



# Rapid formation of adventitious roots and partial ethylene sensitivity result in faster adaptation to flooding in the *aerial roots* (*aer*) mutant of tomato



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## ABSTRACT

The frequency of extreme events such as droughts and floods has increased as a consequence of climate change. Many crops have not been improved to tolerate soil anoxia and, therefore, floods cause important economic losses. During submergence, *Solanum lycopersicum* L. exhibits three distinct responses which are adventitious root production, epinasty and aerenchyma formation. The development of a new adventitious root system is crucial as it can replace the original roots that succumb to the hypoxic environment. *Aerial roots* (*aer*) is a tomato mutant characterized by the presence of numerous adventitious root primordia along the hypocotyl and older internodes. In this work, we have analyzed the *aer* mutant behavior to flooding to determine whether preformed adventitious roots represent an adaptive advantage with respect to biomass accumulation. We have also examined other morphological and anatomical responses of *aer* plants to detect differential adaptations under flooding. *Aer* plants form an abundant adventitious root system faster than Ailsa Craig cultivar, which results in flooded plants accumulating as much biomass as non-flooded *aer* plants. In addition, several ethylene-induced responses such as epinasty, hypertrophy, aerenchyma production, and apical hook formation are reduced in *aer*, suggesting a lower sensitivity of some tissues to ethylene. The *E4* expression level, an ethylene-induced gene, confirmed this observation since *E4* transcripts are less abundant in petioles and stems of ethylene-treated *aer* plants, coinciding with the tissues that present a lower degree of morphological and/or anatomical response. Evidence from the *Never ripe* mutant suggests a reduction in ethylene sensitivity could contribute to the attenuation of flooding effects. Therefore, our results indicate that the rapid formation of a new root system together with a reduction in ethylene sensitivity is responsible of a faster adaptation to flooding stress in the *aer* mutant.

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## 1. Introduction

Climate change has brought about an increase in the frequency of climate extremes (Niu et al., 2014). Heat waves, frosts, droughts and heavy rainfall are some of the effects due to an increase in greenhouse gas emissions. In particular, intense precipitation that causes surface water flooding, river floods and snow melting have resulted in important losses in crop production all over the world (Bailey-Serres et al., 2012). This scenario is particularly alarming as most crops have not been selected for tolerance/resistance to flood-

ing (Setter and Waters, 2003). Considering the increasing world population, one of the main challenges for the years to come is the development of high yielding varieties that are able to withstand extreme rainfall events – and therefore flooding – due to a continuously changing climate (Tester and Langridge, 2010). A better mechanistic understanding of how plants cope with the excess of water in the soil would provide a useful resource in breeding programmes aimed at maintaining or increasing agricultural productivity in flooded lands (Voeselek et al., 2014).

Tomato (*Solanum lycopersicum*) is the second most important vegetable in the world market after potatoes (FAO, 2015). It has been used as a model species to study different aspects of plant physiology and genetics, especially for those traits for which *Arabidopsis* is not a suitable option (Carvalho et al., 2011). Furthermore, tomato is more closely related to other horticultural crops such as lettuce than other widely studied species (Jiménez-Gómez and

Abbreviation: AR, adventitious root.

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Maloof, 2009), making it easier to transfer knowledge to those species.

Tomato has an additional advantage when used as model plant, which is the number of monogenic mutants that are available, most of them through the Tomato Genetics Resource Center (TGRC). Some of these mutants have been well characterized with respect to their physiology such as *Never ripe* (Lanahan et al., 1994), *diageotropica* (Kelly and Bradford, 1986), *epinastic* (Barry et al., 2001), *entire* (Mignolli et al., 2015), *ripening inhibitor* and *non ripening* (Osorio et al., 2011) whereas others, such as *aerial roots* (*aer*), have never been studied. Phenotypically, the *aer* tomato mutant resembles a wild type plant except for the fact that numerous quiescent adventitious root (AR) primordia are formed along the stem.

After the onset of flooding, tomato plants exhibit some distinct responses, three of which are AR development (Jackson, 1955), leaf epinasty (Jackson and Campbell, 1976) and aerenchyma formation (Kawase, 1981). All three responses seem to act together to mitigate the impact of flooding. In particular, the contribution of a new AR system has long been associated with tomato plant recovery from flooding stress (Kramer, 1951; Jackson, 1955; Aloni and Rosenshtein, 1982; McNamara and Mitchell, 1990; Else et al., 2009). Indeed, tomato plant ability to produce a new root system allows the plant to adapt by replacing the original roots when damaged by the hypoxic/anoxic environment (Jackson and Drew, 1984; Colmer and Voeselek, 2009). Moreover, the production of ARs proves also beneficial when pathogens attack the original root system (Román-Avilés et al., 2004). However, the ability to respond to environmental stress depends on plant life cycle stage, as young plants are more plastic than older ones (Zhang et al., 2015).

The commercial use of submergence tolerant plants requires fundamental knowledge of basic aspects of tomato adaptive responses, as well as the identification of promising genotypes. In this paper, we characterized for the first time the *aer* mutant behaviour under flooding, considering morphological and anatomical changes (AR formation, stem porosity, stem hypertrophy, aerenchyma development and leaf epinasty) as well as the plant ability to resume growth while flooded. In particular, we tested the hypothesis whether preformed ARs present in *aer* stems result in faster adaptation to flooding during early life stages. Following, based on our morphological and anatomical observations, we addressed the question whether partial ethylene sensitivity in certain tissues contributes to mitigate the flooding stress effect on biomass accumulation.

## 2. Materials and methods

### 2.1. Plant materials and growing conditions

Tomato (*S. lycopersicum*) cv Ailsa Craig (AC, accession LA2838A) and *aerial roots* mutant seeds (*aer*, accession LA3205) were provided by the Tomato Genetics Resource Centre (TGRC, University of California, Davis). Since the genetic background of *aer* is unknown and nearly isogenic lines were not available, we selected the AC cultivar as a control line for our experiments. AC has been used as a control cultivar in physiological studies regarding AR formation (Negi et al., 2010; Vidoz et al., 2010) and in studies looking at anthocyanin production when near isogenic lines did not exist (Povero et al., 2011). The lack of spontaneous production of AR primordia along the stem, make AC a useful wild type to perform valid comparisons. To assess the effects of ethylene insensitivity, an experiment was performed using the ethylene perception mutant *Never ripe* (*Nr*, accession LA0162) and its wild type Pearson (accession LA0012) (Lanahan et al., 1994; Clark et al., 1999), provided by the TGRC.

One-week-old seedlings were transplanted on peat-based substrate (pH 5.5–6.5) amended with perlite (Dynamics 2 Q80, Buenos Aires, Argentina) in 220 mL plastic pots and irrigated every two days with 150 mL 1/4 strength Hoagland solution after the second week from sowing. Plants were maintained in a climatically controlled room with a temperature of  $26 \pm 1$  °C with 15 h photoperiod provided by high pressure sodium lamps (Vialox®, 400W, OSRAM GmbH, Germany). Average light intensity at the plant height was  $254 \mu\text{mol m}^{-2} \text{s}^{-1}$  and relative humidity fluctuated between 50 and 70%. Plants were grown for up to four weeks from sowing.

Unless specified otherwise, all flooding experiments were conducted with 4-week-old plants and lasted seven days. Groups of eight to fifteen plants were placed in  $60 \times 40 \times 25$  cm ( $h \times w \times d$ ) tanks and hypocotyls were submerged in tap water up to the cotyledons. Control plants were placed in similar containers and watered regularly, allowing soil to freely drain. When we assessed the effect of flooding duration on plant biomass, plants were flooded in 1/4 strength Hoagland solution so that the only factor affecting plants was flooding and not nutrient deficiency. In this case, control plants were regularly watered with 1/4 strength Hoagland solution as required.

### 2.2. Plant growth parameters

Biomass of roots, stems, leaves, and ARs of flooded and control plants was determined by oven-drying the material at 70 °C until constant weight.

Leaf area was determined by placing the leaves on a flat surface and covering them with a glass lamina to keep the material flat. Photos were taken and processed with the public-domain digital image processing software ImageJ (National Institutes of Health, <http://rsb.info.nih.gov/ij>) to determine the area.

### 2.3. Hypocotyl porosity determination

A modified pycnometer method (Jensen et al., 1969) was used in order to determine porosity. Hypocotyls from control and flooded plants approximately 1 cm long were excised and those from treated plants were carefully blotted with tissue paper. Hypocotyls were weighed ( $Z$ ) and then infiltrated with distilled water under vacuum ( $-0.9$  atm for 3 min) before being weighed again ( $Y$ ). Their volume was determined by weighing a pycnometer full of water ( $X$ ), and then the pycnometer with the infiltrated hypocotyl fully submerged ( $W$ ). The volume of the water equivalent to the volume of the hypocotyl was determined with the following calculation:  $[X - (W - Y)] / \text{water density} = V_{\text{hypocotyl}}$ . The volume occupied by air ( $V_{\text{air}}$ ) was calculated as the difference between the weight of the hypocotyl infiltrated with water ( $Y$ ) and the hypocotyl before this procedure ( $Z$ ) divided by the density of water. Finally, the porosity was calculated as follows:  $V_{\text{air}}/V_{\text{hypocotyl}} \times 100$ .

### 2.4. Anatomical observations of flooded hypocotyls

Hypocotyl segments of control and 72 h flooded plants were first fixed in FAA (10 formaldehyde 40%: 5 acetic acid: 50 ethanol: 35 water v/v) applying a vacuum for 15 min. Samples were dehydrated using the tertiary butyl alcohol series and finally embedded in paraffin. Sections of 30  $\mu\text{m}$  were stained with safranin for 2 h and counter-stained with Fast Green FCF for 5 min. Digital microphotographs were acquired with a Leica ICC50HD digital photographic camera coupled with a Leica DM LB2 (Leica Microsystems, Wetzlar, Germany) optical microscope.

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