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Water deficit effects on tomato quality depend on fruit developmental stage and genotype

Julie Ripoll[a,b], Laurent Urban[b], Béatrice Brunel[a], Nadia Bertin[a,*]

[a] INRA—Centre d'Avignon, UR1115 Plantes et Systèmes de Culture Horticoles, Domain Saint Paul—Site Agroparc, 228 route de l'aérodrome, CS 40509, 84 914 Avignon, Cedex 9, France

[b] Université d'Avignon et des Pays du Vaucluse—Laboratoire de Physiologie des Fruits et Légumes EA4279, Bât. Agrosciences, 301 rue Baruch de Spinoza, B.P. 21239, 84916 Avignon, Cedex 9, France

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ABSTRACT

Many studies have advocated that water deficit (WD) may exert beneficial effects on fruit quality. However, the fruit response to WD at specific developmental stages was seldom investigated, although different mechanisms could be involved at each stage and lead to different effects on final fruit quality. In the present study, a moderate WD (−60% of water supply compared to control) was applied during each of the three major phases of fruit development, namely cell division (CD), cell expansion (CE) and maturation (MT). Two cocktail tomato (*Solanum lycopersicum* L.) genotypes were studied, one producing poor quality fruits (LA1420), and the other one producing tasty fruits (PlovdivXXIVa named Plovdiv). Contrasted responses were observed between the two genotypes. For both of them, fruit fresh mass and size were not significantly reduced by WD, whatever the developmental phase affected. Osmotic regulations were likely involved in the CD treatment for LA1420 fruits, which accumulated more sugars (both on a dry and fresh matter basis) and less acids (on a dry matter basis). In the CE treatment, other adaptive strategies involving sugar metabolism and sub-cellular compartmentation were suggested. In contrast, the composition of Plovdiv fruits changed only under the MT treatment, with less sugars, acids and carotenoids compared to control fruits (both on a dry and fresh matter basis). Total ascorbic acid (AsA) was not significantly influenced by treatments in both genotypes. On their whole, results suggest that, depending on genotypes, fruits are sweeter and less acidic under WD, but that the nutritive value related to vitamin and carotenoid contents may be lessened. The sensitivity of each developmental phase highly depends on the genotype. All phases were sensitive to WD for LA1420, but only the ripening phase for Plovdiv. Interestingly, major changes in fruit composition were observed in LA1420 which presents poor fruit quality under control conditions. This suggests the onset of fast adaptive response to WD at the fruit level in this genotype.

1. Introduction

In the context of the climate change, limitation of water resources is expected to exert an adverse impact on plant growth and crop productivity (Shao et al., 2008). To cope with stress conditions induced by water deficit (WD), different innovative irrigation strategies have been evaluated such as partial root zone drying (PRD) and regulated deficit irrigation (RDI), which both improve the soil exploration by roots and thus may increase water use efficiency (Stikic et al., 2003, 2014). However plant growth and crop productivity under PRD and RDI conditions may be adversely affected depending on intensity, timing and duration of WD, as well as on genotype, as observed in tomato *Solanum lycopersicum* L. (Davies et al., 2000; Marjanovic et al., 2012). Plant responses to WD have been extensively studied (reviewed by Costa et al., 2007). In terms of stomatal conductance and water potential regulations, these responses are species-specific and highly dependent on stress intensity and duration (Hetherington and Woodward, 2003; Tardieu et al., 2011). Water deficit usually induces a decrease in stomatal conductance and in water losses by transpiration (Blum,

Abbreviations: AsA, ascorbic acid; C, control; CD, cell division treatment; CE, cell expansion treatment; DAA, days after anthesis; DM, dry matter; MT, maturation treatment; NS, not significant; PAR, photosynthetically active radiation; PRD, partial root zone drying; RDI, regulated deficit irrigation; $\Psi_{predawn}$, predawn water potential; Ψ_{midday}, midday water potential; Ψ_{π}, leaf osmotic potential; Ψ_F, fruit water potential; $\Psi_{\pi F}$, fruit osmotic potential; Plovdiv, genotype PlovdivXXIVa *Solanum lycopersicum* L; SLA, specific leaf area; WD, water deficit.

* Corresponding author. Fax: +33 4 32 72 24 32.
E-mail addresses: julie.ripoll87@gmail.com (J. Ripoll), laurent.urban@univ-avignon.fr (L. Urban), beatrice.brunel@avignon.inra.fr (B. Brunel), nadia.bertin@avignon.inra.fr (N. Bertin).

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1996). Unfortunately, more substantial decreases in stomatal conductance result in decreased photosynthesis, carbon gains, plant growth and crop productivity (Chaves, 1991; Xoconostle-Cazares et al., 2010). Aside from the negative impact on plant growth, beneficial effects on fruit quality may be expected, related to higher sugar accumulation and increased antioxidant activity (Ripoll et al., 2014). However, contradictory effects of WD on fruit quality have been reported depending on the genotype and on the plant and fruit developmental stages at the time of stress (reviewed by Ripoll et al., 2014). As stressed by these authors, to take full advantage of innovative irrigation management techniques we need to increase our understanding of the way WD impacts the processes involved in yield and quality during fruit development and to assess their genetic variability.

In most studies dealing with the effects of WD on fruit quality, a constant WD is applied over the whole fruit development period. Few of them are dealing with the effect of WD as a function of fruit development stage, although different processes may be affected at each stage and lead to contrasted effects on final fruit quality. Fleshy fruit development is divided into three phases: cell division, cell expansion and ripening. The duration of the cell division period varies according to genotypes (about 10 days for small fruit types and 25 days for big fruit types) (Gillaspy et al., 1993; Bertin et al., 2007). This phase strongly influences the final fruit size in many species, like tomato, through the number of cells and the sink activity of developing seeds (Varga and Bruinsma, 1976; Bohner and Bangerth, 1988; Bertin et al., 2003; Prudent et al., 2010). It has been suggested that WD applied during the cell division phase could induce carbon starvation and thus negatively regulate cell division and fruit tissue development in tomato (Bertin, 2005; Baldet et al., 2006; Prudent et al., 2010). However controversial studies suggest that WD applied during the cell division phase could improve carbon supply to the remaining fruits by exerting a negative effect on fruit setting and fruit load. Regarding the fruit composition, moderate WD has been shown to improve fruit quality (sweetness and flavor) in peach *Prunus persica* L. provided that WD is applied during the phases of cell division and of rapid endocarp hardening (Li et al., 1989; Vallverdu et al., 2012). Furthermore, a low carbohydrate supply (i.e., a low supply in soluble sugars) during cell division was shown to promote the synthesis of carotenoids in clementine *Citrus clementina* (Hort ex. Tan) (Poiroux-Gonord et al., 2013).

Cell expansion starts as cell division declines and is triggered by water entering in the cell. The water influx depends on the stem-to-fruit gradient of water potential generated by the gradient of osmotic potential which exists between source and sink tissues (Münch, 1930). Cell expansion is therefore related to sugar metabolism and sub-cellular compartmentalization (Lockhart, 1965; Ho, 1988). WD applied during cell expansion is expected to have the greatest impact on fruit growth considering the changes in water relationships and in cell wall properties occurring at that specific stage of fruit development (Schopfer, 2001). In peach, a negative impact on yield was observed associated to a decrease in water content (Li et al., 1989; Girona et al., 2004). Finally, fruit ripening consists in a rapid slowdown of cell expansion and an increase in metabolic changes and hormonal regulations. During this phase, WD may interact with the stress-induced increase in ethylene synthesis (Fray et al., 1994; Barry and Giovannoni, 2007). Furthermore, the accumulation of phytochemicals such as carotenoids or ascorbic acid (AsA) was reported to be ethylene-dependent (Iglesias et al., 2001). In peach, deficit irrigation applied during ripening induces a yield reduction proportional to the reduction of water supply (Wang and Gartung, 2010). In tomato, WD shows the greatest increase in fruit quality (soluble sugars, organic acids, aromas and AsA) at the red stage when compared with the mature green or orange stages (Veit-Köhler et al., 1999).

In this study, a comprehensive experimental approach on tomato fruit was developed with the objective: (i) to analyze the effects of WD on tomato fruit growth and quality traits as a function of the fruit developmental phases and (ii) to evaluate the influence of genetic factors on fruit responses. Moderate WD (−60% of water supply compared to the control) was applied during the three major phases of fruit development, namely cell division, cell expansion and maturation. Two cocktail tomato genotypes known for their contrasted fruit quality traits were investigated. Fruit fresh and dry masses, cell pericarp number and size, seed weight, and the contents in soluble sugars, organic acids, AsA and carotenoids were measured along with indicators of plant and fruit water status. Results support the idea that fruit quality may be improved under moderate WD without yield reduction. However, significant interactions between genotype and developmental phases were observed. Results are consistent with similar observations made on other plant species and contribute to a better understanding of tomato plant and fruit responses to moderate WD.

2. Materials and methods

2.1. Plant material & experimental conditions

The study was performed on two indeterminate cocktail-type genotypes of *S. lycopersicum* L. The first genotype, PlovdivXXIVa (here called Plovdiv), is a cultivated tomato, and the second one, LA1420, is a wild tomato. LA1420 seeds were provided by the Tomato Genetics Resource Centre, Davis, California. Plovdiv seeds were provided by the Genetic Resource Centre of INRA, Avignon (France). These genotypes were selected among the eight parents of the MAGIC TOM population which is the population with the highest rate of allelic variability in tomato (Ranc, 2010). LA1420 and Plovdiv genotypes show important allelic variability (SNP differences on chromosomes 3, 4, 5, 7, 8, 9, 11 and 12) (Causse et al., 2013).

The trial was conducted during autumn 2012 in a glasshouse located near Avignon, France. 110 plants were grown in 4 L pots filled with compost (substrate 460, Klasmann, Champety, France) at a density of 1.3 plant m^{-2} and 72 plants were actually used for the experiment. Plants were supplied daily with a nutrient solution (Liquoplant Rose, Plantin, Courthézon, France) diluted between 0.4‰ and 0.8‰ according to the plant development stage, which corresponds to an average electroconductivity of 1.8 mS cm^{-1} for the whole period. All trusses were pruned to 6 set fruits per truss, just after fruit set (no effect of WD was observed before pruning), in order to have a similar fruit load on all plants. Flowers were pollinated three times a week using an electrical bee.

Day–night temperature control was set at 25–15 °C. Over the whole trial period, the mean daily photosynthetically active radiation (PAR) decreased due to seasonal effects (from 15.6 to 8.5 mol m^{-2} day^{-1}), whereas the air temperature and relative humidity remained relatively stable (on average the day temperature ranged between 20.4 and 24.5 °C, the night temperature between 15.1 and 19.7 °C, and the air humidity between 56 and 72%).

2.2. Water deficit treatments applied during different fruit developmental phases

Control plants were irrigated, according to current practises, in order to maintain soil humidity and drainage around 70% (maximum water retention capacity of the substrate) and 15%, respectively. Soil humidity was measured every two days in all pots using water content sensors (WCM-control, Grodan, Roermond,