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Abstract

The aim of the present study was to investigate the effect of long term moderate drought stress on fruit yield and quality of four parents of the MAGIC TOM population and to gain insight into the differences in sensitivity to drought between large fruited and cherry tomatoes. Results showed that long term water deficit had a negative effect on fresh mass and fruit diameter that were more expressed in cherry tomatoes than in large fruited ones. Long term moderate water deficit can improve fruit taste in large fruited tomato genotypes by active metabolic accumulation of soluble sugar and organic acid (sucrose and citric acid), which are also osmotic active compounds. The reduction in fruit growth of cherry tomatoes compared to large fruits could be compensated for by improving fruit nutritional value (ascorbic acid, carotenoids and antioxidant activity) through both concentration and metabolic responses.

Keywords: antioxidant compounds, drought, MAGIC TOM, nutritional value, *Solanum lycopersicum*.

Introduction

Drought limits productivity of crops and vegetables by inducing different morphological, physiological and molecular changes in plants, which consequently reduces the yield and its quality (Ashraf, Harris, 2013). Adaptation measures to mitigate the reduction of yield induced by climate change besides the application of different irrigation strategies (including partial root drying) also include the use of drought resistant genotypes to increase crop water productivity (Jovanovic, Stikic, 2012; Sun et al., 2014). However, the prerequisite for the development of resistant genotypes is a better understanding of the plant response and adaptation to drought stress, the improvement of phenotyping, the selection of key-genes involved in the resistance to drought and the evaluation of the impact of resistance on crop yield and quality. These are very difficult tasks, because reactions of plants to drought are the complex phenomenon, where the plant response depends on the species or genotypes, the type, duration or intensity of drought and on phenological stage, in which drought stress is experienced (Chaves et al., 2003).

Tomato taste and flavour rely on the balance among essential compounds such as sugars, organic acids, secondary metabolites (carotenoids and polyphenols) and ascorbic acid. Crop production and fruit quality are often exposed to several stress factors and their interaction affects plants to a larger intensity than the effect of one individual stress (Lipiec et al., 2013). However, the effects of water deficit on fruit yield and quality mostly depended on the genotype, on the plant and fruit developmental stage at the time stress occurs and on the interactions with other stress factors (Ripoll et al., 2014).

Generally, water deficit is expected to reduce the flux of water to fruit, to stimulate the accumulation of osmotic compounds like soluble sugars and acids and to trigger the synthesis of antioxidant compounds, including vitamin C and carotenoids (Dorais et al., 2008; Fanciullino et al., 2014). However, this increase may result either from concentration effects due to a decrease in the amount of water accumulated in the fruit and/or from a higher synthesis of specific metabolites. Accordingly, Zheng et al. (2013) and Ripoll et al. (2014) demonstrated that water deficit could also have beneficial effects on tomato fruit quality and health value with minimal reduction of the yield.

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Currently, the main challenge is to develop plants not only able to survive stress, but also able to grow under adverse conditions with reasonable biomass production, overcoming the negative correlation between drought resistant traits and productivity, which was often present in previous breeding programs (Chaves, Oliveira, 2004; Causse et al., 2011). For tomato, the MAGIC TOM (the multi-parent advanced generation inter-cross) population encompasses the highest rate of allelic variability in tomato (Ranc, 2010) and offers a potential source of genetic variation to outline traits useful for stress breeding programs for both cherry tomatoes and tomatoes with long fruits.

The aim of the present study was to investigate the effect of long term moderate drought stress on fruit yield and quality of four parents of the MAGIC TOM population and to gain insight into the differences in sensitivity to drought between large fruited tomato and cherry tomatoes.

Materials and methods

Plant material and experimental conditions. The study was performed on four tomato (*Solanum lycopersicum* L.) genotypes from the eight parents of the MAGIC TOM (the multi-parent advanced generation inter-cross) population, which offers the largest allelic variability observed in tomato (Ranc, 2010). The genotypes selected were two cherry or cocktail tomatoes ('Plovdiv' and LA1420) and two tomatoes ('Levovil' and LA0147) with large fruits. The experiment was conducted in the glasshouse in 2014 (March–July) at INRA, Avignon, France.

The plants were raised from the seeds and transplanted into 4 L pots filled with compost mixture: 60% black peat, 30% fibrous peat and 10% white peat, with pH = 6 and with clay. Over the whole experimental period, the mean daily photosynthetically active radiation (PAR) was from 5 to 11 mol m^{-2} day^{-1}, the air temperature and relative humidity remained relatively stable (the average temperature 24–28/17–21°C day/night and the air humidity 51–56/69–73% day/night).

Water deficit treatment. At the stage of 2nd flower truss anthesis, water deficit was implemented and soil humidity was maintained around 25% of maximum water retention capacity until fruit harvesting (red-ripe stage). Control plants were irrigated until the end of experiment in order to maintain optimal soil humidity (70% of maximum water retention capacity of the compost). Soil humidity was maintained by an automated irrigation system and controlled by a Wireless Control Module sensor ("Grodan", The Netherlands).

Measurements of fruit quality parameters. Fruits were harvested at full maturity, red-ripe stage. Soluble sugars (glucose, fructose and sucrose) and organic (citric and malic) acids were extracted following the protocol by Gomez et al. (2002). The high-pressure liquid chromatography (HPLC) analyses were done by HPLC system ("Waters", USA) with a UV detector at 210 nm. The separation of sugars was carried out on a Sugar-Pac I column (300 × 6.5 mm) ("Waters", ref. WAT088141) equipped with a pre-column ("Waters", ref. WAT015209). The mobile phase consisted of Na_2Ca-EDTA (50 mg L^{-1}) and was delivered at a flow rate of 0.6 mL min^{-1}. The separation of organic acids was carried out on a Shodex RS pak KC-811 column (300 × 8 mm) equipped with a pre-column Shodex RS pak KC-G (50 × 6 mm). The mobile phase consisted of 0.1% H_3PO_4 (flow rate 1 mL min^{-1}).

Carotenoids (phytoene, lycopene, β-carotene and lutein) were extracted by micro-method and analysed by HPLC (Serino et al., 2009). Carotenoid analyses were performed with a HPLC system with a diode array detector ("Agilent", USA). The separation was carried out on two columns (VWR Merck, ref. 1.02129.0001, Chromolith® RP-18 endcapped 100 × 4.6 mm monolithic) with a pre-column (VWR Merck, ref. 1.51452.0001, Chromolith® RP-18 endcapped 10 × 4.6 mm monolithic). Mobile phase consisted of acetonitrile, ethyl-acetate and ultrapure water in the range of 53:40:7 with a flow rate of 1 mL min^{-1}. For peak identification and calculation of analysed carotenoids, the HPLC standards (Cayman Chemical, USA) were used.

The ascorbic acid analysis included two assays: total ascorbic acid (with the addition of dithiothreitol – DTT) and reduced ascorbic acid (without of DTT) content according to the protocol by the Stevens et al. (2006). Grounded fruits were homogenized with cold 6% trichloroacetic acid (TCA), vortexed (20 s), centrifuged (15 minutes, 4°C, 13200× rpm), and then the supernatant was used for further analysis. After addition of DTT (total ascorbic assay) and phosphate buffer (reduced ascorbic assay) the microplate was incubated at 37°C for 20 minutes. In the wells with DTT the N-ethylmalemide ($C_6H_7NO_2$) was added. The plate was incubated with a colouring agent for 60 minutes at 37°C. The absorbance was read at 550 nm using a microplate reader ("Tecan", Switzerland) and the results were expressed on fruit fresh weight basis.

The antioxidant capacity of the samples was measured using 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid (ABTS assay), following the modified protocol of Miller et al. (1993). Extraction of ground tomato fruit samples was done by 80% ethanol, and then the samples were vortexed, centrifuged (9000 × rpm) and finally the supernatant was used for analysis. $ABTS^{\bullet+}$ radical cation was prepared by dissolving ABTS in phosphate-buffered saline (PBS) buffer (pH = 7.4) and adding manganese dioxide to oxidize ABTS. The absorbance for standard curve and samples was measured at 734 nm with a Spectro UV-VIS RS 1166 (Labomed Inc., USA). The results were expressed as µmol of Trolox equivalent antioxidant capacity (TEAC) kg^{-1} fresh weight (FW).

Statistical analysis was performed using software *SigmaPlot*, version 11.0 (Systat Software Inc., USA). Descriptive statistic was done for each group of measurement. Standard errors of the means were calculated and they are stated in the tables. Differences between treatments were estimated by a two-way *ANOVA*/*MANOVA* procedure *Statistica 99* (StatSoft Inc., USA), and the *Student's t*-test was used to determine the significant differences between the means.

Results and discussion

Exposure of the plants to long term moderate drought stress had a reducing effect on fruit fresh mass in all investigated genotypes (Table 1), but the effects were more expressed in cherry tomatoes ('Plovdiv' and LA1420) than in large fruits tomatoes ('Levovil' and LA0147).

Table 1. Fruit fresh mass, dry matter content and diameter of tomato fruits exposed to optimal and water deficit conditions

Genotype	Fresh mass g		Dry matter %		Diameter mm	
	control	drought	control	drought	control	drought
Plovdiv	45.20 ± 1.95	19.33 ± 0.70***	7.52 ± 0.13	9.59 ± 0.14***	41.87 ± 0.76	31.41 ± 0.54***
Levovil	104.05 ± 9.08	88.29 ± 9.36 ns	5.26 ± 0.32	6,49 ± 0.38***	65.57 ± 4.33	57.05 ± 2.28 ns
LA1420	64.04 ± 7.11	25.31 ± 5.14***	6.61 ± 0.10	8,83 ± 0.44***	53.83 ± 2.14	38.66 ± 3.36**
LA0147	107.84 ± 12.71	57.30 ± 6.26***	5.94 ± 0.18	7,69 ± 0.47***	60.79 ± 3.16	52.37 ± 3.03 ns

Note. Values are mean ± standard error (n = 6); levels of significance are represented by *$P < 0.05$, ** $P < 0.01$ and *** $P \leq 0.001$, ns – not significant.

In all genotypes the dry matter content of fruit increased, while reduction of fruit diameter was statistically significant only for the cherry tomatoes. The effects of drought could be different depending on the intensity of the stress and the stage of fruit development when a water deficit is applied (Kuşçu et al., 2014; Chen et al., 2015). This could explain the discrepancy of our and Ripoll et al. (2016 b) results, where reduction in fruit fresh weight of cherry genotypes was not found after short term repeated drought and recovery periods at specific developmental stages. Our experiment started at anthesis, prolonged until maturity stage, and our plants were exposed to a much longer period of water deficit.

Soluble sugars and organic acids are major osmotic compounds that accumulate in fleshy tomato fruits and determine its taste. Our results revealed specific genotypic differences between cherry and large fruits. The results showed that in all genotypes glucose and fructose content had a tendency to decrease, although the sucrose concentration, as the most important trait for sweetness perception and marketing value of the fruits (Baldwin et al., 2008), increased in all genotypes, especially in large fruited tomatoes (Table 2).

On the contrary, results of Ripoll et al. (2016 a) demonstrated that the majority of genotypes from MAGIC TOM population were not strongly affected by

Table 2. Soluble sugars content (g 100 g^{-1} dry weight) in tomato fruits exposed to optimal and water deficit conditions

Genotype	Glucose		Fructose		Sucrose	
	control	drought	control	drought	control	drought
Plovdiv	24.74 ± 0.21	24.56 ± 0.33 ns	22.15 ± 0.21	20.95 ± 0.38*	1.19 ± 0.04	2.29 ± 0.08***
Levovil	24.28 ± 0.56	24.98 ± 0.18 ns	23.53 ± 0.34	22.32 ± 0.30*	0.23 ± 0.02	1.19 ± 0.04***
LA1420	22.93 ± 0.16	21.62 ± 0.47**	21.15 ± 0.21	19.25 ± 0.27***	0.63 ± 0.03	1.48 ± 0.10***
LA0147	23.53 ± 0.41	19.65 ± 0.40***	21.64 ± 0.32	17.57 ± 0.19***	0.41 ± 0.03	1.62 ± 0.07***

Explantations under Table 1

the different level of stress in repeated drought. These differences can be explained by the varying degree of stress, to which the plants were exposed. Since large tomato fruits exhibited reduction of fruit fresh weight and fruit diameter under water deficit (Table 1), it could be presumed that the higher accumulation of sucrose in these fruits could contribute to osmotic adjustment necessary for continuing fruit growth in water deficit conditions.

Drought also affected organic acids and increased citric acid in the fruits of all genotypes (Table 3), but the effects were more expressed in the large than in cherry fruit. Results of Sun et al. (2014) showed that the increase of organic acid does not necessarily lower the quality of fruits. Increase of both sugars and organic acids could improve tomato fruit quality under water stress (Nahar et al., 2011).

Table 3. Organic acids content (g 100 g^{-1} dry weight) in tomato fruits exposed to optimal and water deficit conditions

Genotype	Malic acid		Citric acid	
	control	drought	control	drought
Plovdiv	1.86 ± 0.05	2.20 ± 0.08***	4.16 ± 0.04	4.60 ± 0.09***
Levovil	2.57 ± 0.08	2.31 ± 0.09 ns	4.05 ± 0.04	4.81 ± 0.03***
LA1420	0.63 ± 0.03	0.70 ± 0.02 ns	7.35 ± 0.08	8.13 ± 0.09**
LA0147	2.41 ± 0.08	2.64 ± 0.06 ns	5.01 ± 0.09	6.14 ± 0.12***

Explantations under Table 1

Different secondary metabolites, including carotenoids, are responsible for the nutrient and health values of tomato fruits and also are genotype-specific (Schweiggert et al., 2017). Comparison between cherry and large fruits showed that in both optimal and drought conditions fruits of cherry tomato had a higher total carotenoid content than large fruits, mainly due to higher content of lycopene and phytoene (Tables 4 and 5). In this study, the effect of drought stress was more expressed on β-carotene accumulation than lycopene that could

Table 4. Lycopene and β-carotene content (mg kg^{-1} fresh weight) in tomato fruits exposed to optimal and water deficit conditions

Genotype	Lycopene		β-carotene	
	control	drought	control	drought
Plovdiv	73.54 ± 2.12	74.65 ± 2.18 ns	2.58 ± 0.09	3.02 ± 0.07**
Levovil	55.81 ± 1.64	52.19 ± 1.45 ns	4.72 ± 0.04	3.43 ± 0.07***
LA1420	68.03 ± 2.12	101.95 ± 1.44***	3.64 ± 0.06	4.39 ± 0.07***
LA0147	40.31 ± 1.82	40.84 ± 2.30 ns	2.92 ± 0.01	3.27 ± 0.07**

Explantations under Table 1

Table 5. Phytoene and lutein content (mg kg^{-1} fresh weight) in tomato fruits exposed to optimal and water deficit conditions

Genotype	Phytoene		Lutein	
	control	drought	control	drought
Plovdiv	11.57 ± 0.28	14.94 ± 0.49***	0.74 ± 0.02	0.97 ± 0.02***
Levovil	3.70 ± 0.11	4.40 ± 0.1**	0.90 ± 0.03	1.16 ± 0.02***
LA1420	8.36 ± 0.14	14.30 ± 0.10***	0.70 ± 0.02	1.04 ± 0.02***
LA0147	4.24 ± 0.12	4.68 ± 0.04*	1.15 ± 0.03	1.57 ± 0.04***

Explantations under Table 1

be indirectly connected to their role in the biosynthesis of plant water-stress related hormones as abscisic acid (Riggi et al., 2008).

Tomatoes are characterized by high fruit antioxidant capacity, and many literature data indicated that this trait is genotype specific (Nour et al., 2013; Klunklin, Savage, 2017). Our study showed that long term moderate drought stress induced the increase of total antioxidant capacity in all analysed genotypes, but this effect was more expressed in cherry than in large tomato fruits (Table 6).

The high antioxidant activity of cherry tomato cultivars was also induced by oxidative stress generated by moderate water deficit (Sánchez-Rodríguez et al., 2010). Among the plant antioxidants, ascorbic acid (vitamin C) is a major antioxidant playing a vital role in protecting against various environmental abiotic stresses (Venkatesh, Park, 2014). In our experiment long term drought stress significantly increased total and reduced ascorbic acid contents in all analysed genotypes, especially in cherry tomatoes (Table 6). This increase could be a result of the oxidative stress-induced formation

Table 6. Antioxidant capacity, total and reduced ascorbic acid content of tomato fruits exposed to optimal and water deficit conditions

Genotype	Antioxidant capacity µmol TEAC 1000 g^{-1} FW		Total ascorbic acid mg 100 g^{-1} FW		Reduced ascorbic acid mg 100 g^{-1} FW	
	control	drought	control	drought	control	drought
Plovdiv	1582.72 ± 21.03	2863.63 ± 84.68***	20.78 ± 0.47	21.26 ± 0.76***	18.24 ± 0.21	28.70 ± 0.40***
Levovil	1411.54 ± 18.17	1866.33 ± 16.83***	24.88 ± 0.58	27.91 ± 0.40***	23.41 ± 0.59	27.43 ± 0.52***
LA1420	1370.00 ± 12.85	2124.00 ± 22.91***	22.84 ± 0.71	32.58 ± 0.97***	22.62 ± 0.70	29.65 ± 0.54***
LA0147	1613.21 ± 16.79	2546.73 ± 15.39***	22.68 ± 0.59	28.07 ± 0.58***	21.94 ± 0.56	26.77 ± 0.96***

Explantations under Table 1; FW – fresh weight

of reactive oxygen species (ROS), where lycopene and *β*-carotene could also contribute to antioxidant defence mechanisms in fruit (Fanciullino et al., 2014). Although we did not measure the activity of enzyme related to ROS-detoxification mechanisms, the increase of the non-enzymatic antioxidant components such as carotenoids and vitamin C in the fruits indirectly indicated the presence of antioxidant protective mechanism in the investigated tomato plants.

According to Ripoll et al. (2016 a), the comparison of fruit quality parameters on dry and fresh weight basis may explain drought effect on tomato fruits. An increase in a certain compound per dry and fresh weight basis indicates that drought induced both, concentration and metabolic effects, while the significant increase only per fresh weight basis indicates that the drought induced a concentration effect.

Use of such approach for assessment of sugars and organic acid data (Table 7) indirectly showed that hexose sugars and organic acids increased significantly in all genotypes mainly due to the concentration effect, although the tendency of increasing the sucrose content, especially in large fruits indicated both, concentration and metabolic accumulation effects.

Results for lycopene and β-carotene for most genotypes indirectly indicated that their content was mainly the result of decrease in storage / metabolism and can be compensated for by concentration effect, except for LA1420, where the higher accumulation of lycopene was accompanied by metabolic changes.

Table 7. Relative differences in metabolite components of tomato fruits expressed on fresh and dry matter basis

	Fresh matter basis				Dry matter basis			
	'Plovdiv'	'Levovil'	LA1420	LA0147	'Plovdiv'	'Levovil'	LA1420	LA0147
Glucose	**+26.61**	**+26.94**	**+26.01**	**+8.08**	−0.73	+2.88	**−5.71**	**−16.5**
Fructose	**+20.59**	**+17.14**	**+21.60**	**+5.21**	**−5.42**	**−5.11**	**−9**	**−18.78**
Sucrose	**+146.36**	**+527.64**	**+216.42**	**+418.67**	**+92.68**	**+408.12**	**+137.06**	**+298.77**
Total sugars	**+26.52**	**+24.65**	**+25.89**	**+10.45**	−0.58	+0.98	**−5.28**	**−18.45**
Citric acid	**+40.90**	**+46.48**	**+47.74**	**+58.92**	**+10.73**	**+18.72**	**+10.55**	**+22.59**
Malic acid	**+50.71**	+11.11	**+47.03**	**+41.96**	**+17.91**	−9.88	+10.05	+9.72
Total acids	**+43.93**	**+32.76**	**+47.68**	**+53.41**	**+12.96**	**+7.70**	**+11.60**	**+18.03**
Phytoene	**+29.15**	**+18.96**	**+71.08**	**+10.55**	+1.27	−3.57	**+28.06**	**−14.61**
Lutein	**+31.12**	**+28.21**	**+48.36**	**+40.72**	+2.77	+3.90	**+11.08**	+8.71
β-carotene	**+16.87**	**−27.39**	**+20.7**	**+12.16**	−6.83	**−41.06**	**−7.76**	**−13.54**
Lycopene	+1.51	−6.49	**+49.87**	+0.57	**−20.40**	**−24.21**	**+12.85**	**−22.31**
Total carotenoids	**+5.82**	**−6.11**	**+50.72**	**+5.87**	**−16.98**	**−23.87**	**+13.50**	**−20.42**
Total vitamin C	**+50.46**	**+12.18**	**+42.63**	**+23.74**	+9.9	+6.75	+13.61	**−13.83**
Reduced vitamin C	**+57.38**	**+17.15**	**+31.08**	**+22.01**	**+25.85**	−0.6	−6.71	**−8.64**

Note. Values are relative differences expressed as % (% = (mean drought-mean control / mean control) × 100); significant differences ($P < 0.05$) between control and treatments are indicated by bold fonts.

Conclusions

1. Long term water deficit can influence fruit quality in large tomato fruit genotypes by active metabolic accumulation of sucrose and citric acid, which are also osmotically active compounds.

2. Higher reduction of the fruit growth of cherry tomatoes compared to the large fruited tomatoes can be compensated for by improved fruit nutritional value: higher content of ascorbic acid and carotenoids as well as antioxidant activity.

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Drėgmės trūkumo įtaka vyšninių ir didžiavaisių pomidorų vaisių kokybei

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Santrauka

Tyrimo metu siekta ištirti ilgalaikio vidutinio sausros streso įtaką keturių tėvinių MAGIC TOM populiacijos formų pomidorų vaisių derliui bei kokybei ir nustatyti vyšninių bei didžiavaisių pomidorų jautrumo sausrai skirtumus. Tyrimo rezultatai parodė, kad ilgalaikis vidutinio sunkumo drėgmės trūkumas turėjo neigiamos įtakos žaliai masei bei vaisių skersmeniui, ir tai labiau pasireiškė vyšniniuose nei didžiavaisiuose pomidoruose. Ilgalaikis drėgmės trūkumas gali pagerinti didžiavaisių pomidorų vaisių skonį dėl aktyvaus metabolinio tirpiųjų cukrų ir organinių rūgščių (sacharozės ir citrinos rūgšties) kaupimosi, kurie taip pat yra osmotiškai aktyvūs junginiai. Lyginant su didžiavaisiais pomidorais, sumažėjęs vyšninių pomidorų augimas gali būti kompensuojamas gerinant vaisių mitybinę vertę – didinant askorbo rūgšties bei karotenoidų kiekį ir antioksidacinį aktyvumą, dėl medžiagų koncentracijos bei metabolizmo ir spartinant metabolines reakcijas.

Reikšminiai žodžiai: antioksidantų junginiai, MAGIC TOM, mitybinė vertė, sausra, *Solanum lycopersicum*.