Journal of Horticulture and Forestry Vol. 3(10), pp. 294-300, October 2011
Available online http://www.academicjournals.org/jhf
ISSN 2006-9782 ©2011 Academic Journals

Full Length Research Paper

Physiological responses of six tomato (*Lycopersicon esculentum* Mill.) cultivars to water stress

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Accepted 22 November, 2010

The aim of the present study was to investigate the physiological responses of six tomato (*Lycopersicon esculentum* Mill.) cultivars to water stress. To this end, plants were exposed to slow dehydration at the third unfolded leaf stage for 23 days. The relative water content (RWC), leaf area and leaf L-proline were determined at 10, 17 and 23 days after treatment application. Our results showed that during slow dehydration, the leaf RWC declined in all studied genotypes, whereas L–proline accumulated. A statistically significant effect of the sampling date (water stress duration) on RWC values was also observed. In addition, the differences in proline content were significantly influenced by tomato genotype, sampling date and the level of substrate saturation. Putting all these together, the results of this study indicate that the adaptive potential of the studied genotypes was expressed in a different relationship between the relative water content and growth of the leaf area. However, three of the tomato genotypes exhibited reduced growth in leaf area in response to the decreased RWC, whereas other tomato genotypes retained a balanced RWC accompanied by further growth of the leaf area.

Key words: Tomato, genotypes, growth, water stress, L-proline, relative water content.

INTRODUCTION

Higher plants, which are continuously exposed to intense or moderate water deficit, use morphological, cellular and molecular adaptive mechanisms to survive (Bohnert and Jensen, 1996; Zhu et al., 1997; Hasegawa et al., 2000; Pedrol et al., 2000). Plant responses to drought include changes of growth intensity in shoots and roots, and an acceleration of the plant development (Lannucci et al., 2000, Ma et al., 2006). In addition, drought has been demonstrated to be extremely negative at the reproductive stage of plant development (Ludlow and Muchow, 1990; Ma et al., 2006). Therefore, plants tend to avoid dangerous periods by changing the intensity of the physiological processes and the position of organs, or by leaf rolling (Fernandez and Castrillo, 1999; Kadioglu and Terzi, 2007; Saglam et al., 2008).

It has been demonstrated that for many plant species, a decrease in leaf water potential (-1.0 MPa) induces an osmoregulatory mechanism through the accumulation of some primary and secondary metabolites, such as: amino acids, amides, carbohydrates and salt cations (Serraj and Sinclair, 2002; Zhu, 2002; Ashraf and Foolad, 2006). Among these osmoprotective substances, the amino acid L-proline has been shown to be accumulated under stress conditions (Taylor, 1996; Ben-Rouina et al., 2006), particularly under drought conditions, and many other plants have also displayed significant increases in L-proline levels (Delauney and Verma, 1993; Hasegawa et al., 2000; Adejare et al., 2006; Umebese, 2008). In experiments with transgenic plants, it has been shown that plants overexpressing the Δ^1-pyrolin-*5*-carboxylate synthetase, a gene involved in proline biosynthesis (Kavi-

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Table 1. Characteristics of the studied tomato genotypes.

Tomato variety	Origin	Description
Premium	Collection of genetic sources in Slovak Republic	Determinate, bush tomato, main season variety,
Denár	Collection of genetic sources in Czech Republic	Determinate, bush tomato, semi-fast ripening variety
Hana	Collection of genetic sources in Czech Republic	Semi-determinate tomato, semi-fast ripening variety
Robura	Collection of genetic sources in Slovak Republic	Determinate, bush tomato, late variety
Moldeny	Collection of genetic sources in Slovak Republic	Bush tomato, semi-fast ripening variety
UC-82		Determinate, bush tomato, fast ripening variety

Kishor et al., 1995; Nanjo et al., 1999; Hong et al., 2000), have a good capacity to tolerate drought. In our opinion, proline indicates plant stress and it shows a considerable adaptive plant response against stress. The present work is focused on the study of selected physiological responses of tomato genotypes and the determination of the adaptation model to drought during the process of slow dehydration.

MATERIALS AND METHODS

In this study, six tomato (*Lycopersicon esculentum* Mill.) genotypes, namely: Hana, UC-82, Premium, Denar, Moldeny and Robura, were used. The genotypes were selected according to the heterogeneity of their growth type and in terms of tomato fruit ripening (Table 1); although tomato seeds were pre-germinated on Petri-dishes. In the second decade of March, the root tips were detected and seeds were sown to seedbeds and placed in greenhouse. As such, the seedlings germinated within one week.

At the second unfolded leaf stage, 30 days old plants were individually transplanted in containers (5 L contents) with sowing substrate (pH = 5.0 – 6.5, content of salts < 1.5 g/l, N = 50 - 300 mg /l, P_2O_5 = 80 - 300 mg/l, K_2O = 80 – 400 mg/l), after which the content of dry mass (38%) and water (62%) in the substrate was analysed at the beginning of the experiment. During the experiment, the average daily air temperature was 21.9°C and the average air humidity was 77.8%. Before treatment application, the substrate was maintained at 70% of its full water capacity. At the vegetative growth stage, 30 tomato plants of each genotype were divided into two groups (15 individuals in each group). For the first one, plants were watered at only 40% of their full water capacity (stress) for 23 days; while for the second group, plants were retained at 70% substrate saturation (control). However, the water regime was maintained by daily watering of the individual plants to constant weight. From each tomato genotype, 10 plants (5 stressed and 5 controls) were analysed and their samples were taken from the control and stressed plants at the 10^{th}, 17^{th} and 23^{rd} day after treatment application. After exposure period of the treatment, the flowers appeared on lateral shoots. The following parameters were analysed: content of water in the whole plant and its vegetative organs, leaf area (A) in square meters (m^2) determined from leaf scanning using the Corel SCAN 8 software and Corel OCR-TRACE 8, content of L-proline in leaves determined colorimetrically in the toluene extract according to Bates et al. (1973) after tissue homogenisation and filtration. Excitation (E) was determined at 519 nm using a Merck spectrophotometer (NOVA 400). The relative water content (RWC%), which represents the relationship between the content of water in the plant organs and the content of water during their full turgescence was calculated according to the method of Gonzáles et al. (2001), while the relative growth rate of the leaf area ($RGR_A = \ln A_2 – \ln A_1 / t_2 – t_1$) was calculated according to the method of Květ (1971). However, Hunt (1982) and Kolb and Steiner (1990) used the same basic calculation for the mentioned parameter.

The data obtained in this study were analyzed using multifactor ANOVA, and the mean values were compared using the Tukey test at a confidence interval of 95% and a significance level of $p \leq 0.05$. The regression analysis on 95% significance level was applied for assessment of the associations between RWC content and leaf area (A). However, all assessments were carried out using the statistical software package, Statgraphics Centurion XV.

RESULTS

The study of the physiological responses of six tomato genotypes growing in conditions with good and low water supply revealed the extreme heterogeneity of the analysed genotypes in their responses to water stress. Cultivar efficiency retains or only slightly reduces the intensity of physiological processes under conditions of water stress and hence can be a significant indicator of their drought tolerance. According to Umebese et al. (2009), water stress reduces the shoot elongation rate of tomato and amaranth in vegetative growth stages and decreases shoot biomass production of both species in the reproductive growth stage.

The influence of tomato cultivar, water regime and stress duration (sampling date) was analysed on values of the relative water content (RWC) in tomato leaves. The differences in the RWC values between cultivars and treatment (stress and control) were not statistically significant (Table 2). The RWC was significantly influenced by the sampling date (water stress duration). From the beginning of the experiment (0-day), the leaf RWC decreased significantly with the lowest value (77.08%) obtained at the 17th day of the treatment, while on the next sampling date, a moderate increment of the average RWC to 82.33% was recorded (Table 3).

One plausible cause of these changes is the accumulation of L-proline in plant leaves (Jureková et al., 2003; Gubiš et al., 2006). The differences in proline content are significantly influenced by genotype, sampling date and the level of the substrate saturation (Table 4). The results of multifactorial analysis of variance confirmed the

Table 2. Multifactor analysis of variance for parameter RWC of different tomato cultivars.

Source of variation	Sum of squares	Df	Mean square	F-value	P-value
Main factor					
A: Cultivar	100.589	5	20.1178	1.74	0.1872 $^{n.s.}$
B: Sampling date	1470.28	3	490.093	42.28	0.0000 ***
C: Water regime	45.2408	1	45.2408	3.90	0.0669 $^{n.s.}$
Interaction					
AB	179.763	15	11.9842	1.03	0.4747 $^{n.s.}$
AC	109.569	5	21.9138	1.89	0.1558 $^{n.s.}$
BC	39.4408	3	131.469	1.13	0.3670 $^{n.s.}$
Residual	173.879	15	11.5919		
Total	2118.76	47			

Table 3. Average values of RWC (%) and Tukey-test at a significance level of p ≤0.05. Data are given for particular tomato cultivars, sampling dates and different levels of substrate saturation.

Cultivar	N	Average	Sampling date	N	Average
Premium	8	82.92 ^{a}	0^{th} day	12	91.27 ^{c}
Moldeny	8	83.81 ^{a}	10^{th} day	12	78.45 ^{ab}
Hana	8	83.78 ^{a}	17^{th} day	12	77.08 ^{a}
Denar	8	80.19 ^{a}	23^{rd} day	12	82.33 ^{b}
Robura	8	80.50 ^{a}	Water regime	*N*	*Average*
UC-82	8	82.49 ^{a}	70%	24	83.25 ^{a}

Table 4. Multifactor ANOVA of L-proline content in the leaves of tomato cultivars.

Source of variation	Sum of squares	Df	Mean square	F-value	P-value
Main factor					
A: Cultivar	6.81352	5	1.3627	3.99	0.0167 *
B: Sampling date	5.50345	3	1.83448	5.37	0.0103 *
C: Water regime	4.26021	1	4.26021	12.48	0.0030 **
Interaction					
AB	6.6102	15	0.44068	1.29	0.3136 $^{n.s.}$
AC	2.21904	5	0.443808	1.30	0.3156 $^{n.s.}$
BC	4.94688	3	1.64896	4.83	0.0151 *
Residual	5.12038	15	0.341358		
Total	35.4737	47			

statistically significant interactive effect of sampling date and water regime on proline content (Table 4).

The significant differences in the average values of proline content were confirmed for cultivars Moldeny and Denar (Table 5). In comparison to other studied cultivars, Denar showed quite a high average value of proline, which indicates the highest expressive adaptation of this tomato genotype to stress conditions. A similar adaptation mechanism was confirmed for all studied genotypes in the variant with lower substrate saturation (40%), which accumulated an average proline content of 0.99 µmol. g^{-1} of fresh mass (Table 5).

As part of the study of proline accumulation in relation to the duration of water deficit, a significant increase of proline content was confirmed on the 17th day of the experiment. This date was duplicated in the assay of the changes in water content of the leaves. At the 23^{rd} day of treatment, the content of proline decreased to an average

Table 5. Average values of L-proline (µmol.g-1) and Tukey-test at significance level of p ≤0.05. Data are given for particular tomato cultivars, sampling dates and different levels of substrate saturation.

Cultivar	N	Average	Sampling date	N	Average
Premium	8	0.30 [ab]	0[th]day	12	0.52 [a]
Moldeny	8	0.22 [a]	10[th]day	12	0.50 [a]
Hana	8	0.80 [ab]	17[th]day	12	1.28 [b]
Denar	8	1.25 [b]	23[rd]day	12	0.48 [a]
Robura	8	1.05 [ab]	Water regime	*N*	Average
UC-82	8	0.54 [ab]	40	24	0.99 [b]
			70	24	0.40 [a]

Table 6. Correlation (R-squared values) between RWC and the leaf area (A) of three tomato genotypes with balanced growth of the leaf area.

Cultivar	Parameter	RWC (%)
Premium	A	98.40***
Robura	A	84.01**
UC-82	A	77.89*

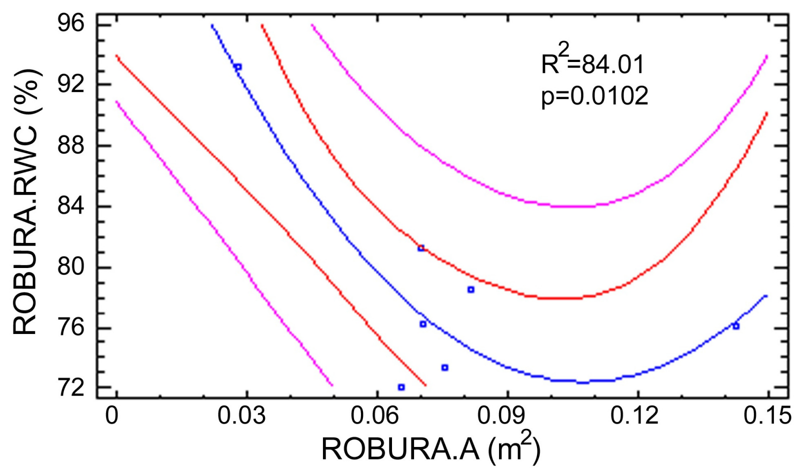

Figure 1. Polynomial correlation between relative water content RWC) and leaf area (A) of tomato cultivar ROBURA growing in conditions of differentiated water regime. Blue line: fitted regression model; red lines: 95% confidence intervals for mean values of RWC; pink lines: 95% prediction limits for new observations.

value of 0.48 µmol.g^{-1}, which was similar to that at the beginning of the experiment.

Plants grown at a low level of substrate saturation (40%) had significantly higher proline content as compared to the control plants (Table 5). During the 23-day period of water deficit, differences in leaf area growth were recorded for particular genotypes. On the 10th day of water stress, the most sensitive reactions were recorded on cultivars Hana, Denar and Moldeny, which reduced the leaf area growth. However, the final leaf area depletions were 45.3, 43.5, and 31.7% for Hana, Denar and Moldeny cultivars, respectively.

Premium, Robura and UC-82 cultivars did not reduce the growth of their leaf area (A). For these genotypes, quite a significant correlation between the leaf area (A) and RWC was observed (Table 6). The relationship can be described with a second order polynomial (Figures 1, 2 and 3). For the mentioned cultivars, there is an evident decrease in the RWC with increasing leaf size. Later, RWC values became stable and did not change with later

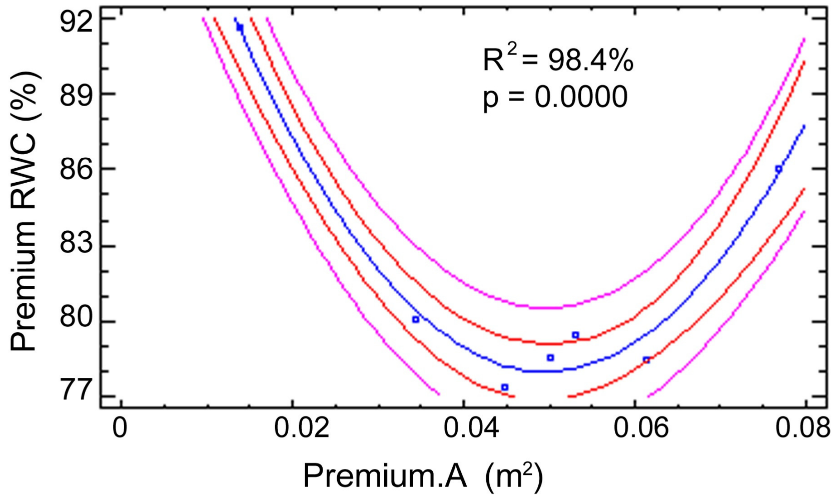

Figure 2. Relationship between relative water content (RWC) and leaf area (A) of tomato cultivar Premium growing in conditions of differentiated water regime. Blue line: fitted regression model; red lines: 95% confidence intervals for mean values of RWC; pink lines: 95% prediction limits for new observations.

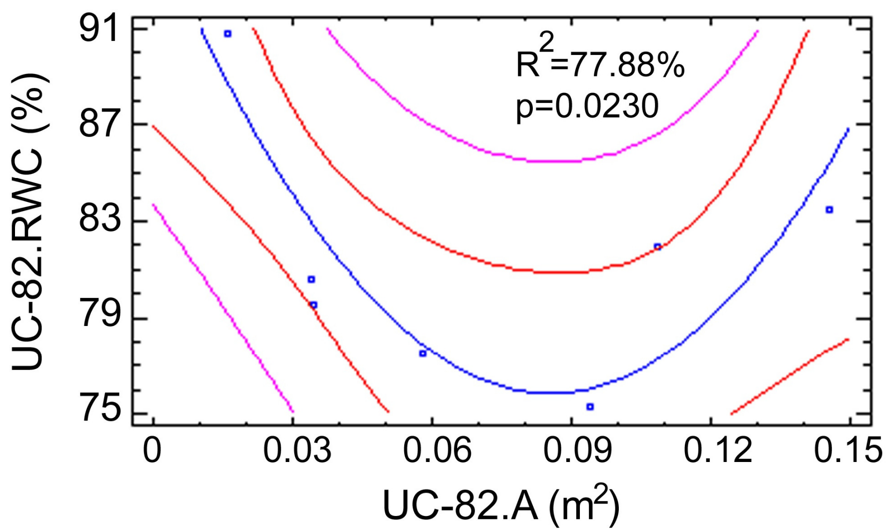

Figure 3. Relationship between relative water content (RWC) and leaf area (A) of tomato cultivar UC-82 growing in conditions of differentiated water regime. Blue line: fitted regression model; red lines: 95% confidence intervals for mean values of RWC; pink lines: 95% prediction limits for new observations.

growth of the leaf area (Figures 1, 2 and 3). Besides the plant responses already mentioned, low values of proline in leaves accompanied by an increase of the relative water content (RWC) and relative growth rate of the leaf area (RGR_A) were recorded after 17 days of water deficit. As such, the highest values of RGR_A were obtained in the interval between the 17^{th} and 23^{rd} day of drought for the six tomato genotypes.

DISCUSSION

Some genotypes of cultural plants have a specific growth and productive potential. Its realisation depends on environmental conditions. There is an increasing demand for identification of such genotypes tolerant to unfavourable factors including drought. However, the exact identification of genetic conditioning in plant reactions to drought has not yet been successful. Many papers have studied the osmoprotectant accumulation, in which the parameter has been used in selection for tolerance to environmental stresses (Ozturk and Demir, 2002; Hsu et al., 2003; Kavi-Kishore et al., 2005; Ashraf and Foolad, 2007). The results of the experiments with six tomato cultivars in conditions of increasing drought, however, revealed some physiological reactions of tomato cultivars, which may be regarded as significant traits of adaptation to water deficiency.

Reduction of the relative water content (RWC) in leaves of all the studied genotypes was detected during slow plant dehydration. Differences in this parameter among the studied genotypes were not significant. Depending on the duration of the plant hydration, the lowest values of relative water content were measured on the 17th day of the experiment. However, these values were maintained on 85 to 78%, which correlated (Gonzáles and Gonzáles-Vilar 2001) with changes in the composition of the tissues and some alterations in the relative rates of photosynthesis and respiration.

There is much information in the literature about osmotic adjustment as a result of osmoprotectant accumulation in plants (Hsu et al., 2003; Nayyar and Walia, 2003; Kavi-Kishore et al., 2005). For instance, proline accumulation is considered to be a part of osmotic adjustment, which allows turgor maintenance, decrease in water potential and an increase of water uptake from the soil (Ali et al., 1999). In our experiments, the accumulation of L-proline was observed in leaves of tomato plants with reduced RWC values. Proline content was influenced by tomato genotype, sampling date and water deficiency. However, statistically significant differences in proline content among genotypes were recorded (Tables 3 and 4). The question is whether the differences mentioned are symptoms of stress, or a result of genotype adaptation to stress. Garcia et al. (1997) and Lutts et al. (1999) consider proline accumulation to be rather a symptom of damage, than an indicator of plant resistance. According to our findings, the significant influence of the time factor (stress duration) and dehydration on proline content confirms its role in plant adaptation to water stress as postulated by Taylor (1996) and Hasegawa et al. (2000).

According to some authors, the adaptive potential of some particular plant species includes curbing of water losses, achieved by a reduction of both the leaf area growth rate (Hsiao, 2000) and the permeability of the cuticle towards water (Riederer, 2001), a closing of stomata and a reduction in the transpiration rate (Tardieu et al., 1996).

Our results refer to genotype conditioning in the mentioned plant responses. Under conditions of water stress, the three genotypes (Hana, Denar and Moldeny) reduced relative water content (RWC) and growth rate of the leaf area. Under the same conditions, Premium, Robura and UC-82 cultivars maintained quite a number of elevated values of leaf area, while the relative water content (RWC) in their leaves was significantly correlated with the leaf area. After reduction of RWC at the beginning of the experiment, these genotypes maintained a stable RWC which did not change following growth of the leaf area. Thus, this study confirms the significant differences in physiological responses among tomato genotypes and their adaptation to water deficiency. However, relative water content correlated with leaf area growth and proline accumulation, and these correlations can be regarded as indicators of genotype drought tolerance.

Conclusions

Due to the current climate changes exemplified by longer drought periods and higher temperatures during the growing season, a description of the principles and processes of plant adaptation to unfavorable conditions is essential. According to results obtained in our experiments with tomato cultivars, all genotypes studied responded to water deficiency with physiological responses on the level of plant water regime, growth response and osmoregulation. However, some tomato cultivars like Premium-determinate (main season variety), Robura-determinate (late variety) and UC-82 determinate (fast ripening variety) had significantly correlated RWC values and growth of leaf area. For the three tomato genotypes studied (Hana, Denar and Moldeny, which are all determinate semi-fast ripening varieties), the growth of the leaf area was limited by reduction of relative water content (RWC) in the leaves; whereas the other genotypes, after initial reduction, maintained stable RWC. Nonetheless, the values of this parameter did not change with growth of the leaf area.

Fundamentally, statistically significant differences in the average L-proline content were noted between the tomatoes' genotypes studied. Also, a significant influence of stress duration (sampling date) and substrate saturation (water regime) was confirmed. The highest average proline content was found in the cultivar Denar, which displays the most evident adaptation of a tomato genotype (vs. other cultivars) to stress conditions through osmotic adjustment. A similar mechanism of plant adaptation was also confirmed for other tomato cultivars growing in conditions with lower substrate saturation.

ACKNOWLEDGEMENTS

This study was supported by the Grant Agency of the Ministry of Education, Slovak Republic. The authors wish to acknowledge the Slovak Academy of Sciences (VEGA grant No. 1/0426/09). The adaptability and vitality of plants as a criterion of their utilization in urban spaces

and landscape).

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