (Fig. 1C). Foliar application of BAP in control plants increased  $E$  significantly.  $E$  significantly decreased at drought. GA and BAP significantly alleviated the detrimental effects of drought. ABA and ETH further decreased  $E$  at drought (Fig. 1D). In control plants CE

significantly increased with application of BAP while it reduced with ABA and ETH. At drought CE decreased significantly. GA and BAP significantly nullify

detrimental drought effect on CE, while ABA and ETH further significantly reduced CE at drought (Fig. 1E). WUE in control plants increased with IAA and GA

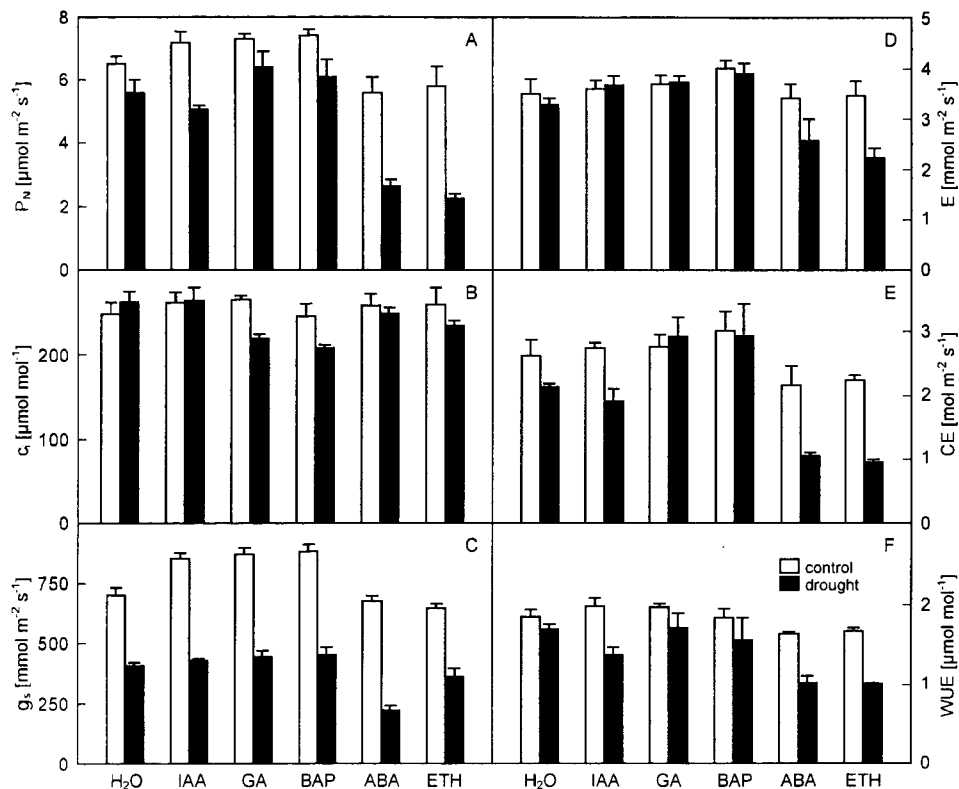


Fig. 1. Effect of plant hormones on net photosynthetic rate ( $P_N$ , A), internal carbon dioxide concentration ( $c_i$ , B), stomatal conductance ( $g_s$ , C), transpiration rate, (E, D), carboxylation efficiency (CE, E), and water use efficiency (WUE, F) in cotton leaf under drought stress. Plants were sprayed with various hormones at 5  $\mu\text{M}$  concentration before imposing to drought. Bars represent SE,  $n = 3$ .

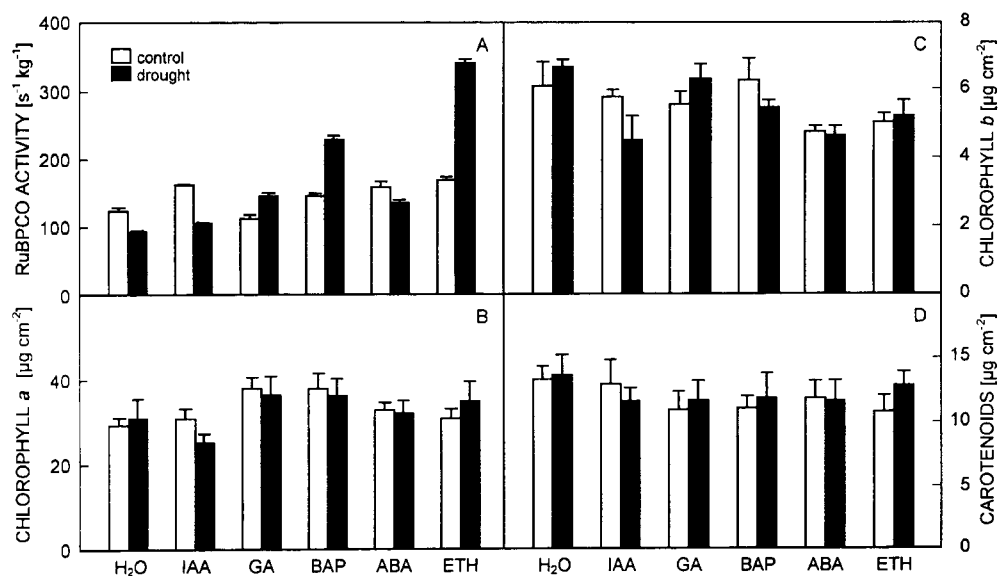


Fig. 2. Effect of plant hormones on ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity (A) estimated by radiochemical method and contents of chlorophyll a (Chl a, B), chlorophyll b (Chl b, C), and total carotenoids (D) in cotton leaf under drought stress. Plants were sprayed with various hormones at 5  $\mu\text{M}$  concentration before imposing to drought. Bars represent SE,  $n = 3$ .

while BAP, ABA and ETH were inhibitory. WUE significantly decreased at drought. ABA and ETH reduced WUE nonsignificantly (Fig. 1F).

**RuBPCO activity and pigment contents:** In control plants all hormones except GA enhanced RuBPCO activity and ETH was most stimulatory. Its activity reduced at drought. Foliar application of all hormones alleviated detrimental effect of drought and BAP and ETH were more effective (Fig. 2A). Content of Chl *a* in control plants significantly increased by GA and BAP. At drought Chl *a* content nonsignificantly increased with exogenous application of GA, BAP and ETH while it reduced further with IAA and ABA (Fig. 2B). In control except IAA and BAP, all hormones significantly decreased Chl *b* content. Under drought Chl *b* increased significantly and its content decreased with exogenous application of IAA (Fig. 2C). In control as well at drought carotenoids content nonsignificantly decreased with all hormones (Fig. 2D).

**Yield:** In control plants flower number per plant increased significantly with ETH. Under drought flower number increased significantly. BAP and ETH were more effective and significantly enhanced flower number at drought (Fig. 3A). In control GA and ETH enhanced boll number per plant nonsignificantly. With drought number of retained boll reduced significantly while foliar application of BAP and ABA retained it maximally (Fig. 3B). In control seed number per plant reduced with IAA and BAP while increased significantly with ABA and ETH. Under drought its number reduced significantly. Foliar application of IAA, GA and ETH further reduced its number while with BAP and ABA it increased significantly (Fig. 3C). In control plants IAA, BAP and ETH significantly reduced lint mass per plant while ABA increased its content significantly. At drought it decreased significantly. At drought lint mass was further significantly decreased with IAA and ETH while, it significantly increased with GA, BAP and ABA (Fig. 3D).

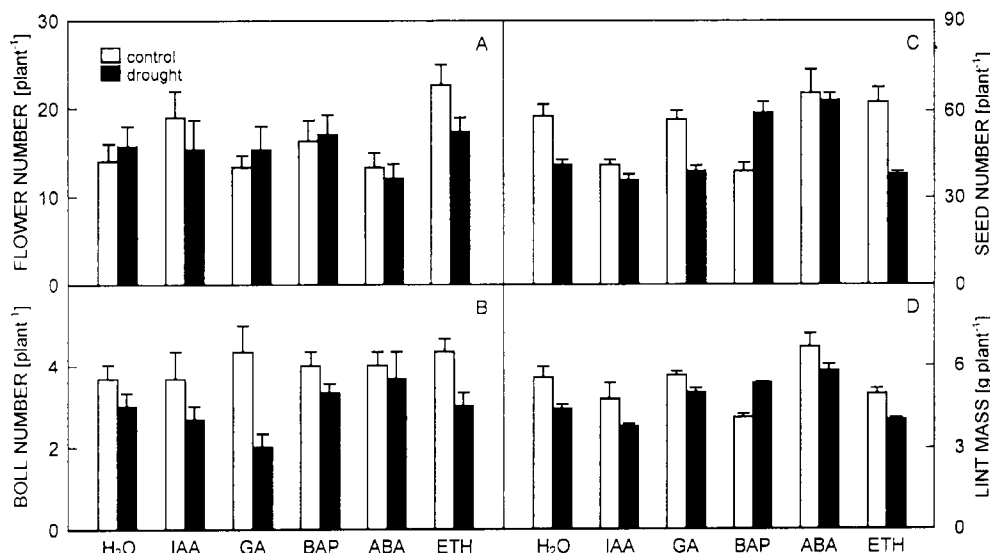


Fig. 3. Effect of plant hormones on flower number (A), boll number (B), seed number (C), and lint mass (D) per plants in cotton under drought stress. Plants were sprayed with various hormones at 5  $\mu$ M concentration before imposing to drought. Bars represent SE,  $n = 3$ .

## Discussion

In this work we found that under drought  $P_N$ ,  $g_s$ , E, CE and WUE significantly decreased while  $c_i$  increased (Fig. 1) which is agreement with the reduction in  $P_N$  under drought in cotton (Cadena and Cothren 1996, Favre *et al.* 1996, Kumar *et al.* 2001). Exogenous application of GA and BAP significantly increased  $P_N$  while ABA reduced further. Similar results were reported by Kumar *et al.* (2001). Reduced  $g_s$  in cotton is in agreement with Iersel *et al.* (1996). In support to our results PGR-IV treatment on cotton plants increased  $P_N$  and  $g_s$  (Zhao

*et al.* 1997) and also ABA treatment minimizes the water loss in cotton under drought by lowering  $g_s$  (Gadallah 1995). Controversial trend of  $c_i$  in response to drought have been observed in different crops *i.e.* in cotton decreased  $c_i$  under moderate stress and increased  $c_i$  under severe stress (Ephrath *et al.* 1990) or constant  $c_i$  (Downton *et al.* 1988). Drought reduced CE in cotton supported results obtained by Leidi *et al.* (1999) and Kumar *et al.* (2001). WUE significantly reduced with drought. ABA and ETH decreased WUE nonsigni-

ificantly. Droughted reduced WUE was observed by Van Rensburg and Krüger (1993) in tobacco, which supports our results. In contrast to our findings WUE did not change in drought because proportion reduction in  $P_N$  and E was similar (Kumar *et al.* 2001). According to Nilsen and Orcutte (1996) ABA induced higher WUE was due to ABA induced stomatal closure. Under drought condition ABA reduced WUE because reduction in  $P_N$  was much greater than reduction in E.

RuBPCO activity reduced under drought (Fig. 2A). In severely dehydrated leaves RuBPCO activity decreased considerably (Kicheva *et al.* 1994) which supports our findings. RuBPCO activity under drought either remained unchanged or increased, slightly decreased or even fell sharply depending upon the intensity of drought and plant type (Chernyad'ev 1997). Drought induced decrease in RuBPCO activity should be attributed not only to proteolytic decomposition of enzyme protein but also to the partial inhibition of its catalytic activity, because decrease in RuBPCO activity was more than that in RuBPCO content (Chernyad'ev and Monakhova 1998). BAP or 6-furfurylamino purine affected photochemical activity (Doushkova *et al.* 1989), carboxylating activity and the content of RuBPCO (Chernyad'ev 1994). Kartolins affects the activities of RuBPCO and other photosynthetic enzymes and ultrastructure of leaf plastids in crop plants exposed to drought (Baskakov 1988) and BAP increased RuBPCO activity (Pandey *et al.* 2000). Under drought condition Chl *b* content increased significantly (Fig. 2). In contrast to our findings chlorophyll content in cotton decreased with drought (Gadallah 1995). However, with increasing severity of drought stress its content decreased (data not shown). At drought exogenous application of GA and BAP nonsignificantly increased Chl *a* while IAA significantly

reduced Chl *b* (Fig. 2). In support to our findings Dayal *et al.* (1993) observed that droughted pigeon pea (*Cajanus cajan* cv. H-77-216) spray of 0.64 or 3.2 mmol dm<sup>-3</sup> cycocel (chlomequate) increased chlorophyll content. In contrast, proline alone or with ABA increased chlorophyll stability index at low water potential (Gadallah 1995).

We found that at drought flower number per plant increased significantly while boll number, seed number and lint mass per plant reduced (Fig. 3). Similarly drought influenced economic yield (Bagga *et al.* 1985, Bharadwaj *et al.* 1987) and also, drought after flowering aborted young fruits, reduced fruit number and yield (Krieg *et al.* 1993). Drought reduced total seed cotton yield (Marur 1991) and yield components (Mc Michael and Hesketh 1982). Under drought foliar application of BAP increased flower number, boll number, seed number and lint mass per plant while ETH significantly reduced lint mass per plant (Fig. 3). It is well known that IAA and ETH are directly or indirectly linked in the enhancing of the flowering, senescence and abscission of flower and fruits resulted reduced lint mass per plant. In support of our results Guinn and Mauney (1984) observed that seed yield enhancers such chlorodimeton, which are insecticides, may function primarily by increasing the retention of fruit form.

From present study it was concluded that gas exchange ( $P_N$ ,  $g_s$ , E, CE, WUE), RuBPCO and yield (boll number, seed number and lint mass per plant) significantly decreased at drought while Chl *b* and flower number per plant increased. BAP significantly alleviated detrimental drought effect on  $P_N$ ,  $g_s$ , E, CE, RuBPCO and lint mass per plant while ABA significantly increased seed number and lint mass per plant.

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