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The effect of endogenous hormones on plant morphology and fruit quality of tomato under difference between day and night temperature

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Abstract

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The difference between day and night temperature (DIF) was reported to influence plant morphology and fruit quality, but the mechanism was poorly known. Therefore, controlled-environment experiments were carried out to investigate the mechanism of DIF influenced plant morphology and fruit quality attributes of tomato during fruit stage. Five day/night temperature regimes 16/34, 19/31, 25/25, 31/19 and 34/16°C with respective DIFs of –18, –12, 0, +12 and +18 at a common 25°C mean daily temperature were used. The results showed that gibberellin 3, indoleacetic acid and zeatin content of stem tip were enhanced significantly by positive DIF and inhibited by negative DIF, while abscisic acid was not significantly influenced by DIF. Plant height, stem diameter, fruit diameter and leaf area were enhanced significantly by positive DIF regimes and inhibited by negative DIF regimes. The soluble sugars, vitamin C and soluble protein content increased under positive DIF while decreased under negative DIF. Both plant morphology and fruit quality of tomato were significantly related to endogenous hormones.

Keywords: growth hormone; plant height; leaf area; solubel sugar; vitamin C

Tomato (*Lycopersicum esculentum* Mill.) is one of the most important fruit crops grown throughout the world (Sun et al. 2014). For tomato plants during fruit stage, to keep the proper stem length, elongation rate and leaf area is very important to achieve high yield (Jiang 1996). The difference between day and night temperature (DIF) was found effective in control internode length and plant height in chrysanthemum (Lepage et al. 1984), *Lilium longiforum* (Erwin et al. 1989), cucumber (Grimstad et al. 1993) and DIF had been applied widely in greenhouse horticulture to regulate plant morphology (Berghage et al. 1998). DIF was defined as day temperature minus night temperature. Positive DIF indicated day temperature was higher than night temperature, while negative DIF indicated night temperature was higher than day temperature. However, the mechanism how DIF influenced plant morphology is poorly understood. The endogenous hormones were reported to influence plant growth and development. For example, gibberellins were reported to regulate stem elongation (Moe 1990; Ihlebekk et al. 1995). Indoleacetic acid (IAA) was reported to exert a strong influence

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on the development of the lateral buds (Li et al. 1995). DIF was reported to influence the content of endogenous hormones. Thingnaes et al. (2003) reported that IAA content of *Arabidopsis* stem decreased 56% under negative 10 DIF compared with that of positive 10 DIF. Therefore, it is possible that DIF regulated plant morphology through endogenous hormones.

It was also reported that DIF influenced crop quality. For example, carbohydrate content decreased dramatically in *Lilium longiflorum* under negative DIF (Miller et al. 1993). The sucrose, lupeose and starch content of cucumber leaf significantly increased under positive DIF (Miao et al. 2009). However, the mechanism by which DIF influenced crop quality was unclear. Endogenous hormones were reported to influence quality of crops. For example, Xie et al. (2003) indicated that endogenous hormones under post-anthesis drought might indirectly affect protein and starch accumulation in grains. Therefore, it was possible that DIF regulated fruit quality through endogenous hormones.

To our best knowledge, the effect of DIF on endogenous hormones and the mechanism of DIF influenced plant morphology and fruit quality of tomato have not been reported. Therefore, the main aim of this research was to investigate the mechanism of DIF influencing plant morphology and fruit quality of tomato. Our hypothesis was: DIF regulates plant morphology and fruit quality of tomato through changes in endogenous hormones.

MATERIAL AND METHODS

Plant material, and experimental design. Two controlled-environment experiments were carried out during 2015 in climate chambers (TPG-2900, Australia) in Nanjing University of Information Science and Technology, Nanjing, China. Tomato (*Lycopersicum esculentum* Jinguan 5) seeds were germinated and grown in vermiculite media for 20 days. At third-leaf stage, the young tomato plants were transplanted into 25-cm-diameter pots containing 15 kg of a sandy loam soil with 2.5% organic matter content and nutrient availability of 180 mg N/kg, 90 mg P/kg, and 210 mg K/kg. Each pot contained one plant. The plants were watered regularly with a nutrient solution containing N, P, and K in concentrations of 14.3, 1.0, and 5.1 mM, respectively, and with other microelements. During the fruit setting stage, uniform tomato plants were selected and placed into the chambers. Five day/night temperature regimes were set as: 16/34, 19/31, 25/25, 31/19 and 34/16ºC (12 h DT/12 h NT), with five DIFs of –18, –12, 0, +12 and +18 at a common 25°C mean daily temperature. 500 μmol (photon) m^2/s PPFD, a CO_2 concentration of 380 ± 10 μ mol (CO_2) mol^{-1}, and a relative humidity of 60–70% were set in all chambers at the same time. A completely randomized design was use for the experiments. Each chamber contained 18 plants and each DIF treatment consisted of three replicates. Pots in each chamber were changed in position every 3 days in case the light intensity in the chambers was not uniform. No disease symptoms were visible in any plants. When the first order of tomato fruits was red-ripening, the DIF treatments stopped. The DIF treatments started from May 1 until June12, and were repeated from November 1 until December 12, 2015.

Hormone extraction and analysis. Determination of endogenous hormones (GA_3, IAA, ZT and ABA) content was according to the method described by Yang et al. (2014) with small modifications. Stem tip of tomato plants were taken for each treatment at interval of 7 days until ripening of the first order fruits. Sample was quickly preserved in liquid nitrogen and kept in a low temperature freezer (–80°C). About 0.5 g of tissue was weighed and homogenized in small volumes of pre-cooled 80% methanol. The samples were extracted with 5 ml of pre-cooled 80% methanol for 24 h at 4°C. After centrifugation at 2×10^4 g for 20 min at 4°C, the supernatant was collected and concentrated to the aqueous phase by placing in a 37°C water bath with Rotary Evaporator (RE-100, Bibby Sterlin LTD, Stone Staffordshire, England). The organic phase was treated with 0.2g polyvinylpolypyrrolidone (PVPP). After centrifugation again at 2×10^4 g for 20 min at 4°C, the supernatant was collected and adjusted to pH 2.8, extracted with an equal volume of ethyl acetate three times, and finally evaporated to dryness with Rotary Evaporator at 37°C as above. The dried samples were redissolved in chromatography grade methanol with 0.1 M glacial acetic acid as the mobile phase. The flow rate was adjusted to 0.7 ml/min. Samples of 10 μl was injected for HPLC analysis, and the detection wavelength was 254 nm. HPLC analysis was performed with an HP1100 (Agilent, Palo Alto, USA) coupled with a Diode

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Array Detector. An Agilent ZORBAX SB-C18 clumn (5 µm 4.6 × 250 mm) was used in analysis and Mobile phases were 100% methanol (A) and 0.1M acetic acid (B). The elution was performed as A 45% and B 55%. Flow rate was 0.7 ml/min and column temperature was set at 30°C. Chromatograms were used for quantification via Agilent chromatography workstation.

Measurement of morphogenesis. Plant height, stem diameter, fruit diameter and leaf area (measured by LI-COR Model 3100 Area Meter, USA) were determined by destructive measurements on three tomato plants per time over a period of six weeks. Plants were removed out of climate chamber after measurements. Increment of plant height, stem diameter, leaf area and fruit diameter represented the difference value between two contiguous determinations.

Measurement of fruit quality. Fruit quality attributes were determined on 28, 35, and 42 days after treatment. Soluble sugars were determined using anthrone method (Fales 2000). About 0.5 g of fresh sample was placed in a 25 ml of cuvette and then 10 ml distilled water were added. Samples were heated at 100ºC for 1 h, and then filtered into 25 ml volumetric flasks. Reaction mixture (7.5 ml) contained 0.5 ml extracts, 0.5 ml mixed reagent (1 g anthrone + 50 ml ethyl acetate) and 5 ml H_2SO_4 (98%), plus 1.5 ml distilled water. The mixture was heated at 100°C for 1 min and absorbance was read at 620 nm.

Vitamin C concentration was determined using the 2,6-dichlorophenol-indophenol (DIP) method (Ghasemnezhad et al. 2011). Twenty grams of each fruit sample was homogenised in 10 ml of 3% [weight/volume (w/v)] metaphosphoric acid, then filtered. The extract was made up to 100 ml with 3% (w/v) metaphosphoric acid. Ten millilitres was then titrated using DIP (Ghasemnezhad et al. 2011), which had been standardised against standard ascorbic acid solutions. The results were expressed in mg ascorbic acid per 100g fresh weight (FW) of the tissue.

A modified soluble protein assay (Bradford 1976) was used to determine the concentration of soluble protein in the extracted samples. The tests were carried out in triplicate. Firstly, Coomassie Brilliant Blue staining solution (G250 solution) was prepared. 100 mg of G250 dye was weighed, dissolved in 50 ml of 95% ethanol, added with 100 ml of 85% phosphoric acid, dissolved completely by magnetic stirring and added with distilled water to a final volume of 1,000 ml and transferred to a brown bottle and preserved at 4°C. Then 1 ml of protein extract of sample was added with 5 ml of G250 solution, mixed evenly and placed at room temperature for about 2 minutes. Absorbance was measured at 595 nm using a spectrophotometer UV 1800 (Shimadzu, Japan). Standards containing 0–100 µg/ml of standard protein solution were measured following the same procedures.

Statistical Analysis. All data were subjected to analysis of variance (ANOVA) using SAS software (Version 9.0; SAS Institute, Cary, NC, USA). The least significant difference (LSD) method was used to separate means at a probability value of $P \leq 0.05$.

RESULTS AND DISCUSSION

DIF significantly influenced endogenous hormone content in the tip of tomato plants. Positive DIF caused an increase in GA_3 content of tomato plants, while negative DIF caused a decrease (Fig. 1). GA_3 content was found the most in tomato plants under +12 DIF, while the least under −18 DIF was similar to GA_3, both IAA and ZT contents were promoted by positive DIF while inhibited by negative DIF during the whole experiment (Fig. 1). However, DIF did not have significant effect on ABA content of tomato plants (Fig. 1). Similar results obtained by Thingnaes et al. (2003) indicated IAA and GA_9 of *Arabidopsis* stem increased 56% and 13% under +10 DIF compared to −10 DIF, and by Stavang et al. (2010) reported that GAs content of pea leaf decreased under negative DIF compared to positive DIF. In the initial period of experiment, GA_3, IAA and ZT under all DIF treatments increased, while declined afterward. While ABA increased sharply in the middle period, and decreased afterwards.

DIF significantly influenced plant height and stem diameter of tomato (Fig. 2). Positive DIF caused tomato plants grow longer and larger compared with that of 0 DIF, while negative DIF caused tomato plants grow shorter and thinner during the experiment. This is parallel to the results by Moe (1990) who indicated that plant height of *Campanula isophylla* under +12 DIF increased 230% compared −12 DIF. Plant height was enhanced by +12 IF, while this was not observed

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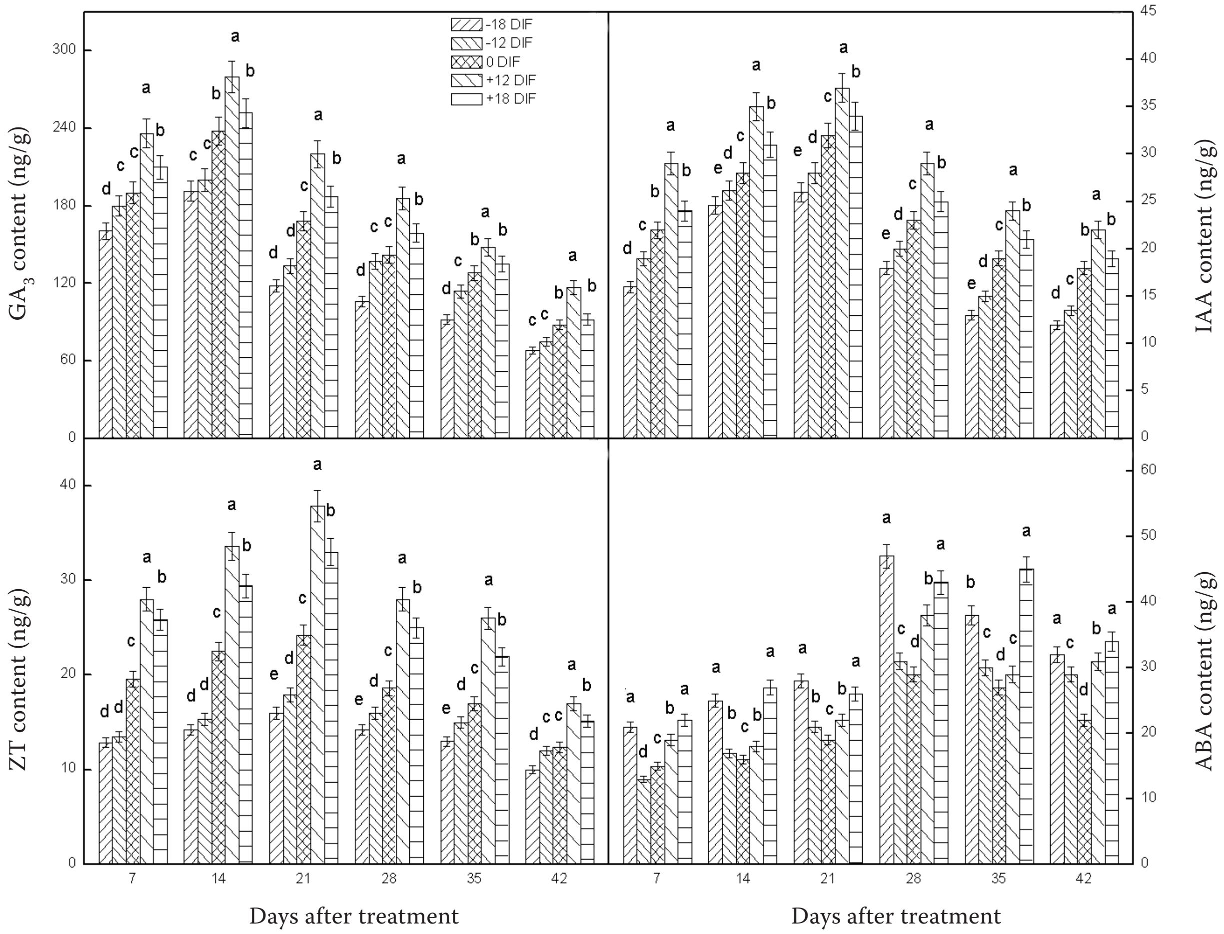

Fig. 1. Effect of difference between day and night temperature (DIF) in endogenous hormones concentrations of tomato during fruit stage

mean values with the same lower-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test

in +18 DIF (Fig. 2), in accordance with Davies et al. (2002) who reported that stem length increased by 55% as DIF increased from –6 to +12, but a further increase to DIF +18 resulted in markedly shorter stems in *Sandersonia aurantiaca*. Similarly, leaf area and fruit diameter increased under positive DIF, while decreased under negative DIF compared with that of 0 DIF (Fig. 2). It was consistent with Slack and Hand (1983) who found that cucumber plants at the transplanting stage under +5 DIF had 6% more leaf area than plants grown at +2 DIF, and Miller et al. (1993) who indicated Easter lily under +8 DIF had more leaf area than that under –8 DIF. The reason for an increase in leaf area by positive DIF may be that positive DIF increased photosynthetic rate, resulting in more assimilate accumulation, thus more leaf area (Mao et al. 2012). During the experiment, plant height, stem diameter, fruit diameter and total leaf area of tomato plants under all treatments increased fast in the beginning, while the growth rate of them decreased thereafter. Their growth rates were consistent with variations of endogenous hormones such GA_3, IAA and ZT.

DIF significantly influenced soluble sugars of tomato fruit (Table 1). During the whole experiment, it was much more under positive DIF, compared to 0 DIF, similar to Miller et al. (1993) who indicated that total carbohydrate content of 'East lily' leaves under +8 DIF was significantly higher than that under –8 DIF. The reason may be that plants grown under positive DIF had a higher photosynthetic rate than plants grown in a negative DIF or constant temperature (Bunce 1985; Berghage et al. 1990), therefore more soluble sugars were synthesized. The response of vitamin C and soluble protein content to DIF was similar to soluble sugars (Tables 2 and 3). During the experiment, soluble sugars content under all treatments gradually increased, while soluble protein content gradually

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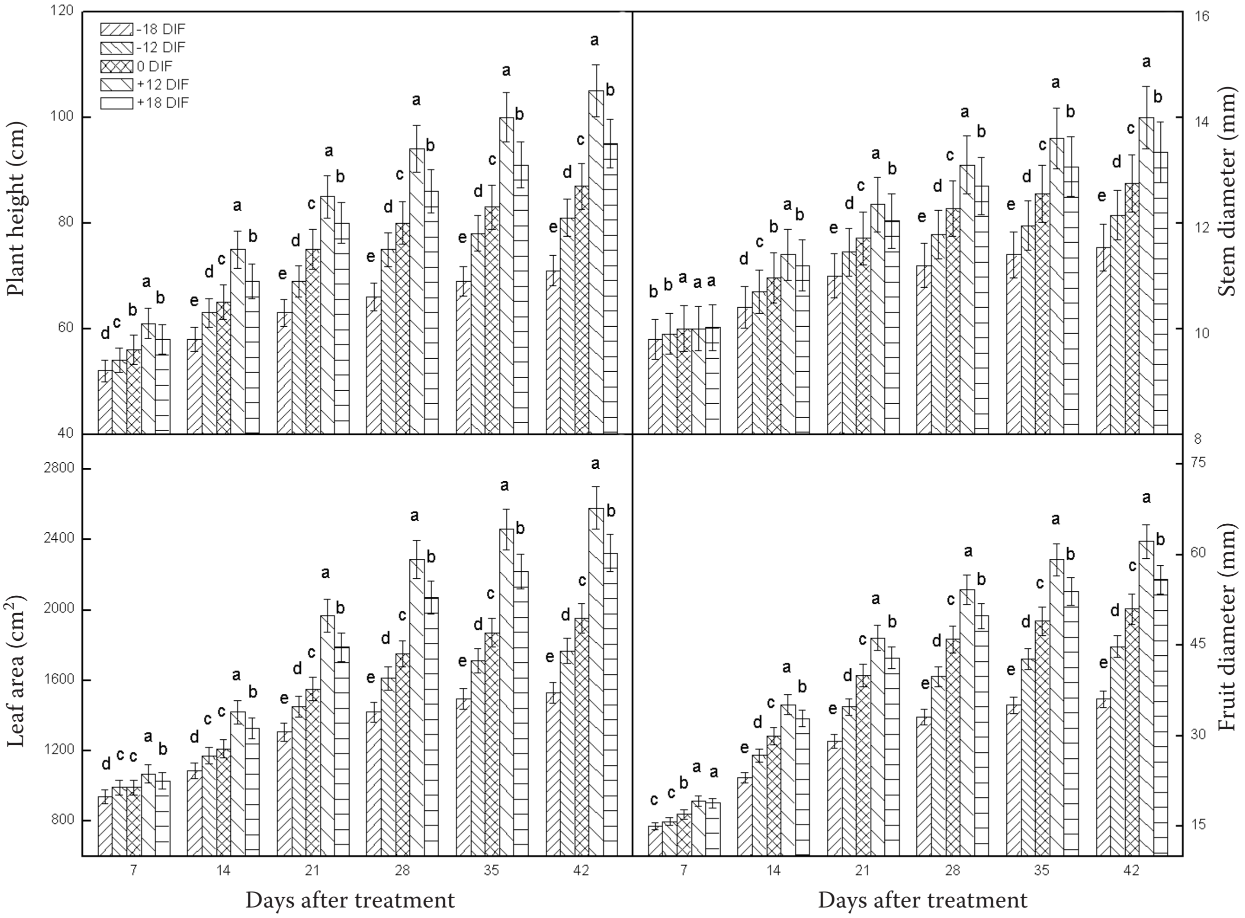

Fig. 2. Effect of difference between day and night temperature (DIF) in plant morphology of tomato during fruit stage mean values with the same lower-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test

decreased. Vitamin C content increased initially but deceased at the end.

GA_3 was significantly positive correlated with plant height increment (Table 4), in accordance with Fujioka et al. (1988) who indicated plant height of *Zea mays* seedlings were positively correlated to GA_3. GA_3 is known to have a positive effect to promote stem growth by stimulating both cell division and cell elongation (Swarup et al. 2002). Plant height increment was also positively correlated IAA, in accordance with Wu et al. (2009), who also suggested that IAA promoted normal stem elongation. Evidence from physiological studies indicates that IAA affects cell expansion during shoot elongation (Jacobs, Ray 1976). ZT was positively correlated with stem diameter increment (Table 4), in agreement with Xu (2008), who also pointed out higher level of cytokinins was a key factor in controlling stem swelling processes. Similar to plant height increment, leaf area increment, and fruit diameter increment were also significantly positive correlated with all of GA_3, IAA and ZT (Table 4).

The soluble sugars content of tomato fruit was significantly positively correlated with GA_3, IAA and ZT, in agreement with Booth and Lovell (1972), Brenner (1989) and Li et al. (2016). Booth and Lovell (1972) indicated that GA increased sugar content of potato. Brenner (1989) indicated that exogenous GA_3, IAA and ZT increased sugar content of fruit in different fruit development stages. Li et al. (2016) indicated that a high content of endogenous ZT favoured sugar accumulation in tubers. However, soluble sugars were not significantly correlated with ABA, while Archbold (1988) indicated that exogenous ABA increased soluble sugars content of fruit. (Table 5). Similar to soluble sugars, vitamin C and soluble protein were also significantly positive correlated with all of GA_3, IAA and ZT (Table 5). The results were consistent with Brenner and Cheikh (1995) who indicated that IAA increased protein synthesis.

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Table 1. Effect of difference between day and night temperature (DIF), days after treatment, and their interaction on soluble sugars concentrations (mg/g FW) in tomato fruit

DIF	Days after treatment			mean DIF
	28	35	42	
−18 DIF	40.12^{e}	48.27^{d}	52.78^{d}	47.06^{D}
−12DIF	49.24^{d}	60.57^{c}	64.42^{c}	58.08^{C}
0 DIF	63.37^{c}	78.34^{b}	83.74^{ab}	75.16^{B}
+12 DIF	79.45^{b}	91.78^{a}	96.42^{a}	89.22^{A}
+18 DIF	74.69^{b}	88.45^{a}	92.68^{a}	85.28^{A}
Mean days after treatment	61.38^{B}	73.49^{A}	78.01^{A}	

means of interaction effects followed by the same lower-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test. Means of the main effects (DIF or days after treatment) followed by the same upper-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test

Table 2. Effect of difference between day and night temperature (DIF), days after treatment, and their interaction on Vitamin C concentrations (mg/100 g FW) in tomato fruit

DIF	Days after treatment			mean DIF
	28	35	42	
−18 DIF	17.52^{c}	15.36^{d}	13.23^{d}	15.37^{C}
−12DIF	20.74^{b}	18.48^{c}	16.35^{c}	18.52^{C}
0 DIF	25.56^{ab}	22.45^{b}	20.74^{b}	22.92^{B}
+12 DIF	31.44^{a}	29.35^{a}	27.46^{a}	29.42^{A}
+18 DIF	28.49^{a}	25.43^{ab}	23.74^{b}	25.89^{A}
Mean days after treatment	24.76^{A}	22.22^{A}	20.31^{B}	

means of interaction effects followed by the same lower-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test. Means of the main effects (DIF or days after treatment) followed by the same upper-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test

Table 3. Effect of difference between day and night temperature(DIF), days after treatment, and their interaction on soluble protein concentrations (mg/g FW) in tomato fruit

DIF	Days after treatment			Mean DIF
	28	35	42	
−18 DIF	3.88^{e}	3.52^{f}	3.34^{f}	3.58^{D}
−12DIF	4.15^{d}	3.82^{e}	3.62^{e}	3.86^{D}
0 DIF	4.62^{c}	4.22^{d}	3.86^{e}	4.23^{C}
+12 DIF	5.92^{a}	5.14^{b}	4.53^{c}	5.20^{A}
+18 DIF	5.27^{b}	4.51^{c}	4.14^{d}	4.65^{B}
Mean days after treatment	4.77^{A}	4.25^{B}	3.90^{C}	

means of interaction effects followed by the same lower-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test. Means of the main effects (DIF or days after treatment) followed by the same upper-case letters are not significantly different at $P \leq 0.05$ by the least significant difference test

Table 4. Correlation coefficients between endogenous hormone and growth of tomato during fruit stage (*n* = 90)

	Plant height increment	Stem diameter increment	Leaf area increment	Fruit diameter increment
GA_3	0.55*	0.61*	0.54*	0.62*
IAA	0.60*	0.58*	0.59*	0.67*
ZT	0.46*	0.54*	0.61*	0.61*
ABA	–0.12	–0.08	–0.11	–0.09

*significant at 0.01 level

Table 5. Correlation coefficients between endogenous hormone and fruit quality attributes of tomato during fruit stage (*n*=15)

Days after treatment	GA_3 & soluble sugar	IAA & soluble sugar	ZT & soluble sugar	ABA & soluble sugar
28	0.85*	0.86*	0.87*	–0.11
35	0.89*	0.83*	0.85*	–0.06
42	0.88*	0.84*	0.89*	–0.04
	GA_3 & vitamin C	IAA & vitamin C	ZT & vitamin C	ABA & vitamin C
28	0.84*	0.87*	0.85*	–0.17
35	0.91*	0.90*	0.79*	–0.14
42	0.85*	0.82*	0.76*	–0.19
	GA_3 & soluble protein	IAA & soluble protein	ZT & soluble protein	ABA & soluble protein
28	0.86*	0.84*	0.79*	–0.15
35	0.83*	0.75*	0.81*	–0.19
42	0.78*	0.81*	0.76*	–0.11

*means significant at 0.01 level

CONCLUSION

Our results suggest that endogenous hormones, growth rate and fruit quality attributes could be enhanced significantly by positive DIF and inhibited by negative DIF. DIF may regulate plant morphology and fruit quality of tomato through changes in endogenous hormones.

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