



Inhibition of ethylene synthesis reduces salt-tolerance in tomato wild relative species *Solanum chilense*



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ABSTRACT

Exposure to salinity induces a burst in ethylene synthesis in the wild tomato halophyte plant species *Solanum chilense*. In order to gain information on the role of ethylene in salt adaptation, plants of *Solanum chilense* (accession LA4107) and of cultivated glycophyte *Solanum lycopersicum* (cv. Ailsa Craig) were cultivated for 7 days in nutrient solution containing 0 or 125 mM NaCl in the presence or absence of the inhibitor of ethylene synthesis (aminovinylglycine (AVG) 2 μ M). Salt-induced ethylene synthesis in *S. chilense* occurred concomitantly with an increase in stomatal conductance, an efficient osmotic adjustment and the maintenance of carbon isotope discrimination value ($\Delta^{13}\text{C}$). In contrast, in *S. lycopersicum*, salt stress decreased stomatal conductance and $\Delta^{13}\text{C}$ values while osmotic potential remained higher than in *S. chilense*. Inhibition of stress-induced ethylene synthesis by AVG decreased stomatal conductance and $\Delta^{13}\text{C}$ in *S. chilense* and compromised osmotic adjustment. *Solanum chilense* behaved as an includer and accumulated high amounts of Na in the shoot but remained able to maintain K nutrition in the presence of NaCl. This species however did not stimulate the expression of genes coding for high-affinity K transport but genes coding for ethylene responsive factor *ERF5* and *JREF1* were constitutively more expressed in *S. chilense* than in *S. lycopersicum*. It is concluded that ethylene plays a key role in salt tolerance of *S. chilense*.

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1. Introduction

Soil salinization is a major environmental stress affecting plant productivity. Salinity can cause nutritional imbalance, ion toxicity, water deficit and oxidative damage in plants (Munns 2002; James et al., 2011). Tomato (*Solanum lycopersicum*) is one of the most important crops in the world but is considered to be salt-sensitive and encounters drastic yield decrease in response to NaCl (Chen et al., 2015).

Some plants, however, are able to cope with high levels of NaCl in the surrounding media and for this purposes induce different mechanisms allowing adaptation against the stress (Ruan et al., 2010). Analysis of wild-related halophytes species can be consid-

ered as a useful tool to improve the salt tolerance of cultivated plant species (Munns, 2005). Several halophyte plant species are available within the genus *Solanum* and could be considered as a valuable source of salt tolerance genes for transfer to the cultivated tomato (Albacete et al., 2009; Fischer et al., 2013). In its natural environment (salt desert of Atacama, Chile), the wild tomato species *Solanum chilense* is frequently exposed to extreme temperatures, drought, and high salt concentrations in the soil (Chetelat et al., 2009; Nakazato et al., 2010). This species is considered as a good model to study adaptation to biotic stress and as a source of genes coding for resistance to several pathogens such as *Topovirus* species and *Pseudomonas syringae* (Dianese et al., 2011; Thapa et al., 2015). It also displays a promising behavior in relation to drought tolerance (Fischer et al., 2013; Tapia et al., 2016). Considering its halophytic nature, salinity resistance in *S. chilense* also recently started to be studied. Martínez et al. (2014) reported that salt-resistance in *S. chilense* can be related to the optimal management of the water and the oxidative status compared with *S. lycopersicum*.

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Our previous results confirmed that *S. lycopersicum* and *S. chilense* exhibited contrasting levels of salt-resistance. In *S. chilense*, salinity induces a marked burst in ethylene synthesis occurring concomitantly with ACC2 gene induction (Gharbi et al., 2016). These data are contrasting with those obtained in the cultivated glycophyte *S. lycopersicum*. Indeed, Albacete et al. (2008) and Ghanem et al. (2008) demonstrated that the accumulation of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) may explain the onset of salt-induced oxidative damage in the leaves of cultivated tomato preceding massive Na⁺ accumulation.

Ethylene involvement in salinity resistance is highly complex and still remains unclear. Although ethylene is commonly considered as a senescing stress hormone, some recent data also suggest that it may have a dual impact in salt resistance (Amjad et al., 2014; Kazan, 2015; Pan et al., 2016). Ethylene was reported to induce stomatal closure through NADPH oxidase activation leading to H₂O₂ in the guard cells (Desikan et al., 2006). According to Ge et al. (2015), ethylene-induced stomatal closure is mediated through the heterotrimeric G protein G α subunit GPA1. In contrast, Tanaka et al. (2005) reported that ethylene inhibits abscisic acid-induced stomatal closure in Arabidopsis. Benlloch-González et al. (2010) provided evidences that K⁺ starvation inhibits water-stress-induced stomatal closure via ethylene synthesis in sunflower plants.

Potassium deficiency is commonly observed as a consequence of salt stress in plants but Jiang et al. (2013) reported that in Arabidopsis, ethylene promotes soil-salinity tolerance via an improved Na/K homeostasis associated with elevated *HIGH-AFFINITY K⁺ transporter5 (HAK5)* transcripts levels. Besides HAK5, the inward-rectifier Shaker K⁺ channel AKT1 also mediates K⁺ uptake and the expression of the corresponding gene is mainly detected in the root epidermal cells (Alemán et al., 2011).

Gharbi et al. (2016) demonstrated that leaf sodium concentration of salt-treated plants was higher in *S. chilense* than in *S. lycopersicum*, while an opposite trend was recorded for the roots. According to this study, salicylic acid (SA) may positively influence K⁺ nutrition in salt-treated plants. Exogenous SA however decreased ethylene production in *S. chilense* but increased polyamine (PA) content. Polyamine and ethylene share a common precursor (S-adenosylmethionine) and the two corresponding biosynthetic pathways are therefore often considered to be competitive (Lutts et al., 2013). Polyamines are thought to assume key functions in mineral nutrition of salt-stressed plants and a specific interaction of PAs with several types of cation channels may contribute to salt stress resistance (Pandolfi et al., 2010). Both salicylic acid and PAs should thus be regarded as important determinants of salinity resistance in *S. chilense* but the influence of ethylene on their synthesis still requires further investigations.

Beside ethylene synthesis itself, transduction through ethylene responsive factors (ERFs) may also assume crucial functions in the tomato plant response to NaCl stress. Zhang et al. (2004) demonstrated that the ethylene- and NaCl responsive tomato transcription factor JERF1 modulates expression of GCC box-containing genes and salt resistance in tobacco. Similarly, ectopic overexpression of tomato *JERF3* in tobacco activates downstream gene expression and enhances salt resistance (Wang et al., 2004) while ERF5 is promoting adaptation to drought and salt tolerance in tomato (Pan et al., 2012). By contrast, mutants deficient for ethylene responses display salt hypersensitivity at different developmental stages (Achard et al., 2006; Lei et al., 2011).

The present work was undertaken in order to confirm the putative involvement of ethylene in salinity resistance exhibited by the halophyte wild tomato *Solanum chilense*. Since no mutants impaired in ethylene synthesis are available in this species, the potent inhibitor of ethylene production aminovinylglycine (AVG), which inhibits ACC synthase (Amrhein and Wenker, 1979) was applied on plants cultivated in the absence or presence of salt.

Stomatal conductance and water use efficiency estimated through carbon isotope discrimination were analyzed in relation to mineral nutrition, endogenous SA and PAs concentration and expression of genes coding for ethylene responsive factors.

2. Material and methods

2.1. Plant material and growth conditions

Seeds of tomato *Solanum lycopersicum* L. cv. Ailsa Craig (TGRC accession number LA2838A) and of the wild species *Solanum chilense* (TGRC accession number LA4107) were obtained from the Tomato Genetics Resource Center (University of California, Davis, USA). Seeds were germinated in peat compost in a germination chamber at 25 °C. Sixteen-day-old seedlings of the two species were transferred to a hydroponic culture system into a growth chamber at 24 °C/22 °C under a 16 h day/8 h night period. Light intensity was 245 $\mu\text{mol m}^{-2} \text{s}^{-1}$ provided by fluorescent lamps (Master TL-D reflex Super 80 58W/840 from Philips) and relative humidity was maintained at 70 \pm 5%. Seedlings were fixed on polystyrene plates floating on aerated half-strength Hoagland nutrient solution containing (in mM): 5 KNO₃, 5.5 Ca(NO₃)₂, 1 NH₄H₂PO₄, 0.5 MgSO₄, and (in μM) 25 KCl, 10H₃BO₄, 1 MnSO₄, 0.25 CuSO₄, 1 ZnSO₄, 10 (NH₄)₆Mo₇O and 1.87 g L⁻¹ Fe-EDTA. Solution was renewed every week and pH was adjusted daily to 5.5–6 using 5 M KOH. For each treatment, seedlings were distributed among four tanks (six seedlings per tank) containing 1.5 L of solution in a complete randomized block design. After 7 days of acclimatization in control conditions the seedlings were randomly divided into four groups: (1) control: plants grown in half-strength Hoagland solution, (2) NaCl: plants grown in half-strength Hoagland solution containing 125 mM NaCl, (3) AVG: plants grown in half-strength Hoagland solution containing 2 μM AVG, (4) NaCl + AVG: plants grown in half-strength Hoagland solution containing 125 mM NaCl + 2 μM AVG. Two actively growing leaves, present at the moment of treatment application (leaf number 3 and 4, numbering from the base of the plant) were tagged for subsequent physiological measurements and biochemical analysis. After 7 days of treatment, the plants (30 days old) were harvested and divided into roots and leaves for physiological and biochemical parameter determinations.

2.2. Plant growth, water content, and osmotic potential

Plant growth was determined on the basis of the shoot and root dry weight (DW) per plant (estimated on 6 individual plants per treatment). Roots of harvested plants were quickly rinsed in deionised water, blotted dry and weighed for fresh weight (FW) determination. For dry weight determination, roots and shoots were incubated in an oven at 70 °C for 72 h. Water content (WC) was calculated as WC = (FW – DW)/FW \times 100. To determine leaf osmotic potential (Ψ_s), leaves were cut into small pieces and immediately frozen into a perforated Eppendorf tube. After two thaw-freezing cycles, sap was collected after 15 min of centrifugation (15,000g) at 4 °C. Leaf and root osmotic potential was estimated on the extracted sap using a Wescor 5500 vapour pressure osmometer as previously detailed (Lutts et al., 1999).

2.3. Gas-exchange parameters, stomatal conductance and carbon isotope discrimination

The instantaneous CO₂ assimilation under ambient conditions (400 ppm CO₂) (A), the instantaneous transpiration (E) and inter-cellular CO₂ concentration (Ci) were taken from the fourth fully expanded leaf of six plants per treatment using an infrared gas analyser (LCA4 8.7 ADC, Bioscience, Hertfordshire, UK). The gas exchange was measured using a Parkinson leaf cuvette, on intact

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