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Expression of a monothiol glutaredoxin, *AtGRXS17*, in tomato (*Solanum lycopersicum*) enhances drought tolerance

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ABSTRACT

Abiotic stresses are a major factor limiting crop growth and productivity. The *Arabidopsis thaliana* glutaredoxin *S17* (*AtGRXS17*) gene has conserved functions in plant tolerance to heat and chilling stress in *Arabidopsis* and, when expressed ectopically, in tomato. Here, we report that ectopic expression of *AtGRXS17* in tomato also enhanced tolerance to drought and oxidative stress. *AtGRXS17*-expressing tomato plants contained twice the shoot water content compared to wild-type plants under water limiting conditions. This enhanced drought tolerance correlated with a higher maximal photosynthetic efficiency of photosystem II (Fv/Fm). Ectopic *AtGRXS17*-expression was concomitant with the expression of *Solanum lycopersicum* catalase 1 (*SlCAT1*) and mitigated defects in the growth of primary roots in response to methyl viologen exposure. In addition, *AtGRXS17* expression was found to prolong elevated expression levels of the *Solanum lycopersicum* ABA-responsive element binding protein 1 (*SlAREB1*) during drought stress. The findings demonstrate that expression of *AtGRXS17* can simultaneously improve the tolerance of tomato, and possibly other agriculturally important crops, to drought, heat, and chilling stresses.

1. Introduction

Drought stress is a major environmental factor that poses a threat to the food security of 3 billion people [1–3]. Each year, billions of dollars are lost in agricultural production as a result of drought stress. In 2012, drought in the U.S. resulted in a 12% decrease in corn production [4,5]. To meet the demands for food and fiber in the face of an increasing world population and climatic changes, it is critical to optimize yield stability [6,7]. Genetic engineering has proven to be an effective approach to improve plant performance under water-limiting conditions [4,8–10]. Recent progress in deciphering the molecular, biochemical, and physiological basis of plant adaptation to drought stress has expanded the molecular toolbox of candidate genes for use in crop improvement [1].

Plants have multiple means of adapting to drought stress [11]. The activation of the abscisic acid (ABA)-dependent signaling pathway is a part of these adaptive mechanisms [11]. The phytohormone, ABA, is induced by drought stress and subsequently perceived by a receptor complex consisting of pyrabactin resistance (PYR)/PYR1-like (PYL)/regulatory component of ABA response (RCAR), protein phosphatase 2C (PP2C), and sucrose non-fermenting 1-related protein kinase 2 (SnRK2) [12,13]. The activated ABA-signaling pathway coordinates a complex regulatory network enabling plants to cope with decreased water availability by regulating downstream transcription factors, such as a set of AREB master regulators which are involved in the activation of drought responsive genes [14–16]. One of the responsive genes in tomato is the *Solanum lycopersicon AREB1*. A previous study has shown that *SlAREB1* antisense lines have a hypersensitivity to drought stress while over-expression lines have increased drought resistance [17].

Induction of the ABA-signaling pathway also leads to an increase

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in reactive oxygen species (ROS) production through the activation of NADPH oxidase (RBOH) [18]. This accumulation of ROS triggers stomatal closure reducing water loss during instances of drought [19]. Although ROS can serve as a signal in stress responses [20–23], excessive ROS accumulation can result in oxidative damage to macromolecules and cellular structures, leading to an inhibition of plant development [20,24,25]. Therefore, the level of ROS must be judiciously regulated in plants through the coordination of ROS production, signaling, and scavenging [26,27].

To maintain cellular redox homeostasis and regulate redox-dependent signaling pathways plants have evolved a versatile ROS scavenging system that functions in conjunction with the regulation of ROS production to control cellular ROS concentrations. Glutaredoxins (GRXs) are small ubiquitous oxidoreductases that are involved in maintaining cellular redox homeostasis by mediating reversible reduction of disulfide bonds of substrate proteins in the presence of glutathione (GSH) via a dithiol or monothiol mechanism [27,28]. Plant GRXs represent a large protein family, the members of which have emerged as key regulators of diverse cellular processes including oxidative stress responses (reviewed in Refs. [27–29]). The plant GRXs can be subdivided into four groups based on the active site motifs [30]. Class I and class II have CxxG/S and CGFS active site motifs, respectively, while Class III has a CCxx and Class IV harbors an N-terminal GRX domain with a CxDC/S or CPxC active site motif, respectively [28].

The class II/CGFS GRXs are involved in development, iron homeostasis, and abiotic stress resistance (reviewed in Ref. [28]). GRXS17, a member of the class II GRXs, has been intensively studied [31–37]. The AtGRXS17 was first reported to modulate auxin signaling in response to heat stress [31], and subsequent studies have unraveled roles for AtGRXS17 in tomato tolerance to heat and chilling stress [32,36]. These results suggest that *AtGRXS17*-expressing tomato plants could confer enhanced tolerance to multiple abiotic stresses including drought stress via modulating expression levels of stress-responsive genes and reducing excessive ROS accumulation.

In this study, we investigated whether ectopic expression of *AtGRXS17* in tomato enhances toleration of drought stress. We examine if these transgenic lines alter water content, photosynthetic efficiencies, and oxidative stress signaling. These findings coupled with those from our previous investigations demonstrate that ectopic expression of this single gene, *AtGRXS17*, can improve the performance of tomato under a variety of adverse environmental conditions.

2. Materials and methods

2.1. Construct and tomato transformation

The coding region of *AtGRXS17* was cloned into the *pBICaMV* vector and driven by the *cauliflower mosaic virus (CaMV) 35S* promoter as described (Wu et al., 2012). Seeds of tomato *Solanum lycopersicum* L. (cv Rubion) were surface sterilized and germinated on the Murashige and Skoog (MS) inorganic salt medium [38]. Tomato transformation was performed via *Agrobacterium*-mediated transformation method using cotyledon and hypocotyls explants as described [39]. *A. tumefaciens* LBA 4404 strains containing *pBICaMV-AtGRXS17* was used for generating stable transgenic lines.

2.2. Growth condition and tolerance analyses of tomato

T2 generation of *AtGRXS17*-expressing [32,36] or wild-type tomato seeds were surface-sterilized, germinated, and grown in pots containing Micracle Gro (700) soil growing medium in a growth chamber. The temperature of the growth chamber was maintained at 24 °C/20 °C (day/night) under a 16-h photoperiod, and the light intensity was maintained at 300 μmol/m^2/sec. The plants were regularly watered and fertilized on a weekly basis with 20:20:20 fertilizer (Scotts, Marysville, Ohio). For the drought treatment, 4-week-old *AtGRXS17*-expressing and wild-type seedlings were withheld from watering for 12 days, and then re-watered. The phenotype and the chlorophyll fluorescence were measured during the drought treatment. For oxidative stress treatment, 7-day-old *AtGRXS17*-expressing and wild-type seedlings grown on the MS media were transferred into the MS medium with or without 20 μM methyl viologen (MV) in Magenta boxes and incubated for 14 days. The primary root length was measured, and total RNA was extracted from the seedlings.

2.3. Time-course analysis of drought stress-responsive genes

Drought treatments were applied using 14-day-old *AtGRXS17*-expressing and wild-type seedlings grown in Petri dishes with MS medium. The treatment and sampling were designed according to previous reports with slight modifications [17,40]. For drought treatment, the seedlings were transferred and incubated in Petri dishes containing two layers of dry filter paper for 0, 0.5, 2, 4, 8, and 24 h, respectively according to the previous study [40]. The leaves on the seedlings after drought treatments were harvested, and the RNA was extracted using the method described below.

2.4. RNA extraction and qRT-PCR

Total RNA was isolated using the Qiagen Plant RNeasy kit from leaves of tomato plants according to the manufacturer's instructions. RNA for real time qRT-PCR was treated with RNase-free DNase prior to the synthesis of first-strand cDNA by oligo (dT) priming using moloney murine leukaemia virus-reverse transcriptase (BD Biosciences Clontech, Palo Alto, CA, USA). One microliter of the reverse transcription reaction solution was used as a template in a 25 μl PCR solution. Real-time PCR was performed in 25 μl reactions contain 10.5 μl cDNA, 1 μl 10 mM of each primer, and 12.5 μl SYBR Green PCR Master Mix (Bio-Rad Laboratories, Hercules, CA). Analysis was performed using the Bio-Rad IQ3 (Bio-Rad Laboratories). Primer efficiencies were measured and relative expression level was calculated using the comparative Ct method [36]. *SlPP2ACS* was uses as a normalization control [41]. The primers for qRT-PCR are listed below:

SlABRE1_F: ACC AAC AAT CAC AGC CAC AG; **SlABRE1_R:** TGC TCT TCC CAA GTC CAT CT. **SlPP2Acs_F:** CGA TGT GTG ATC TCC TAT GGT C; **SlPP2Acs_R:** AAG CTG ATG GGC TCT AGA AAT C. **SlCAT1_F:** ATT GCT GCT GGA AAC TAT CCT GAG; **SlCAT1_R:** GGT CCA ATA CGG TGT CTC TGA GTA.

2.5. Measurement of Fv/Fm ratio

Injury to plants was characterized by measuring chlorophyll fluorescence of leaves as described by Oh et al. [42]. Chlorophyll fluorescence from the adaxial side of the leaf was monitored using a portable chlorophyll fluorometer (PEA, Hansatech Instruments, Ltd. UK). Photochemical efficiency of leaves as determined by chlorophyll fluorescence ratios (Fv/Fm) was monitored during and after drought treatment. Measurements were made during the light cycle on the leaves using the saturation pulse method after 30 min of dark adaption.

2.6. Shoot water content

Shoot water content (SWC) was expressed as the difference between leaf fresh weight and dry weight, and calculated as

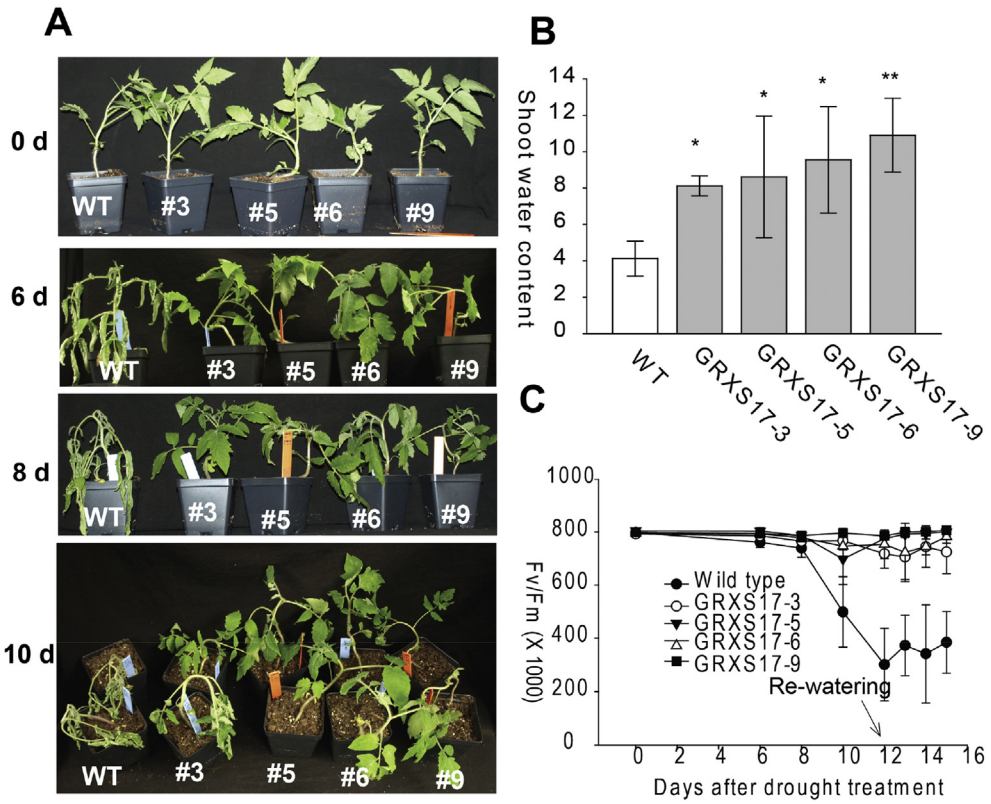

Fig. 1. A phenotype comparison between *AtGRXS17*-expressing and wild-type tomato plants in response to drought stress. (A) *AtGRXS17*-expressing and wild-type plants before, during, and after drought stress. (B) Shoot water content of *AtGRXS17*-expressing and wild-type plants after 10-d withholding of water. (C) Chlorophyll fluorescence of *AtGRXS17*-expressing and wild-type plants during drought treatment. Data represent mean ± SD from three independent biological replicates (Student's *t-test*, *P < 0.05, **P < 0.01).

follows: SWC = (fresh weight-dry weight)/dry weight.

2.7. Statistical analysis

All data were subject to *student's t-test* analysis. Values were considered significantly different at *p*-value < 0.05.

3. Results

3.1. AtGRXS17-expressing tomato plants display enhanced drought tolerance

The four independent homozygous transgenic tomato lines (*AtGRXS17*-3, −5, −6 and −9), which were previously shown to express *AtGRXS17* and to display enhanced tolerance to heat and chilling stress [32,36], were used in this study. Thirty individual *AtGRXS17*-expressing T2 plants from each of the four independent lines along with wild-type controls were visually indistinguishable when grown for 4 weeks under normal conditions (Fig. 1A, 0 d). Upon exposure to drought conditions, wilt symptoms were more evident in the wild-type controls compared to the *AtGRXS17*-expressing tomato lines (Fig. 1A, 6 and 8 and 10 d). Concomitantly, *AtGRXS17*-expressing lines were also found to contain twice the shoot water content of wild-type controls after a 10-day drought treatment (Fig. 1B). In addition, chlorophyll fluorescence of the *AtGRXS17*-expressing tomato plants, as measured by determining the *Fv/Fm* ratio (the maximum quantum efficiency of photosystem II), was higher than that of the wild-type controls (Fig. 1C). Overall, these results demonstrate that ectopic expression of the *AtGRXS17* in tomato improves the plants ability to survive in conditions of drought.

3.2. AtGRXS17-expressing tomato plants show prolonged SlAREB1 expression

To determine whether *AtGRXS17* expression affected the expression of *SlAREB1*, a transcriptional regulator in the ABA-dependent signaling pathway, *SlAREB1* transcript levels were measured in response to drought stress [16]. In both wild-type and *AtGRXS17*-expressing lines (*AtGRXS17*-3 and −6 each contain a single copy of the *AtGRXS17* gene driven by the *35S* promoter), *SlAREB1* expression was found to sharply increase in response to

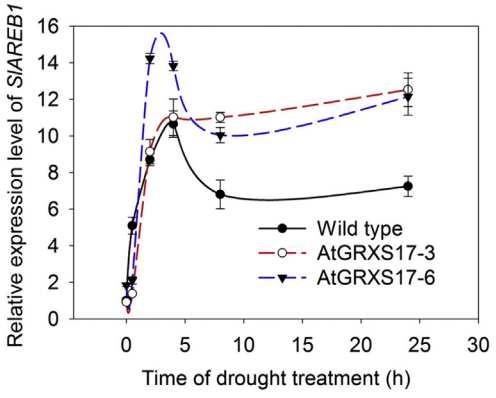

Fig. 2. A comparison of *SlAREB1* transcript levels between *AtGRXS17*-expressing and wild-type tomato plants in response to drought stress. Relative *SlAREB1* mRNA levels in 14 day old *AtGRXS17*-expressing and wild-type tomato seedlings at t = 0, 0.5, 2, 4, 8, and 24 h during drought treatment. Data represent mean ± SD from three independent biological replicates.

drought treatment peaking around the fourth hour. After this peak, transcript abundance appeared to dissipate in both wild-type and transgenic lines. However, the *SlAREB1* transcript abundance in the *AtGRXS17*-expressing lines remained at a higher level than that of wild-type over the entire course of these treatments, indicating expression of *AtGRXS17* prolongs the drought response (Fig. 2).

3.3. *AtGRXS17-expressing tomato plants exhibit increased tolerance to oxidative stress*

To assess whether *AtGRXS17* improved tolerance to oxidative stress wild-type and *AtGRXS17*-expressing tomato seedlings were incubated in MS media with or without methyl viologen (MV), a pro-oxidant herbicide that stimulates the formation of destructive ROS [43]. After 14-d of treatment *AtGRXS17*-expressing tomato seedlings appeared healthier and had longer primary root compared to wild-type (Fig. 3). These observations suggested that expression of *AtGRXS17* reduced the inhibiting effects of MV treatment.

3.4. *AtGRXS17-expressing tomato plants display increased SlCAT1 transcript abundance in response to oxidative stress*

To determine if *SlCAT1*, a ROS scavenging catalase, expression levels were induced by the MV treatment, qRT-PCR analysis was performed utilizing RNA isolated from both wild-type and *AtGRXS17*-expressing tomato lines. The expression of *SlCAT1* was more rapidly up-regulated and higher expression levels were detected in *AtGRXS17*-expressing lines as compared to wild-type plants after being treated by MV (Fig. 4).

4. Discussion

Ectopic expression of *AtGRXS17* has been previously shown to enhance heat and chilling stress tolerance in tomato [32,36], raising the question as to whether *GRXS17* could enhance a plant's ability

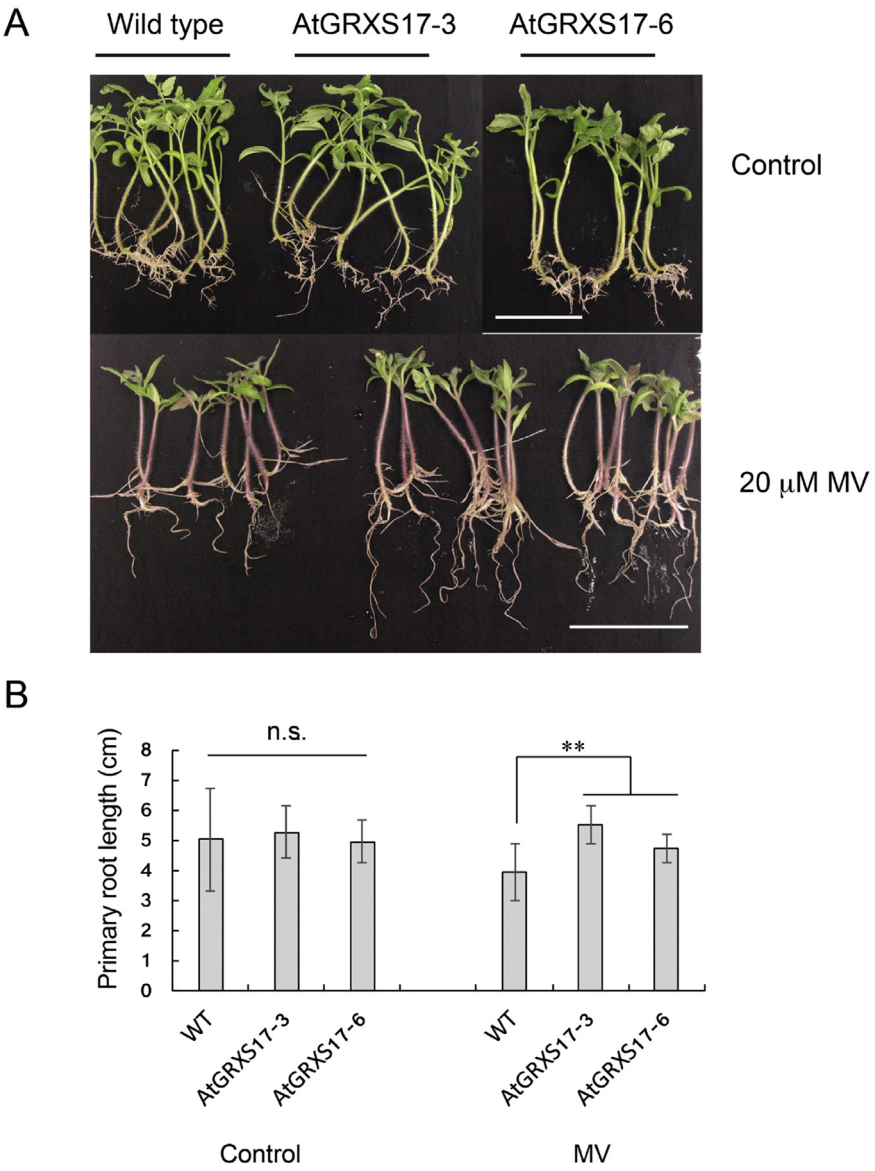

Fig. 3. A phenotype comparison between *AtGRXS17*-expressing and wild-type tomato plants in response to oxidative stress. (A) Seven-day-old *AtGRXS17*-expressing and wild-type tomato seedlings were transferred onto MS media with (lower panel) or without (upper panel) 20 μM MV and incubated for 14 d. Bars = 5 cm. (B) Root length of wild-type and *AtGRXS17*-expressing tomato seedlings from control and MV groups. Data represent mean ± SD from 8 independent biological replicates (Student's *t-test*, $^{**}P < 0.01$).

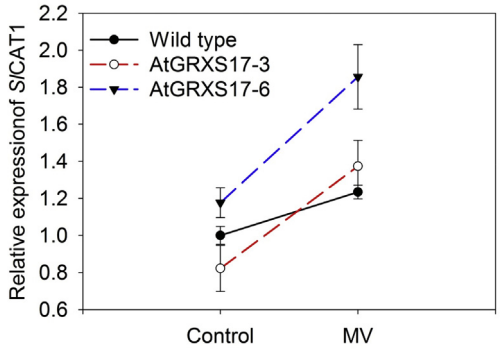

Fig. 4. A comparison of *SlCAT1* transcript levels between *AtGRXS17*-expressing and wild-type tomato plants in response to oxidative stress. RNA was isolated from control and MV treated wild-type and *AtGRXS17*-expressing tomato lines. Relative *SlCAT1* expression was determined by qRT-PCR. Data represent mean ± SD from three independent biological replicates.

to withstand other type of environmental stress conditions, including drought. In this study, we show that *AtGRXS17* expression in tomato also enhanced tolerance to drought and oxidative stresses. This finding coupled with our previous work demonstrating that *AtGRXS17* confers tolerance to heat and chilling stress indicates that a single gene can help alleviate the impact of multiple environmental conditions that can limit crop growth and productivity [32,36]. Our working model for the effects of AtGRXS17-mediated tolerance to heat, chilling, and drought stresses involves both the regulation of stress response pathways and the function of AtGRXS17 in controlling ROS levels.

ROS are known to accumulate during various abiotic stresses causing damage to cell membranes and other cellular components including DNA, proteins, and carbohydrates [24,44]. Therefore, ectopic expression of *AtGRXS17* may lead to ROS scavenging, resulting in enhanced tolerance to drought stress. Our oxidative stress study revealed that *AtGRXS17* expression can relieve the inhibition of primary root growth caused by increases in ROS accumulation. Catalase (CAT), an H_2O_2 scavenger, is an important enzyme in the ROS-scavenging system [45]. Overexpression of *CAT* in tobacco has been reported to enhance tolerance to the pro-oxidant herbicide MV [46]. Here, ectopic expression of *AtGRXS17* resulted in faster induction and higher levels of *SlCAT1* expression compared to wild-type controls in response to oxidative stress (Fig. 4). This increase in *SlCAT1* expression correlates with the alleviation of primary root growth inhibition observed with the *AtGRXS17*-expressing tomato plants in response to oxidative stress conditions. In addition, the activity of CAT has been previously shown to be elevated in the *AtGRXS17*-expressing plants compared to wild-type after heat treatment [36]. Thus, the ectopically expressed *AtGRXS17* may be regulating *CAT* expression at the transcriptional and/or posttranscriptional level in response to these different abiotic stresses. Similarly, ectopic expression of *PtADC* (*Poncirus trifoliata arginine decarboxylase*) was reported to enhance drought tolerance in tobacco and tomato presumably by reducing the accumulation of ROS [47].

As part of the drought responsive signaling pathways, the phytohormone ABA is known to play a key role in regulating abiotic gene expression [19]. Members of the AREB family have been implicated as essential components in the ABA signaling pathway [14–16]. In particular, *SlAREB1* overexpression in tomato has been shown to confer drought tolerance in tomato [17]. An increase in *SlAREB1* expression in response to drought stress was also observed in this study (Fig. 2). Interestingly, *SlAREB1* transcript abundance in *AtGRXS17*-expressing lines remained at a level higher than that of wild-type plants (Fig. 2), suggesting that the presence of AtGRXS17 sustains *SlAREB1* expression during drought exposure.

We demonstrate here that ectopic expression of a member of the class II GRX family, *AtGRXS17*, improves the behavior of tomato during drought and oxidative stresses. This increase in tolerance appears to occur through changes in ROS scavenging and through the modulation of stress-responsive gene expression. Due to the conserved function of GRXs in plant species, manipulation of GRXs across different species may be a useful approach to improve tolerance to various abiotic stresses, including drought, heat, and chilling.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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