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EFFECT OF UNICONAZOLE TREATMENT ON THE DROUGHT TOLERANCE OF SOYBEAN SEEDLINGS

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Abstract

Uniconazole is an important growth regulator in plants in response to abiotic stresses. However, the effects of uniconazole on the leaf physiology and growth of soybean seedlings under drought conditions remain unclear. Thus, this study investigated the effects of uniconazole on the photosynthetic characteristics, antioxidant activities, and morphological structure of soybean varieties Suinong14 (*Glycine max* var.) (drought sensitive) and Heinong64 (*Glycine max* var.) (drought tolerant) under drought conditions through pot experiments. Results showed that drought significantly decreased the growth of the plants. However, the drought-stressed plants with uniconazole treatment showed considerably higher biomass than the drought-stressed plants without uniconazole treatment. Uniconazole treatment showed better effects on Heinong64 than on Suinong14. The uniconazole-treated plants displayed longer roots and thicker stems than the untreated plants. Moreover, the drought-stressed plants with uniconazole treatment exhibited higher chlorophyll contents, photosynthetic rates, transpiration rates, and stomatal conductance but lower lipid peroxidation contents and relative electrical conductivity than the drought-stressed plants without uniconazole treatment. The content of foliar soluble sugar, the content of soluble protein, and the activities of superoxide dismutase, peroxidase, and catalase were increased by uniconazole treatment under drought and well-watered conditions. These results indicate that uniconazole can effectively alleviate the adverse effects of drought partly by modifying the morphology and physiology of the plants.

Key words: Uniconazole, Drought, Soybean, Morphology, Physiology.

Introduction

Soybean (*Glycine max* L. Merr.) is cultivated worldwide as a valuable oil seed and protein-rich crop. However, its nutritional value and plant performance are influenced by environmental stresses (Kosturkova *et al.*, 2014). Among abiotic stresses drought is the major one that affects the growth and development of plants (Farooq *et al.*, 2009). Moreover, drought stress spoils various metabolic, photosynthetic, and physiological processes in plants. Effective improvement of crop drought tolerance has become a concern in agricultural production and research (Passioura *et al.*, 2007). Responses to drought are multidimensional and interconnected. Drought induces several morphological and physiological reactions and resistance mechanisms (Farooq *et al.*, 2009; Jaleel *et al.*, 2009; Ali *et al.*, 2020). Drought tolerance mechanisms include producing longer roots to maintain root growth (Pace *et al.*, 1999; Hossain *et al.*, 2014), inhibiting chloroplast activity and stomatal closing, decreasing the production of reactive oxygen species (ROS), and requiring elevated levels of antioxidants for stress compensation (Xu *et al.*, 2008; Lipiec *et al.*, 2013). Therefore, drought tolerance can be enhanced by promoting these morphological and physiological processes.

Growth regulators are naturally occurring compounds that exert significant effects on the development or metabolism of higher plants, most often when applied in lower doses (Rademacher, 2015). The triazole compound uniconazole is a well-known plant growth retardant that operates by inhibiting gibberellin biosynthesis and reducing stem elongation in higher plants (Izumi *et al.*, 1985). Uniconazole offers potential advantages and serves various functions, such as decreasing plant height in sea marigold (Carver *et al.*, 2014), increasing root length and root volume in soybean (Wan *et al.*, 2013), and increasing root dry weight, chlorophyll content, and net photosynthetic rate in plantlets and duckweed (Cha−Um *et al.*, 2009; Liu *et al.*, 2015). Uniconazole has also been used to induce environmental stress tolerance in certain plants. Uniconazole treatment instigates drought tolerance in apple seedlings (Todoroki *et al.*, 2009), improves the growth of seedlings of rapeseed in response to physiological changes under waterlogging conditions (Qiu *et al.*, 2005), and induces thermotolerance by enhancing antioxidant activity and consequently reducing stress-related oxidative damage to cell membranes (Upadhyaya *et al.*, 1990). Uniconazole also increases the contents of proline and soluble sugars, activities of superoxide dismutase (SOD) and peroxidase (POD) but reduces the malondialdehyde (MDA) content or electrical conductivity of soybean leaves under water stress (Zhang *et al.*, 2007).

Although the alleviation of environmental stress by uniconazole has received attention, little is known about its protective effect on soybean seedlings against drought. In consideration of the importance of uniconazole treatment on soybean under drought, an experiment was conducted in this study to determine the effects of uniconazole treatment on (1) morphology in the roots and shoots; (2) chlorophyll content, photosynthesis rate, transpiration rate, and stomatal conductance; (3) soluble sugar and protein contents; (4) activities of antioxidants such as POD and SOD, which may be valuable in scavenging free radicals that damage membranes during drought; and (5) relative electrical conductivity and MDA content.

Materials and Methods

Planting and uniconazole treatment: Greenhouse experiments were conducted in 2014 and 2015 at Heilongjiang Bayi Agricultural University (45°46′ N, 124°19′ E), Daqing, China. Soybean seeds of drought-sensitive (Suinong14) and drought-tolerant (Heinong64) collected from the Agronomy College of Heilongjiang Bayi Agricultural University were planted in pots (30 cm ×30 cm) containing a mixture of sandy loam soil with 2.2% organic matter content (13 kg) and basal fertilizer (156 mg N·kg^{-1}, 78 mg P·kg^{-1}, and 182 mg K·kg^{-1}). At the first trifoliate leaf stage (V1), the seedlings were thinned to maintain four individuals per pot. The water content of the pots was maintained at 80% of the soil field capacity (oven-drying method) by manual watering until the water treatments were initiated. All experiments were conducted through a completely randomized block design. At V3, uniconazole was applied at 50 mg·L^{-1}. The following four treatment groups were established: 1. 80 uniconazole-treatment seedlings (V3) exposed to drought, 2. 80 untreated control seedlings exposed to drought, 3. 80 uniconazole-treated seedlings (V3) exposed to well-watered conditions (at 80% of soil field capacity), and 4. 80 untreated control seedlings exposed to well-watered conditions. Samples were collected 6 days after treatment for further analysis. For obtaining samples after 6 days of uniconazole treatment, the relative water content of the soil was calculated to be 50%–60% in accordance with the formula provided by Porcel & Ruiz–Lozano (2004).

Measurements

Measurement of morphological parameters: Plant height, stem diameter, root length, biomass (stem and root dry weight), and seed weight were measured 6 days after uniconazole treatment.

Chlorophyll, photosynthetic rate, transpiration rate, and stomatal conductance measurement: Chlorophyll content, photosynthesis rate, transpiration rate, and stomatal conductance in the third leaf from the top were measured 6 days after uniconazole treatment. Chlorophyll content was measured using a portable chlorophyll meter (Minolta SPAD–502, Japan) following the method described by Turner & Jund (1991). Photosynthesis rate, transpiration rate, and stomatal conductance were measured with a photosynthesis system (CID–340, USA). The measurements were recorded between 9 and 11 am when the photosynthetically active radiation above the canopy was 900–1300 μmol·m^{-2}·s^{-1}. A total of 12 leaves from each treatment were adopted to measure the chlorophyll content, photosynthesis rate, transpiration rate, and stomatal conductance.

Biochemical measurements: A total of 12 leaves (third leaf from the top) from each treatment were sampled between 9:30 and 10:30 am, 6 days after uniconazole treatment. Immediately, the samples were separately immersed in liquid nitrogen, ground to fine powder in liquid nitrogen by using a mortar and pestle, and then stored in liquid nitrogen until use. The activities of SOD, POD, and catalase (CAT) and the content of MDA were analyzed using the method described by Leul & Zhou (1999). Soluble sugars were evaluated using the anthrone method described by Fales (1951). Soluble protein was assayed following the method described by Bradford (1976). Relative electrical conductivity was measured by using an EC215 conductivity meter (HANNA Instruments, Portugal) following the method described by Leul & Zhou (1999).

Data analysis: Data were subjected to one-way ANOVA, and differences were compared by the least significance difference test. Each data point was the mean of four replications, and means were compared using the appropriate Duncan's protected LSD (p<0.05).

Results

Effect of uniconazole on morphological parameters under drought: Plant height, stem diameter, root length, stem dry weight, and root dry weight are important indices for evaluating plant growth under drought. In the experiment, uniconazole treatment reduced plant height compared with the controls under drought and well-watered conditions. Conversely, uniconazole significantly increased the stem diameter, root length, and stem and root dry weight under each water condition (except for the stem dry weight in Suinong14). Uniconazole application clearly alleviated the drought-induced inhibition of growth in Suinong14 and Heinong64 (Table 1).

Uniconazole significantly reduced plant height by 7.32% in Suinong14 and 18.99% in Heinong64 under drought. Furthermore, uniconazole significantly decreased plant height by 3.92% in Suinong14 and 6.05% in Heinong64 under well-watered conditions (Table 1). Uniconazole also significantly increased stem diameter and root length by 14.99% and 5.71%, respectively, under drought conditions and 2.50% and 7.35%, respectively, under well-watered conditions relative to the controls in Suinong14. Similarly, uniconazole significantly increased the stem diameter and root length by 5.95% and 14.64%, respectively, under drought conditions and 4.17% and 2.17%, respectively, under well-watered conditions in Heinong64 compared with the controls. Stem dry weight and root dry weight were significantly increased by 13.58% and 33.73%, respectively, in Suinong14 and 16.79% and 17.82%, respectively, in Heinong 64 under well-watered conditions relative to the controls.

Effect of uniconazole on photosynthetic characteristics under drought: Figure 1 shows the changes in the leaf chlorophyll contents, photosynthetic rate, and stomatal conductance of soybean. Drought significantly decreased the leaf photosynthetic rates of Suinong14 and Heinong 64. However, the photosynthetic rate of the drought-stressed plants with uniconazole treatment was higher than the photosynthetic rate of the drought-stressed plants without uniconazole treatment. Under well-watered conditions, the photosynthetic rate of the uniconazole-treated plants was 26.89% higher in Suinong14 and 16.61% higher in Heinong64 compared with the untreated plants (Figs. 1a and 1b). The stomatal conductances of uniconazole-treated Suinong14 and Heinong64 were significantly higher than the stomatal conductances of the control plants (without unicanazole treatment) and presence of water stress (Figs. 1c, d). Under well-watered conditions, the leaf chlorophyll contents of the uniconazole-treated plants were 3.49% higher in

Suinong14 and 10% higher in Heinong64 compared with the leaf chlorophyll contents of the untreated plants (Figs. 1e, 1f). Drought significantly decreased the leaf chlorophyll contents in Suinong14 and Heinong64. However, the leaf chlorophyll contents of the drought-stressed plants with uniconazole treatment were also significantly increased by 4.66% and 4.77% compared with the leaf chlorophyll contents of the drought-stressed plants without uniconazole treatment.

Effect of uniconazole on the transpiration rate: Figure 2 shows the changes in leaf transpiration rate of soybean. Drought significantly decreased the leaf transpiration rate in Suinong14 and Heinong64. However, the transpiration rate of the drought-stressed plants with uniconazole treatment was higher than the transpiration rate of the stressed plants without treatment. Under drought, the photosynthetic rate of the uniconazole-treated plants was 85.54% higher in Suinong14 and 65.79% higher in Heinong64 compared with the photosynthetic rate of the untreated plants (Figs. 2a, b).

Effect of uniconazole on soluble sugar and soluble protein contents under drought: The contents of soluble sugar and soluble protein decreased under drought in the leaves of Suinong14 and Heinong64 (Fig. 3). Under well-watered conditions, the soluble sugar contents in the uniconazole-treated plants of Suinong14 and Heinong64 were 4.98% and 28.75% higher, respectively, than the soluble sugar contents of the untreated plants (Figs. 3a, 3b). Meanwhile, the soluble protein contents of the uniconazole-treated plants were 19.54% and 10.00% higher, in Suinong14 and Heinong64 respectively than in the untreated plants (Figs. 3c, 3d). When the plants were exposed to drought, the soluble sugar and soluble protein contents of Suinong14 and Heinong64 treated with uniconazole exceeded the soluble sugar and soluble protein contents of the untreated plants (Fig. 3). Moreover, the leaf soluble sugar content in Heinong64 was higher than the leaf soluble sugar content in Suinong14 under well-watered and drought conditions; this result further clarified the superior resistance to drought of Heinong64 compared with Suinong14 (Figs. 3a, 3b).

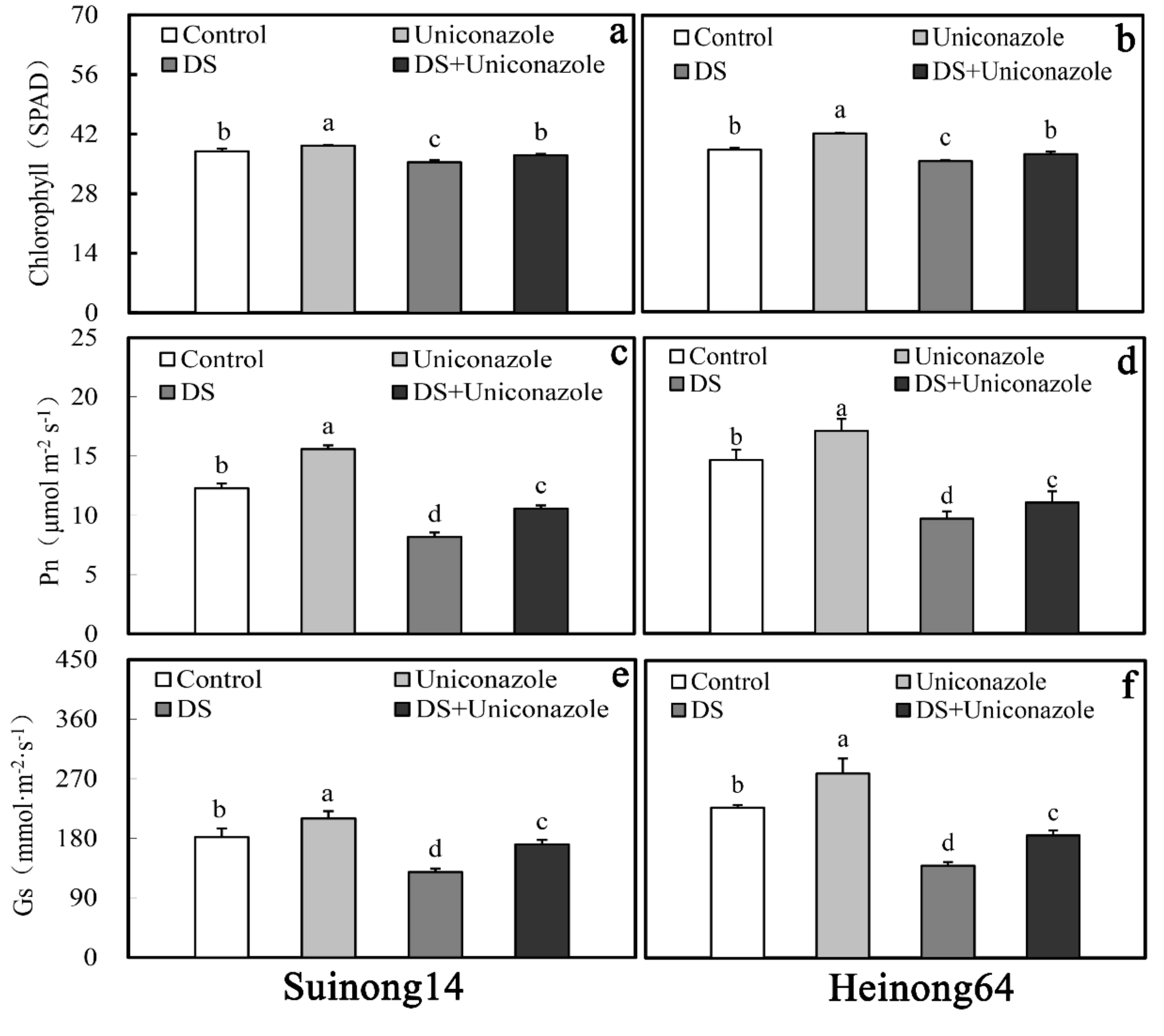

Fig. 1. Effects of foliar application of 50 mg·L^{-1} uniconazole and water on the photosynthetic rates, chlorophyll contents, and stomatal conductances of Suinong14 and Heinong64. DS, foliar application of water under drought; Vertical bars represent ± SEM. *n* = 4 replicates. Values followed by a different lowercase or capital letter within each column are significantly different at the 0.05 probability level.

Table 1. Effects of uniconazole on plant height, stem diameter, root length, and stem and root dry weights under drought and well-watered conditions.Vertical bars represent ± SEM. *n* = 4 replicates. Values followed by a different lowercase or capital letter within each column are significantly different at the 0.05 probability level.

Variety	Treatment	Height (cm)	Stem diameter (mm)	Root length (cm)	Stem dry weight (g)	Root dry weight (g)
Suinong14	Control	25.2 ± 0.0a	2.2 ± 0.0c	38.3 ± 0.3d	0.3 ± 0.0b	0.3 ± 0.0a
	Uniconazole	24.3 ± 0.2b	2.4 ± 0.0a	41.4 ± 0.5a	0.4 ± 0.0a	0.3 ± 0.0a
	DS	22.0 ± 0.5c	2.0 ± 0.0d	39.0 ± 0.2c	0.2 ± 0.0c	0.2 ± 0.0a
	DS+Uniconazole	20.5 ± 0.3d	2.3 ± 0.0b	40.0 ± 0.0b	0.1 ± 0.0d	0.2 ± 0.0d
Heinong64	Control	27.2 ± 0.2a	2.2 ± 0.0b	43.5 ± 0.5d	0.3 ± 0.0b	0.4 ± 0.0a
	Uniconazole	25.6 ± 0.5b	2.5 ± 0.0a	48.0 ± 0.2a	0.4 ± 0.0a	0.4 ± 0.0a
	DS	23.5 ± 0.4c	2.1 ± 0.0c	44.5 ± 0.0c	0.2 ± 0.0c	0.2 ± 0.0b
	DS+Uniconazole	19.8 ± 0.3d	2.2 ± 0.0b	46.0 ± 0.3b	0.3 ± 0.0b	0.4 ± 0.0a

Table 2. Effects of the foliar spraying of 50 mg·L^{-1} uniconazole and water on the plant heights, stem diameters, grain number per plant, pod number per plant and yield per plant of Suinong14 and Heinong64. Values followed by a different lowercase or capital letter within each column are significantly different at the 0.05 probability level.

Variety	Treatment	Height (cm)	Stem diameter (mm)	Grain number per plant (number)	Pod number per plant (number)	yield per plant (g)
Suinong14	Control	51.8 ± 1.4a	5.1 ± 0.2a	31.8 ± 0.7a	11.8 ± 0.7a	5.5 ± 0.2b
	Uniconazole	49.8 ± 2.0b	5.6 ± 0.6a	32.5 ± 1.1a	12.5 ± 1.1a	6.0 ± 0.4a
	DS	45.9 ± 1.0c	4.3 ± 0.3b	22.1 ± 0.9c	7.3 ± 0.9c	4.8 ± 0.9c
	DS+ Uniconazole	42.6 ± 0.7d	4.9 ± 0.2b	23.9 ± 1. 6b	9.9 ± 1.6b	5.0 ± 0.5b
Heinong64	Control	55.6 ± 0.9a	6.1 ± 0.4b	34.6 ± 0.3a	14.6 ± 0.3a	7.0 ± 0.1b
	Uniconazole	52.3 ± 1.1b	7.0 ± 0.3a	34.8 ± 0.5a	14.8 ± 0.5a	8.0 ± 0.8a
	DS	50.6 ± 0.9c	5.5 ± 0.2c	27.3 ± 0.8c	10.1 ± 0.8b	6.2 ± 0.2c
	DS+ Uniconazole	47.8 ± 1.4d	6.4 ± 0.1b	28.9 ± 0.2b	11.9 ± 0.2b	6.5 ± 0.4b

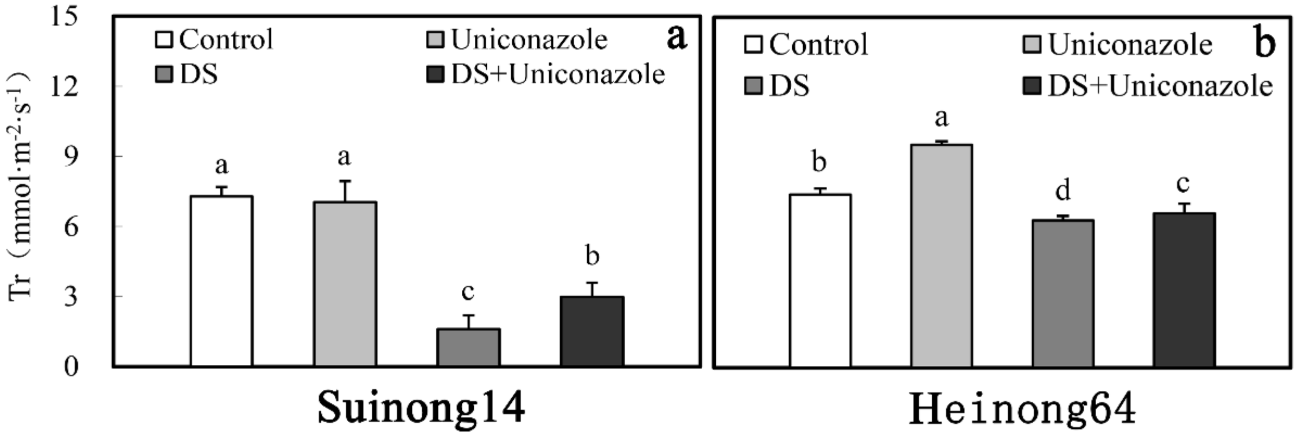

Fig. 2. Effects of foliar application of 50 mg·L^{-1} uniconazole and water on the transpiration rates of Suinong14 and Heinong64. Vertical bars represent ± SEM. *n* = 4 replicates. Values followed by a different lowercase or capital letter within each column are significantly different at the 0.05 probability level.

Effect of uniconazole on SOD, POD, and CAT activities under drought: Under well-watered conditions, uniconazole significantly increased the activities of SOD and POD by 4.56% and 6.81%, respectively, in Suinong14 and 35.71% and 19.66%, respectively, in Heinong64 (Figs. 4a−4d). Drought markedly decreased the SOD and POD activities in the soybean cultivars than in the untreated controls. However, uniconazole significantly raised the SOD, POD, and CAT activities under drought conditions (Fig. 4). Moreover, when the plants were exposed to drought, the SOD activity of the drought-stressed plants wasreduced by 15.01% in Suinong14 and 17.62% in Heinong64 compared with the SOD activity of the untreated controls, whereas the decrements were only 12.10% and 11.94%, respectively, for the DS+uniconazole treatments compared with the uniconazole-treated plants (Figs. 4a, 4b). In Suinong14 and Heinong14, the POD activities of the drought-stressed plants were reduced by 59.88% and 52.07%, respectively, in the uniconazole-treated plants, whereas the reductions were only 35.30% and 30.46%, respectively, for the DS+uniconazole-treated plants compared with the POD activities of the uniconazole-treated plants (Figs. 4c, 4d). Similarly, the CAT activities of the drought-stressed plants were diminished by 56.88% and 26.61%, respectively, compared with the CAT activities of the untreated controls in Suinong14 and Heinong64, whereas the reductions were only 13.61% and 9.75%, respectively, in the DS+uniconazole plants compared with the uniconazole-treated plants (Table 2; Figs. 4e, 4f).

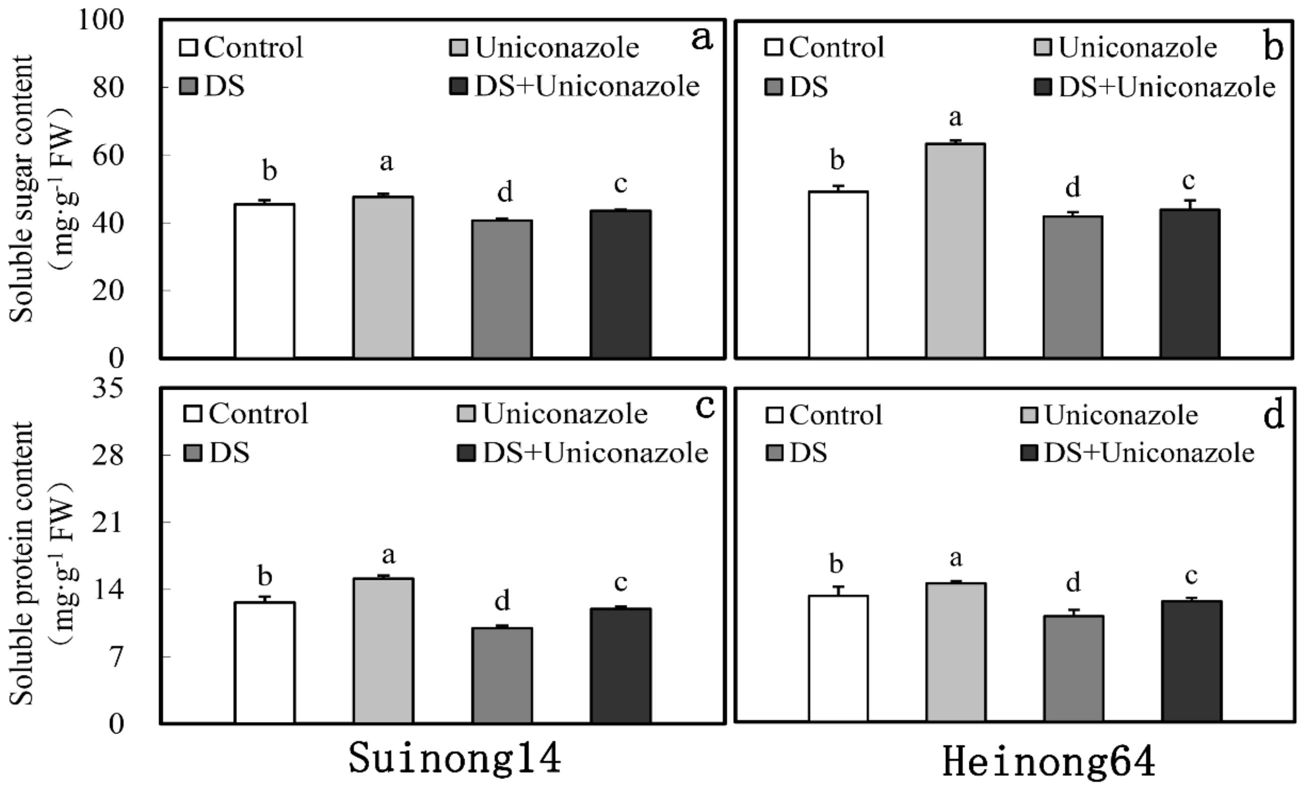

Fig. 3. Effects of foliar application of 50 mg·L^{-1} uniconazole and water on the soluble sugar and soluble protein contents of Suinong14 and Heinong64. Vertical bars represent ± SEM. *n* = 4 replicates. Values followed by a different lowercase or capital letter within each column are significantly different at the 0.05 probability level.

Effect of uniconazole on MDA content and relative electrical conductivity under drought: Drought increased the MDA content and relative electrical conductivity in both soybean cultivars with uniconazole treatment compared with the cultivars without uniconazole treatment (Figs. 5, 6). Uniconazole decreased the MDA content and the relative electrical conductivity in both soybean cultivars under each water condition (Fig. 5). Uniconazole treatment significantly reduced the MDA content under drought and well-watered conditions by 18.51% and 23.51%, respectively, in Suinong14 and 10.48% and 28.46%, respectively, in Heinong64 relative to the controls (Figs. 5a, b). Moreover, uniconazole treatment significantly reduced the relative electrical conductivity by 5.94% and 10.18%, in Suinong14 respectively and 25.58% and 6.26%, in Heinong64 respectively (Figs. 5c, 5d). By contrast, the MDA content and relative electrical conductivity were significantly increased by 21.98%, 98.61% and 45.20%, 11.70% in the untreated controls under drought conditions compared with the untreated controls under well-watered conditions for Suinong14 and Heinong64, respectively (Fig. 5).

Discussion

Drought is a vital limiting factor at the initial phase of plant growth and development (Jaleel *et al*., 2009). In terms of morphological characteristics, plant growth and dry matter (shoot and root) are remarkably reduced in response to drought (Ashraf & Iram, 2005; Harb *et al*., 2010). Uniconazole can induce various morphologies in plants. In particular, rooting is stimulated; hence, the treatment is an ideal candidate for modifying soybean seedling growth and development under environmental stresses (Zhang *et al*., 2007; Wan *et al*., 2013). In the present study, combined ANOVA showed that the morphological characteristics, including plant height, stem diameter, root length, stem dry weight, and root dry weight were decreased after drought (Table 1). By contrast, the plants treated with uniconazole revealed improved morphological characteristics, excluding the plant height; this result indicated the increased tolerance of the soybean seedling to water stress. Under well-watered conditions, the morphological characteristics were enhanced after uniconazole treatment (Table 1). This observation is similar to the findings of Leul & Zhou (1998), that uniconazole treatment significantly improves the growth parameters, including plant height, stem width, root and shoot length, and total dry weight, of plants under waterlogging stress.

Drought reduces the rates of net photosynthesis owing to metabolic limitations, namely, oxidative damage to chloroplasts and stomatal closure (Farooq *et al*., 2014). Stomatal closure guarantees that photosynthesis proceeds well and also helps in controlling excessive water loss (Wang *et al*., 2006). When exposed to drought, plants implement functional measures to reduce water loss by transpiration and protect the appropriate water content in tissues. As recently reported, a drought-tolerant chickpea genotype presents low transpiration; this adaptation may lead to a low photosynthesis rate, which can render the chickpea capable of accessing water available in soil during drought (Saglam *et al*., 2014). By contrast, Lawson &

Blatt (2014) believe that raised stomatal conductance and transpiration rate increase the CO_2 influx into mesophyll cells; as a result, carbon fixation enhances and leads to an augmented photosynthesis rate. In the present study, drought significantly decreased the leaf stomatal conductance in Suinong14 and Heinong64 (Figs. 1e, 1f). However, uniconazole treatment enhanced the stomatal conductance and transpiration rate to maintain a high photosynthesis rate for improving drought tolerance. Uniconazole also significantly increased the chlorophyll content of seedling leaves (Figs. 1a, 1b); this effect is a vital cause for the promotion of photosynthesis in plants. Chlorophyll content can be regarded as an indicator of biochemical modification and quantifier of drought intensity (Leufen *et al*., 2016). Our results are similar to the findings of previous studies (Zhang *et al*., 2007; Duan *et al*., 2008; Zhang *et al*., 2012) where the photosynthetic pigments in uniconazole-treated soybean crops were maintained and resulted in a high photosynthetic rate, transpiration rate, and stomatal conductance under drought.

The accumulation of soluble sugar and soluble protein increases plant resistance to drought (Zhu *et al*., 2003; Ghaderi *et al*., 2015). Coue´e *et al*., (2005) reported that soluble sugar is useful to plants because some defenses and signals function not only in sensing and controlling photosynthetic activity but also in ROS scavenging with a consequent reduction in oxidative damage. Qiu *et al*., (2005) showed that rapeseed film coating with a suitable uniconazole concentration significantly increases soluble sugar concentration to improve rapeseed seedling growth during waterlogging. In the present study, the soluble sugar and soluble protein contents were significantly increased in the leaves of all individuals of the two varieties subjected to uniconazole treatment under well-watered and drought conditions (Figs. 3a, 3b). This result is partly consistent with findings of Zhou *et al*., (2016). The enhanced levels of soluble sugar and soluble protein content in the uniconazole-treated plants exposed to drought may contribute to the buildup of osmolytes and thus help in alleviating stress.

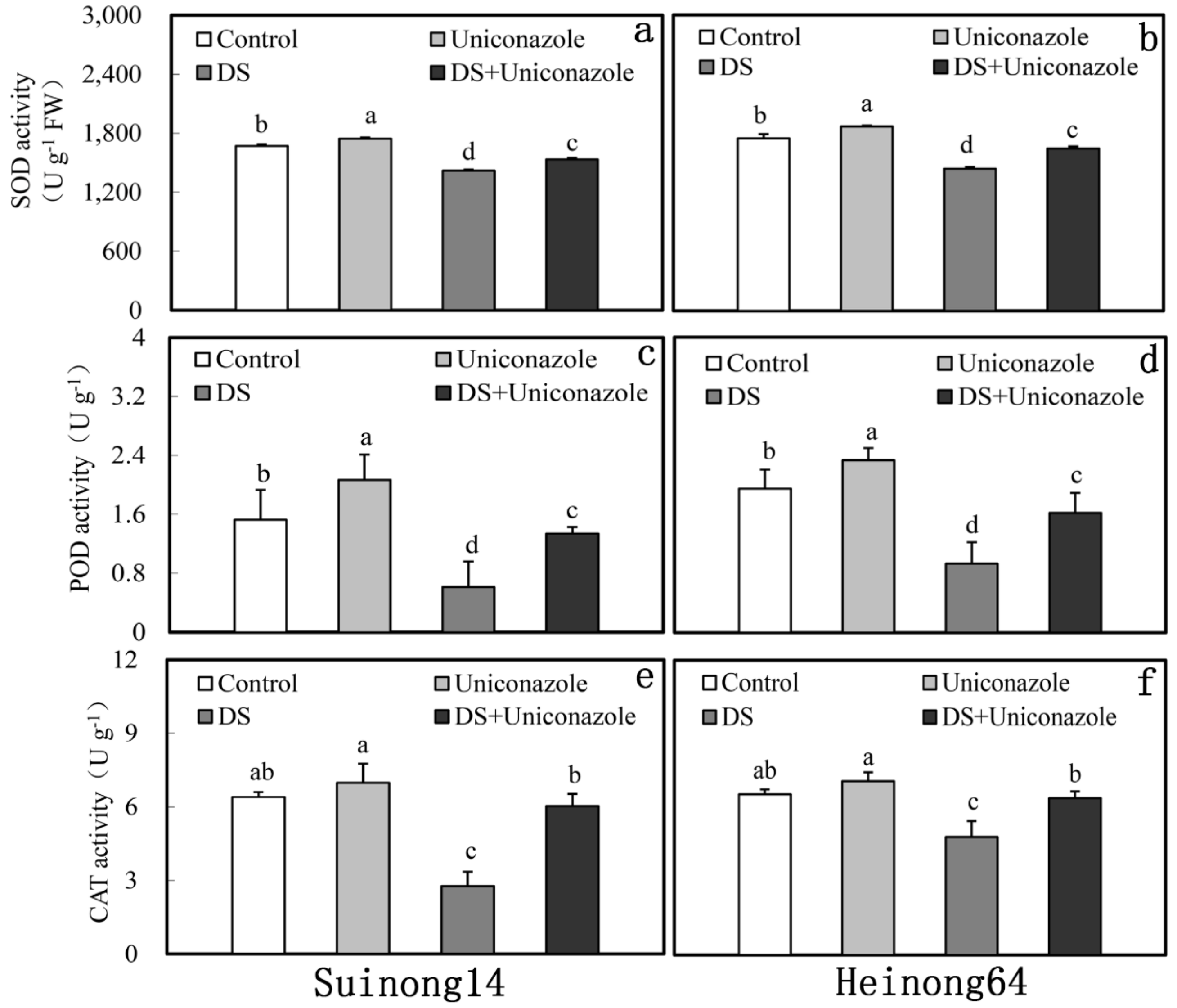

Fig. 4. Effects of foliar application of 50 mg·L^{-1} uniconazole and water on the SOD, POD, and CAT activities of Suinong14 and Heinong64. Vertical bars represent ± SEM. *n* = 4 replicates. Values followed by a different lowercase or capital letter within each column are significantly different at the 0.05 probability level.

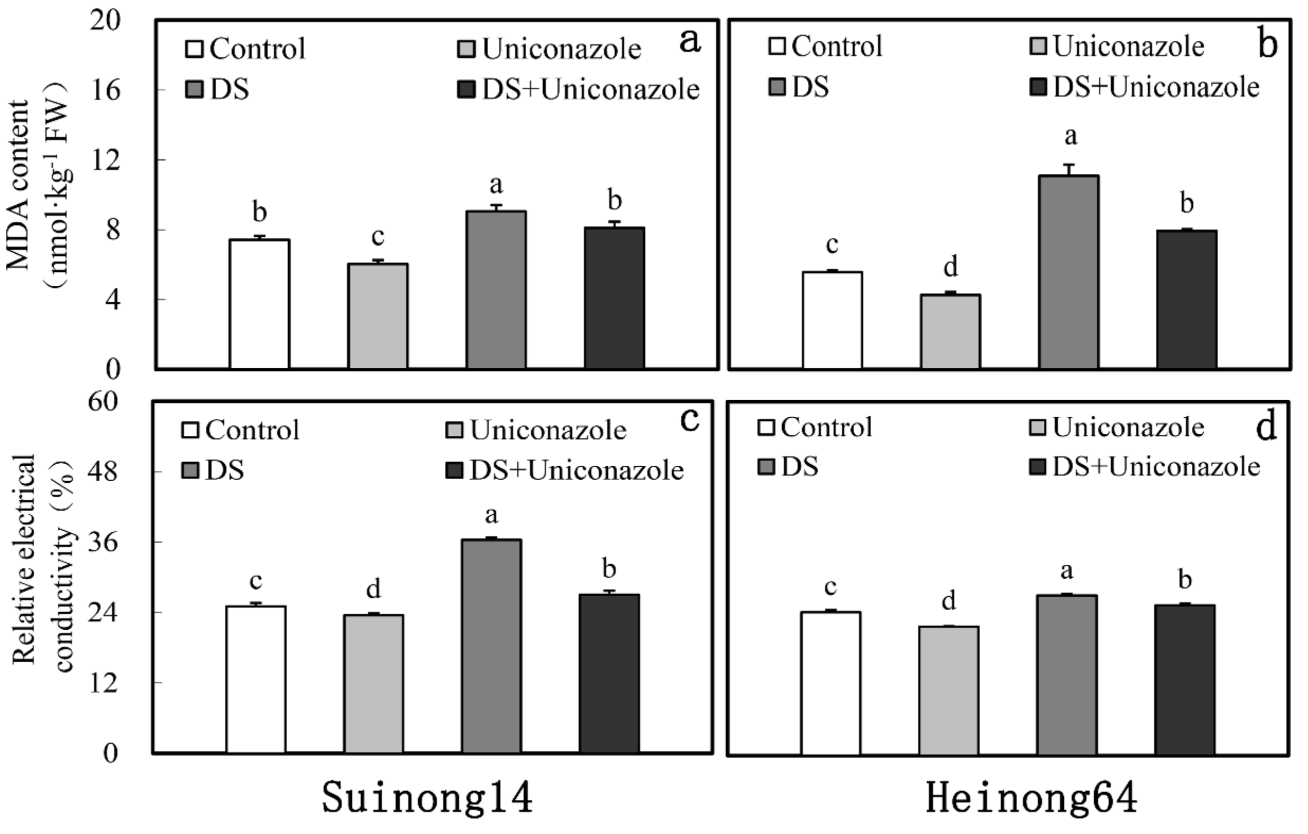

Fig. 5. Effects of foliar application of 50 mg·L^{-1} uniconazole and water on the MDA contents and relative electrical conductivities of Suinong14 and Heinong64. Vertical bars represent ± SEM. n = 4 replicates. Values followed by a different lowercase or capital letter within each column are significantly different at the 0.05 probability level.

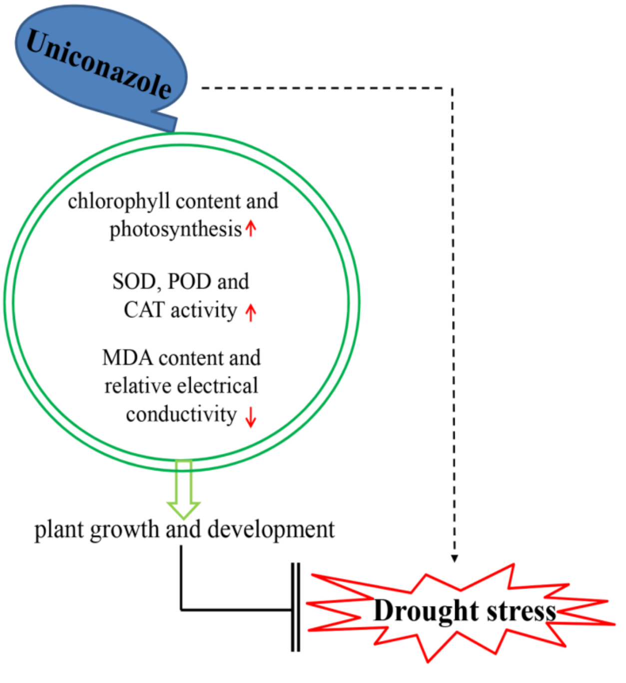

Fig. 6. Soybean seedlings acclimatized under drought environment and treated with uniconazole showing increased chlorophyll contents and photosynthetic rates, transpiration rates, and stomatal conductances; enhanced SOD, POD, and CAT activities; decreased peroxidation of plasma–lemma, as well as MDA content and relative electrical conductivity; and modified growth characteristics. These effects produced strengthened seedlings.

Various environmental stresses often lead to the increased generation of ROS; in this regard, SOD, POD, and CAT are proposed to play important roles in the stress tolerance of plants (Xu *et al*., 2008; Chakhchar *et al*., 2016). SOD activity plays a key role in cellular defense mechanisms against superoxide (O^{2-}) and hydrogen peroxide (H_2O_2), which may cause severe damage to membranes, protein, and DNA (Golldack *et al*., 2014). CAT and POD eliminate H_2O_2 by reducing H_2O_2 to H_2O in plants (Yu *et al*., 2016). Increased SOD, POD, and CAT activities can reduce the damage to plants under drought stress (Jaleel *et al*., 2009). Yan *et al*., (2011) showed that soybean seed treatment with niconazole powder increased SOD and POD activities in soybean seedling roots and leaves, and this effect was beneficial for improving soybean seedling growth and resisting the lodging of corn under shading in relay strip intercropping systems. Our data are consistent with the results of Li *et al*., (1998) or Leul & Zhou (1999), who suggested that the increased tolerance to drought and waterlogging stress induced by uniconazole in resistant cultivars of maize and winter rapeseed seedling, respectively, were due to augmented SOD, POD, and CAT activities. In the present study, the SOD, POD, and CAT activities were enhanced by uniconazole treatment under drought and well-watered conditions (Figs. 4a, 4b, 4c). Hence, the treatment enhanced the efficiency of the antioxidant system and mitigated the damage of drought to seedlings.

MDA is an indicator of the damage extent of membrane lipid peroxidation, which indicates the magnitude of oxidative stress (Møller *et al*., 2007; Chen *et al*., 2011; Piotrowska-Niczyporuk & Bajguz, 2014).

The relative electrical conductivity is also considered an index of stress intensity. For example, under drought, with increasing MDA content and relative electrical conductivity, the extent of peroxidation of plasma–lemma was increased under drought to induce leaf cell membrane damage (Wang *et al*., 2012). Jungklang & Saengnil (2012) showed that the reduction in MDA content by paclobutrazol in patumma is a major cause of the increased tolerance of the plant to water stress. Zhou *et al*., (2016) also reported that although the drought-treated plants show increased relative electrical conductivity, triadimefon-treated plants exhibit decreased relative electric conductivity compared with plants not treated with triadimefon. In the present study, drought significantly increased the leaf MDA content and relative electrical conductivity in the two varieties tested (Figs. 5a, 5b). However, the uniconazole-treated plants showed a smaller incremental proportion than the uniconazole-treated plants (Figs. 5a, 5b). Under drought, uniconazole also significantly decreased the leaf MDA content and relative electrical conductivity to maintain membrane integrity and confer further tolerance to drought.

Conclusion

Soybean seedlings acclimatized under a drought environment through uniconazole treatment showed increased chlorophyll contents, photosynthetic rates, transpiration rates, and stomatal conductances. The seedlings also exhibited enhanced SOD, POD, and CAT activities; decreased peroxidation of plasma–lemma, MDA content, and relative electrical conductivity; and modified growth characteristics, thereby leading to a strengthened seedling. Under well-watered conditions, the soybean seedlings treated with uniconazole showed better growth than the seedlings without uniconazole treatment.

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