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Some morphological, physiological and biochemical characteristics of wheat seedling *Triticum aestivum* L. organs after high-temperature treatment

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Plants as sessile organisms are exposed to persistently changing stress factors. Heat stress adversely affects plant growth and development and induces oxidative stress in plants. To understand the effect of high-temperature stress on plant growth and development, it is necessary to study the physiology and morphology of whole plants and their organs. The oxidative stress level was assessed by increased production of lipid peroxidation (LP) products, such as malondialdehyde (MDA) and conjugated dienes (CD), and cellular membrane permeability, as evaluated by electrolyte leakage (EL) in different wheat (*Triticum aestivum* cv. Harmonija) organs after 24-hour high-temperature (42 °C) treatment. Measurements of relative water content (RWC) in leaf tissues were used to assess water deficits in plants. High-temperature treatment had no effects on RWC in the root, but reduced RWC in the coleoptile at all investigated stages of seedling development and in the first leaf ($p \leq 0.01$) at the late stages of development. A 24-h high-temperature exposure completely inhibited the growth of the first leaf and root ($p \leq 0.001$). LP significantly increased in the coleoptiles of wheat seedlings due to high temperature, but in contrast LP in the root was similar to control at all investigated stages of development. A significant increase of LP products ($p \leq 0.01$) was observed in the first leaf at the late stages of wheat seedling development. Such elevated level of LP led to increase of cellular membrane permeability. 24-h high temperature results in the desiccation of the first leaf and coleoptile. Obviously the root of wheat seedlings is less sensitive to heat stress than the first leaf and coleoptiles. The study revealed that specific effects of high temperature on the root result in increase of electrolyte leakage, but high temperature hardly affects lipid peroxidation processes.

Key words: lipid peroxidation, electrolyte leakage, relative water content, heat stress, oxidative stress, wheat seedling organs

INTRODUCTION

Gradually, increasing temperature is a great threat to agricultural production all over the world. Some reports show that an increase in temperature by a single degree above normal can lead to a significant reduction in growth and yield (Pastori, Foyer, 2002). High temperature affects morphological, biochemical, and physiological processes in plants, and the major effects entail scorching of aerial plant parts, sunburn of branches and stems, leaf death, leaf abscission and senescence, and causes inhibition of shoot and root growth, and reduces yield (Ismail, Hall, 1999; Wahid et al., 2007).

High temperature induced oxidative stress in plants (Gong et al., 1997). In many cases, a result of stress is the formation of reactive oxygen species (ROS). The ROS in plant tissue can initiate lipid peroxidation (LP) that causes damage to cell membranes and is considered to be the most important mechanism of tissue damage, e. g. protein degradation, enzyme inactivation, pigment bleaching

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and disruption of DNA strands (Anderson, Padhye, 2004). Numerous studies have been conducted in order to elucidate the mechanisms and the effects of this oxidative stress, e. g. by monitoring ROS or looking at LP products. The presence of ROS has been investigated for different organs of plants under high temperature and salt stress (Hui et al., 2008; Li, 2009; Savicka, Škute, 2010), light-treated leaves (Wu, von Tiedemann, 2004), etc. The intermediate and the end products of LP have also been explored to monitor the process (Larkindale, Huang, 2004).

A major impact of plant environmental stress is cellular membrane modification, which results in its perturbed function or total dysfunction (Jiang, Huang, 2001). Cell membrane stability has long been taken as an indicator of stress tolerance (Blum, Ebrecon, 1981). For example, cell membrane stability has been widely used for screening against drought and heat tolerance in plant species such as *Sorghum* bicolor (Sullivan, Ross, 1979), wheat (Blum, Ebrecon, 1981), rice (Tripathy et al., 2000), salt tolerance in wheat (Farooq, Azam, 2006), etc. The exact structural and functional modification caused by high-temperature stress is not fully understood. However, the cellular membrane dysfunction due to stress is well expressed in increased permeability and leakage of ions, which can be readily measured by the efflux of electrolytes. Also, plants may experience different types of stress at different developmental stages and their mechanisms of response to stress may vary in different tissues (Queitsch et al., 2000).

The present investigations were undertaken to study the changes in LP, cellular membrane stability and the RWC under heat stress in *Triticum aestivum* L. organs. Morphological, biochemical and physiological changes in wheat organs were investigated to elucidate their relationship to injury from elevated temperature. Four and six days old seedlings of wheat were subjected to high temperature stress (42 °C). These were analysed for products of LP, EL and RWC under control and stress conditions.

MATERIALS AND METHODS

Plant materials

The object of the study was etiolated seedlings of winter wheat (*Triticum aestivum* L., *cv*. Harmonia). Wheat is a convenient object for studying plant morphology, physiology and molecular biology, because the development of cereals is synchronous throughout ontogeny (Kirnos et al., 1997). Etiolated wheat seedlings germinated on moist filter paper in dark at 26 °C for 24 h. After germination, the seedlings were transferred to a plant growth chamber maintained at 26 °C and 75% relative humidity in the dark. The organs of wheat seedlings (first leaves, coleoptiles and roots) used for all the experiments were 4-day-old (the early stage) and 7-day-old (the late stage). Wheat roots were used because high root temperature accelerates senescence of the entire plant (Ferguson et al., 1990). The first leaf and coleoptile were used because the first leaf is a developing organ of wheat, but the coleoptile is a senescent organ of wheat, and processes which occur in these organs during high-temperature stress were expected to differ.

Heat treatment

Heat treatments to wheat seedlings were given in a plant growth chamber by raising its temperature to desired levels from 26 to 42 °C. All the heat treatments were given in the dark. The seedlings were exposed to 42 °C for 24 h, and samples (first leaves, coleoptiles and roots) were taken immediately after high-temperature exposure and at twenty-four hour intervals for measurement of the growth of wheat seedlings (maximum length of root, first leaf and coleoptile length), RWC, LP products (primary LP product, MDA, and secondary, CD) and EL.

Relative water content

The RWC is a useful indicator of the state of water balance of a plant; it is essential because it expresses the absolute amount of water which the plant requires to reach full artificial saturation. The RWC was measured on the wheat seedling organs following the method of Turner (1981). Three wheat organs (first leaf, coleoptile and roots) were examined in each replication. Fresh weight (FW) of plant tissue was determined immediately after harvest, and then wheat organs were allowed to float in distilled water until fully rehydrated. The wheat organs were weighted for turgid weight (TW). The turgid organs were dried in a hot oven at 80 °C to constant weight,

and dry weight (DW) was recorded. The RWC of the first leaves, coleoptiles and roots was calculated as:

$$RWC\ (\%) = (FW - DW) / (TW - DW) * 100.$$

Measurement of malondialdehyde content

The MDA content was determined by the thiobarbituric acid (TBA) reaction as described by Ali et al. (2005) with slight modifications. Leaves, coleoptiles and roots were homogenized in 0.1% trichloroacetic acid (TCA) (1/10, w/v) and centrifuged at 14,000 rpm for 15 min. After centrifugation, 1ml of supernatant was mixed with 2.5 ml 0.5% TBA in 20% TCA and incubated in hot water (95 °C) for 30 min. Thereafter, it was cooled immediately on ice to stop the reaction and centrifuged at 10,000 rpm for 30 min. Absorbance at 532 and 600 nm was determined, and MDA concentration was estimated by subtracting the non-specific absorption at 600 nm from the absorption at 532 nm using a molar extinction coefficient, 155 mM^{-1} cm^{-1}.

Measurement of conjugated diene content

Lipid peroxidation was determined by measuring the primary products of lipid peroxidation – conjugated diene formation (Recknagel, Ghoshal, 1966). For the preparation of measurement of dienic conjugate contents, leaf, coleoptile and root segments were pound in mortar with 1 M Tris – HCl buffer (pH 7.8) (1/5, w/v) and lipids were extracted by a hexane-isopropanol (1 : 1 v/v) mixture (9 ml per 1 ml of the sample) by shaking. After shaking, 1 ml H_2O was added to the mixture to stratify hexane and isopropanol phases. The measurement of dienic conjugate contents was made spectrophotometrically in hexane phase at 233 nm. The dienic conjugate contents in the sample were calculated according to 233 nm molar extinction coefficient to polyunsaturated fatty acids conjugated dienes, 2.2×10^5 M^{-1} cm^{-1}.

Determination of electrolyte leakage

The electrolyte leakage was determined as described before by Guo et al. (2006). Shoots of four seedlings were immersed in 15 ml of distilled water in a test tube overnight at room temperature. The initial conductivity was determined using a conductivity meter. The tubes were then placed in boiling water for 15 min and cooled to room temperature. Conductivity was again determined. The electrolyte leakage was calculated as the ratio of conductivity before boiling to that after boiling:

$$EL(\%) = (C_b - C_w) / (C_a - C_w) * 100,$$

where C_b is the ratio of conductivity before boiling, C_a is the ratio of conductivity after boiling, and C_w is the conductivity of deionized water.

Statistical analysis

Data are presented taking into consideration the standard error (SE) of three replicates. Results were analysed by one-way ANOVA to identify significant differences between the groups, and their significance levels ($p < 0.05$) were determined.

RESULTS

Relative water content and seedling growth

High-temperature stress decreased the RWC of wheat coleoptiles and leaves; the effect increased during the recovery period and depended on time of exposure (Fig. 1, 2). The reduction in the RWC ($p \leq 0.01$) was observed in the first leaf only after high-temperature treatment at the late stages of wheat seedlings development – 24 hours after the beginning of stress at the late stages of the first leaf development it was found to be decreased by 5% and it reached 45% at the end of the investigated period compared to control (Fig. 1*b*). The morphological features of seedlings revealed that a long-term high-temperature stress in wheat seedlings caused inhibition ($p < 0.001$) of the first leaf growth (Fig. 1). The length of the first leaf of experimental seedlings at the early stages of development immediately after exposure was inhibited by 23% (Fig. 1*a*) and at the late stages by 29% compared to control seedlings (Fig. 1*b*). As it is shown in Fig. 1, this effect was also present at the end of the investigated period (55% and 31%, respectively). The coleoptile showed greater reduction in the RWC than the first leaf – 24 hours after the beginning of stress at the early stages of wheat seedling development it was found to be decreased by 6.3%, two days after experiment water loss was 39% and it reached 49% at the end of the investigated period compared

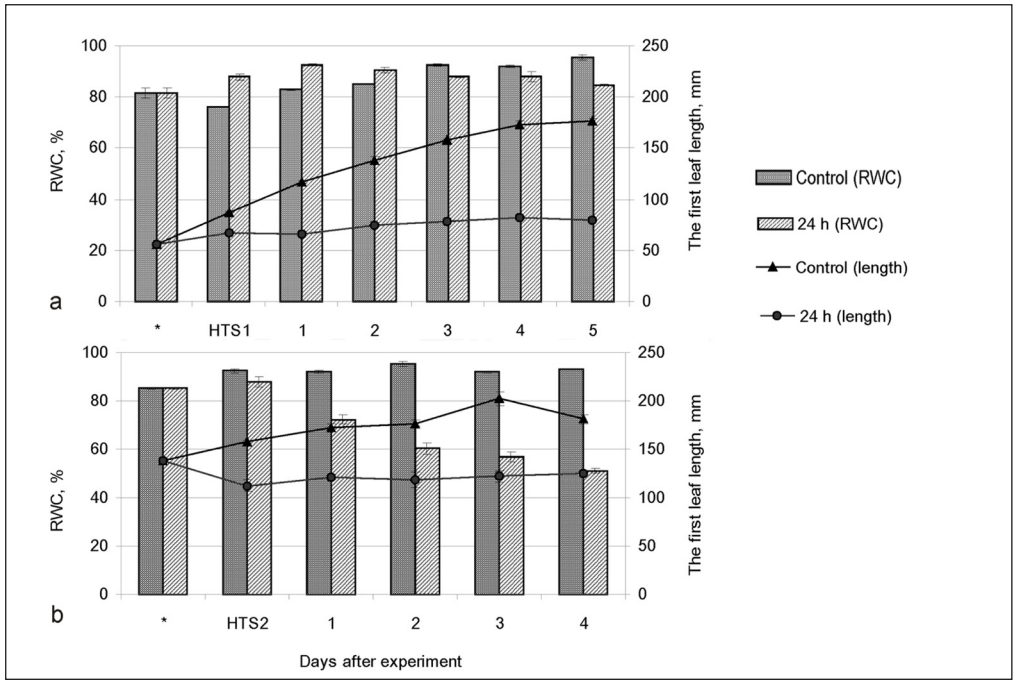

Fig. 1. Relative water content (RWC) and length of the first leaf at the early (a) and at the late (b) stages of wheat seedling development in response to 24-h high-temperature stress (HTS; 42 °C) (* - experiment starting date (4- or 7-day-old seedlings); HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

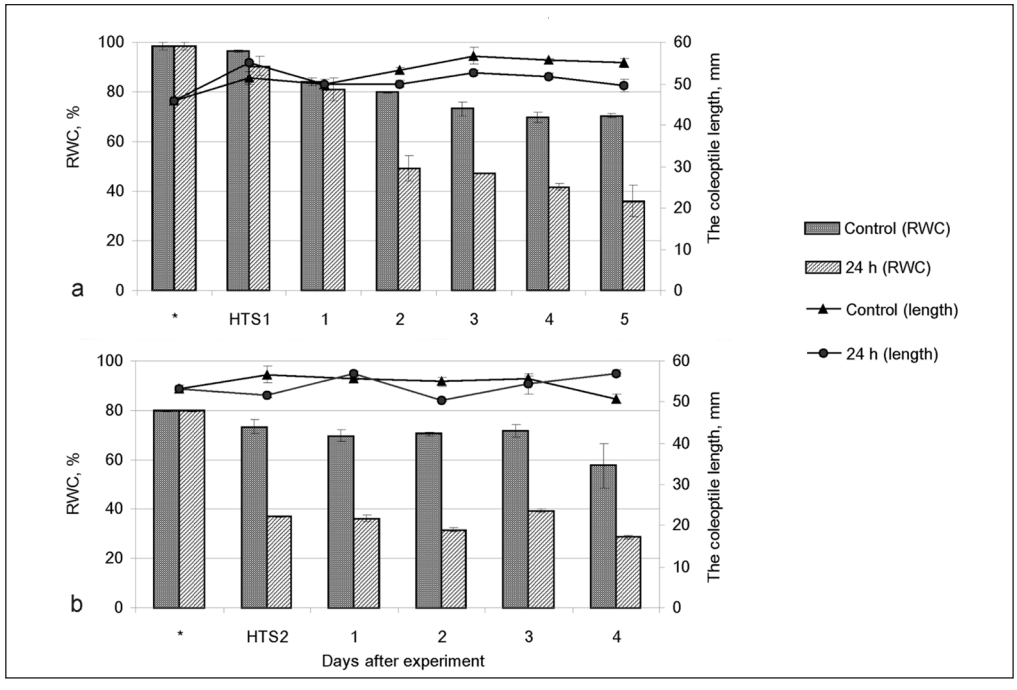

Fig. 2. Relative water content (RWC) and length of the coleoptile at the early (a) and at the late (b) stages of wheat seedling development in response to 24-h high-temperature stress (HTS; 42 °C) (* – experiment starting date (4- or 7-day-old seedlings); HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

to control ($p \leq 0.05$) (Fig. 2*a*). It was observed a statistically significant decrease ($p \leq 0.01$) in the RWC in the coleoptile at the late stages of coleoptile development. The RWC of the treated coleoptile was reduced by 50% immediately after high-temperature treatment and remained steady high during the recovery period compared to the control coleoptile (Fig. 2*b*). Although a long-term high-temperature exposure strongly inhibited the development of roots and first leaves, the heat-treated coleoptile was only insignificantly ($p \geq 0.05$) shorter than the control coleoptile (Fig. 2). High-temperature treatment provoked the statistically significant ($p \leq 0.001$) inhibition of the maximum root length – 24 hours after the beginning of stress at the early stages of root development it was found to be inhibited by 35% and it reached 61% at the end of the investigated period compared to control (Fig. 3*a*). The length of the treated root at the late stages of development was inhibited by approximately 40% immediately after high-temperature treatment ($p \leq 0.001$) and remained steady high during the recovery period ($p \leq 0.001$) compared to the control coleoptile (Fig. 3*b*). However, no significant changes in the RWC of the root were observed at any investigated stages of development (Fig. 3).

Malondialdehyde content

Figure 4 presents changes in the MDA content under control and heat stress conditions in the first leaf at the early and at the late stages of wheat seedling development. A significant decrease ($p \leq 0.001$) of the MDA content was observed in the first leaf immediately after high-temperature exposure at the early (48%) and at the late (32%) stages of seedling development. The MDA content was increased ($p \geq 0.05$) one day after exposure in the first leaf at the early stages of development by 24% compared to the MDA content immediately after stress and became similar to control (Fig. 4*a*), although the MDA content decreased considerably in the first leaf at the early stages of development during the third and fourth day

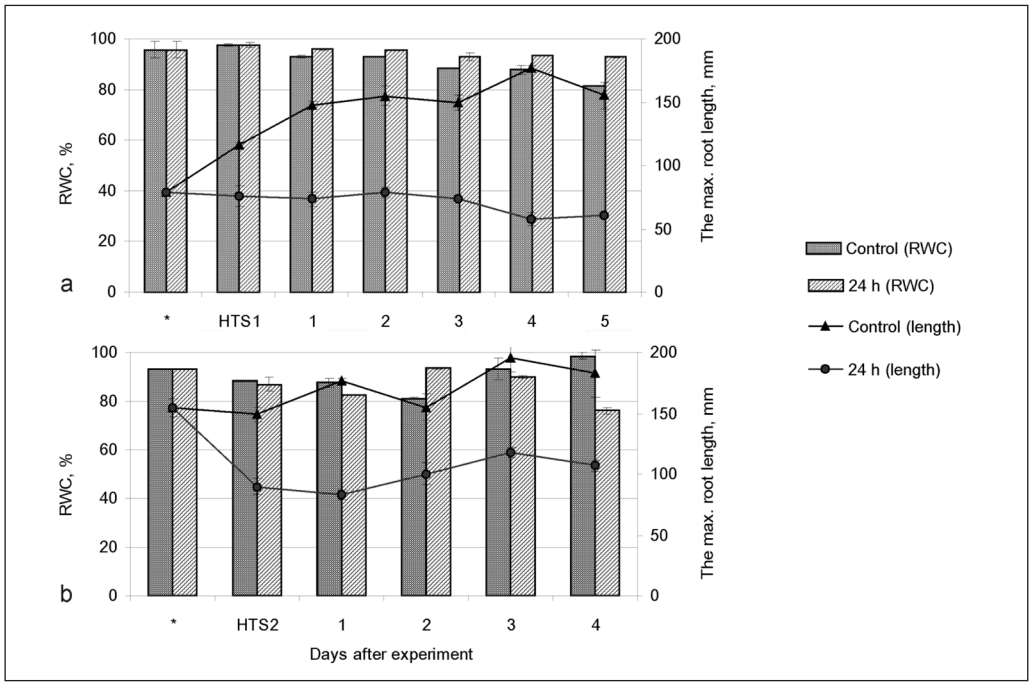

Fig. 3. Relative water content (RWC) and length of the root at the early (a) and at the late (b) stages of wheat seedling development in response to 24-h high-temperature stress (HTS; 42 °C) (* – experiment starting date (4- or 7-day-old seedlings); HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

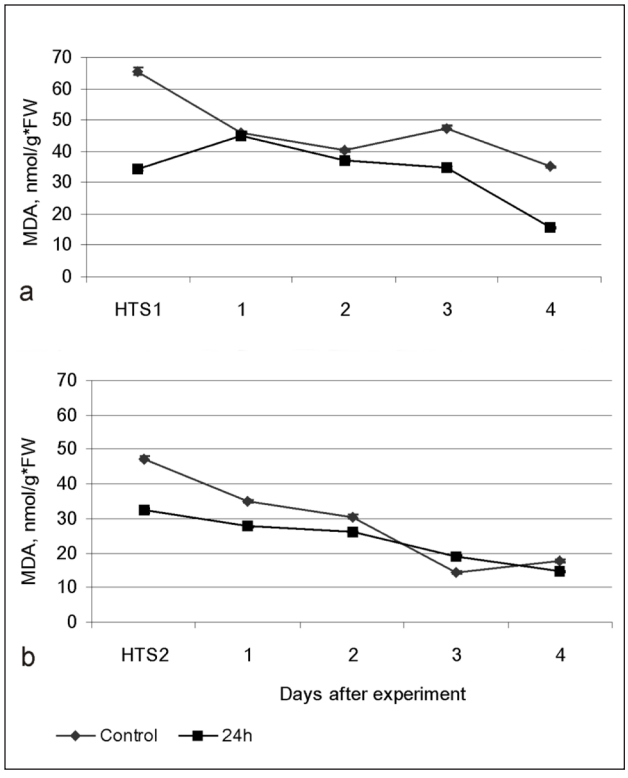

Fig. 4. MDA content (nmol/g*FW) in the first leaf at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

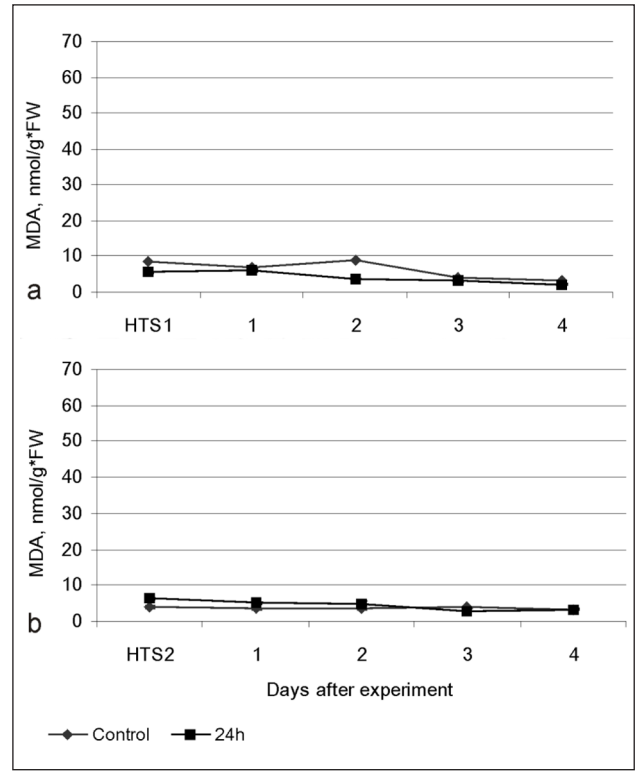

Fig. 5. MDA content (nmol/g*FW) in the coleoptile at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

after exposure in both control and experimental first leaf, however the MDA content was significantly ($p \leq 0.001$) higher in the control first leaf than in the heat-treated first leaf. There were no significant ($p \geq 0.05$) changes in the content of the MDA under heat stress two next days after high-temperature exposure in the first leaf at the late stages of development (Fig. 4*b*). The MDA content started to decrease slightly ($p \leq 0.05$) in the control first leaf, but it remained steady in the first heat-treated leaf at the late stages of seedling development.

Data revealed significant differences under heat stress as well as across different sampling times ($p \leq 0.01$) for the MDA content in the heat-treated coleoptile (Fig. 5). The MDA content in the heat-treated coleoptile was similar to control immediately after exposure at the early stages of development, then it started to increase and was steady high during the recovery period (57%) compared to control ($p \leq 0.001$) (Fig. 5*a*). The MDA content increased slightly with time in the heat-treated coleoptile at the late stages of seedling development – one day after exposure it was found to increase by 26% ($p \leq 0.01$) and it reached 39% ($p \leq 0.001$) at the end of the investigated period compared to control (Fig. 5*b*). The content of MDA remained steady in the control at all stages of seedlings development.

There was no significant ($p \leq 0.01$) change in the content of MDA under control or heat stress conditions in the root at all stages of development (Fig. 6), although during the first days after heat stress the MDA content decreased slightly at

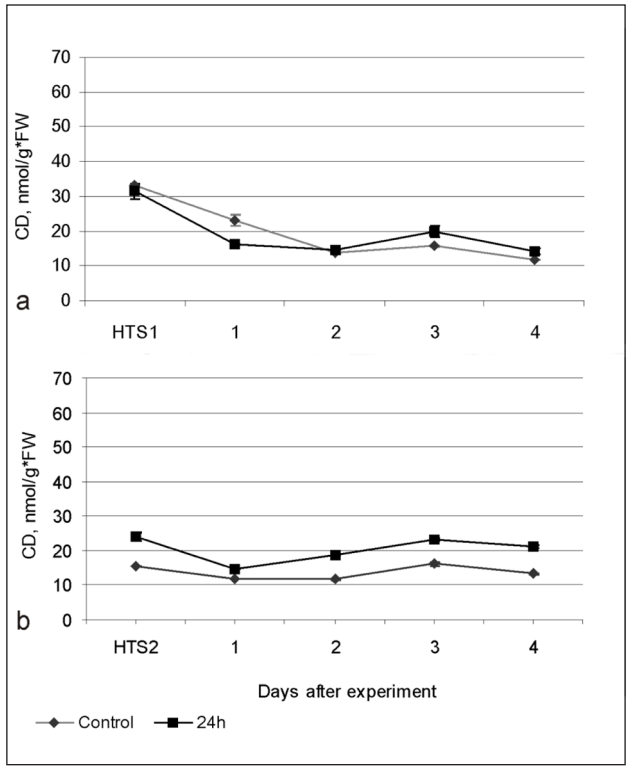

Fig. 6. MDA content (nmol/g*FW) in the root at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

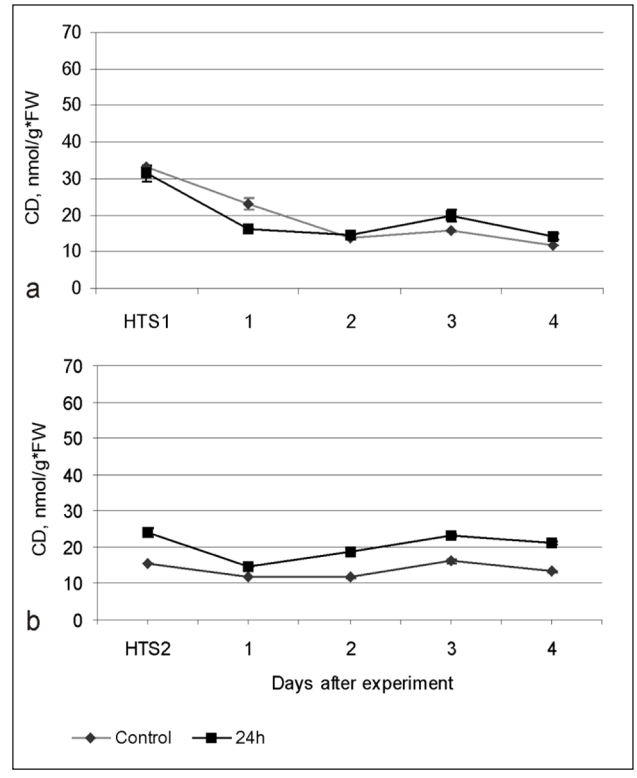

Fig. 7. CD content (nmol/g*FW) in the first leaf at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

the early stages of development, but it increased to a level approaching the control at later days (Fig. 6*a*).

Conjugated diene formation

The CD content decreased slightly in both control and experimental first leaves during first days after stress at the early stages of wheat seedling development (Fig. 7). The CD content was lower ($p \leq 0.05$) in the heat-treated first leaf than in the control first leaf at the early stages of development (5% immediately after heat stress; 30% one day after stress). The CD content in the heat-treated first leaf reached the control level two days after stress and remained steady in both (Fig. 7*a*). Under heat stress at the late stages of development, the CD content was higher in the heat-treated first leaf than in the control immediately after exposure (35%, $p \leq 0.05$) and remained steady high throughout the investigated period ($p \leq 0.01$) (Fig. 7*b*).

In contrast to the first leaf, the coleoptile of wheat seedlings showed significant ($p \leq 0.05$) differences compared to the control coleoptile (Fig. 8). The CD content decreased slightly in both control and experimental coleoptiles during first days after stress, however, the CD content was higher in the heat-treated coleoptile than in the control coleoptile at the early (23% immediately after heat stress; 37% one day after stress; $p \leq 0.05$) (Fig. 8*a*) and at the late (30% immediately after heat stress; 14% one day after stress; $p \leq 0.05$) (Fig. 8*b*) stages of development. The CD content started to increase two days after exposure

and showed a sharp increase three days after exposure in the heat-treated coleoptile at the early (70%, $p \leq 0.01$) and at the late (66%, $p \leq 0.05$) stages of seedlings development compared to control. After a sharp increase, a decrease in the CD content was noted four days after high-temperature exposure in the coleoptile at the early (30%, $p \leq 0.01$) and at the late (14%, $p \leq 0.05$) stages of seedling development, however, it was significantly higher than in the control coleoptiles (Fig. 8).

The CD content did not change in the root immediately after heat stress compared to control and it began to increase ($p \leq 0.01$) on the third day at the early (37%) and at the late (18%) stages compared to control (Fig. 9).

Electrolyte leakage

The EL was measured at the end of the heat-stress period and each 24-h period during four days after the experiment at the early and at the late stages of development in order to find differences in EL as affected by high temperature (42 °C). There was observed a steady high level of EL in the experimental first leaf throughout the investigated period compared to control seedlings (Fig. 10). Although a high level of EL was observed throughout the investigated period ($p \leq 0.05$), at the late stages membrane permeability in the first leaf was higher after high-temperature exposure (approximately 75%; Fig. 10*b*) than at the early stages (approximately 64%; Fig. 10*a*) compared to control.

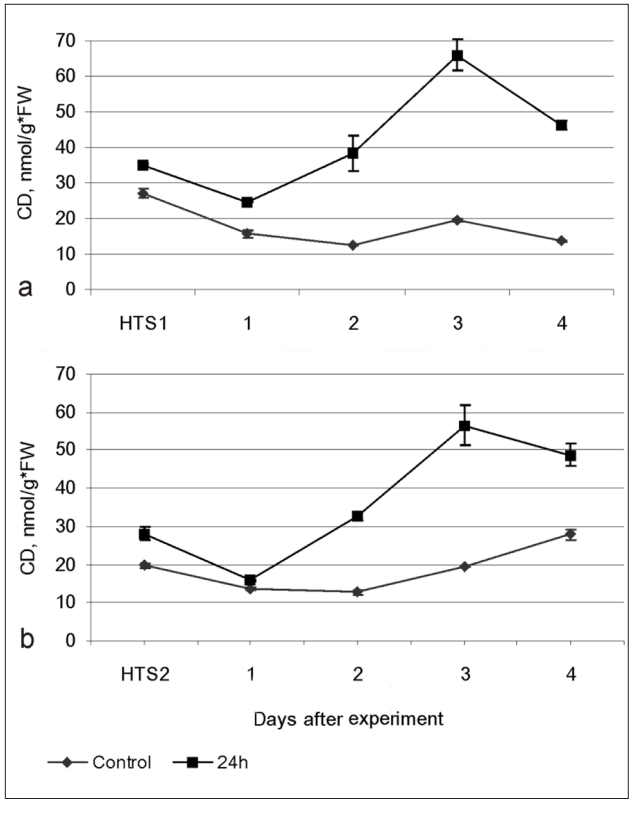

Fig. 8. CD content (nmol/g*FW) in the coleoptile at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

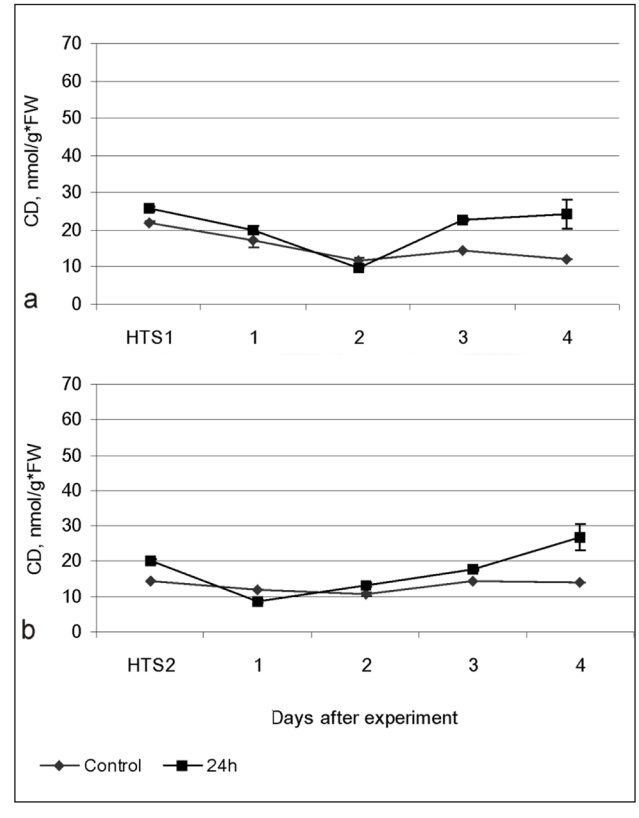

Fig. 9. CD content (nmol/g*FW) in the root at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

Identical increase ($p \leq 0.05$) of EL was observed in the heat-treated coleoptile at the early stages of development (Fig. 11*a*). EL increased by approximately 73% in the coleoptile at the early stages immediately after exposure and remained steady throughout the studied period compared to control. EL was greater in the heat-treated coleoptile at the late stages of seedling development (Fig. 11*b*) immediately after exposure ($p \leq 0.01$) and remained high two days after high-temperature exposure ($p \leq 0.05$), then EL started to decrease but it was higher than in the control coleoptile ($p \leq 0.05$).

EL was slightly higher ($p \leq 0.05$) under high-temperature treatment in the root of wheat seedlings immediately after experiment (9%) at the early stages of development and remained at the similar level next day after high-temperature exposure (Fig. 12*a*). The decrease of EL was observed during the second and third day after the experiment (15% and 36%, respectively) compared to the EL immediately after stress. However, EL in the root was greater at the late stages of development than at the early stages (Fig. 12*b*). There was observed a steady high level of EL in the heat-treated coleoptile at the late stages immediately after exposure (26%) and during the recovery period ($p \leq 0.05$) compared to the control coleoptile (Fig. 12*b*). One day after exposure EL was found to increase by 32%, the increase was 41% on the second and third day after high-temperature treatment and it reached 59% at the end of the investigated period.

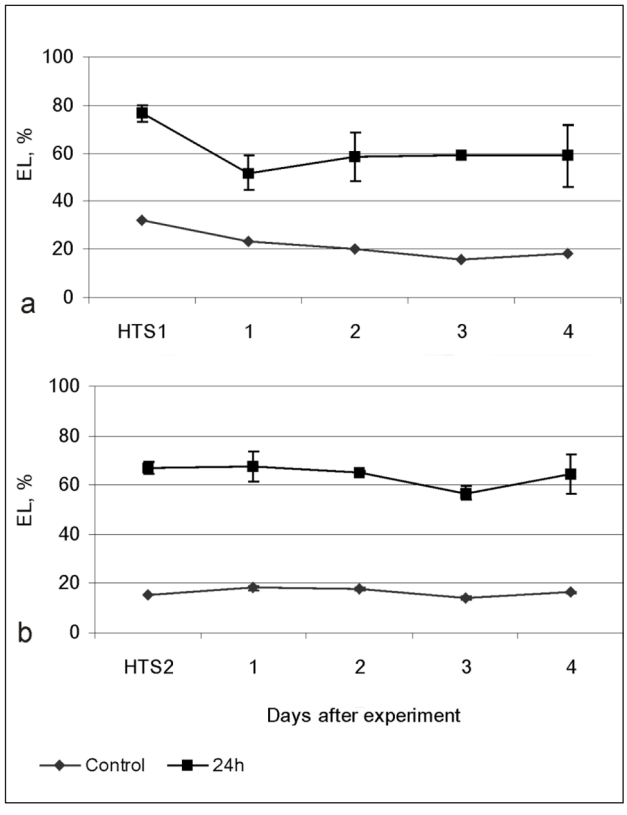

Fig. 10. Electrolyte leakage (EL) in the first leaf at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

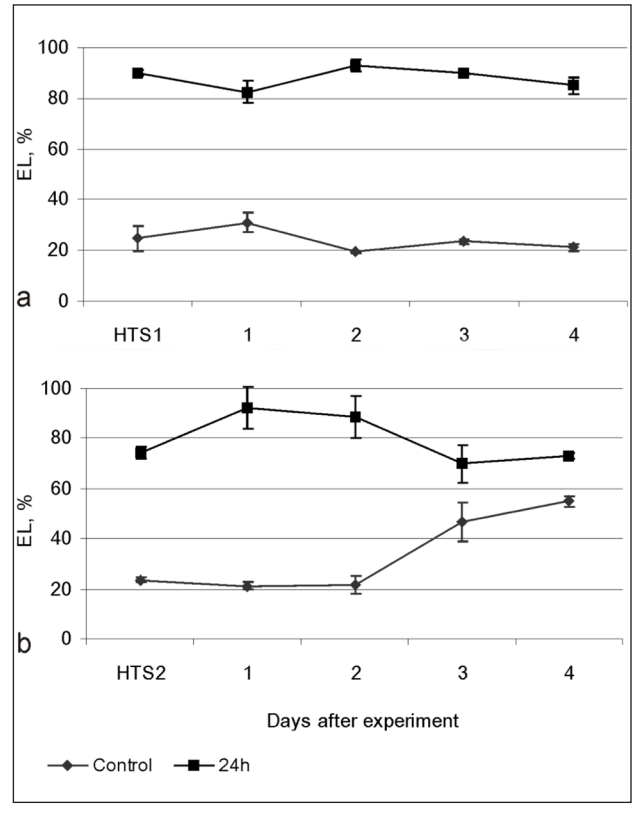

Fig. 11. Electrolyte leakage (EL) in the coleoptile at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

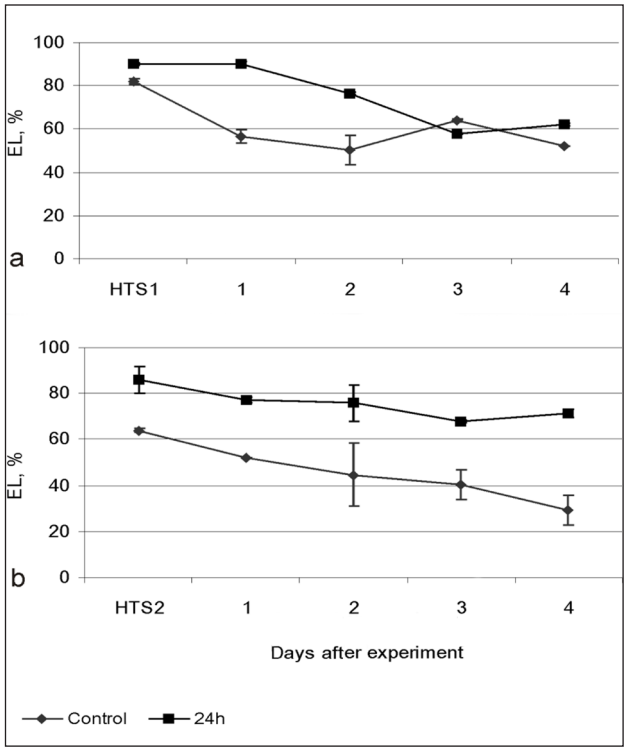

Fig. 12. Electrolyte leakage (EL) in the root at the early (a) and at the late (b) stages of development in response to 24-h high-temperature stress (HTS; 42 °C) (HTS1 (5-day-old seedlings) and HTS2 (8-day-old seedlings) – experiment finishing date). Bars indicate standard errors (n = 3) and missing error bars indicate that they are smaller than the symbol

DISCUSSION

Temperature is a critical factor in the plant environment, and it may play a significant role in growth and development (Źróbek-Sokolnik, 2012). Plant organisms are rarely affected by individual factors, and temperature stress is frequently associated with reduced water availability and, in consequence, oxidative stress. The inhibition of photosynthesis processes, damage of cell membrane, programmed cell death and protein synthesis after high-temperature treatment have been widely studied in separated cell compartments and rarely in whole plants or their organs (Xu et al., 2006); therefore, high-temperature treatment on functionally different organs of wheat seedlings was studied. Morphological, physiological and biochemical changes in the wheat root (high root temperature accelerates senescence of the entire plant (Ferguson et al., 1990)), coleoptile and first leaf (senescent and developing organs of wheat, respectively) were investigated to elucidate their relationship to injury from elevated temperature (42 °C). Our results suggest that high temperature injures plants, at least partially, by promoting senescence processes. The EL was the greatest in the heat-treated first leaf and this high level remained during the recovery period at all investigated stages. This concurs with work described by Zhou, Leul (1999), in which they used the same assay in rape. However, the MDA content decreased in the first leaf after high-temperature treatment, and this reduction further enhanced during the recovery period. The decrease in the CD content was also observed in the first heat-treated leaf at the early stages of development. Similar results were obtained previously in the pea leaves (Kurganova, 2001). Kurganova (2001) reported that a short-term high-temperature exposure led to a significant increase in LP products such as CD and hydroperoxides in leaves. However, the LP content decreased till the control level after a long-term high-temperature exposure. These results are in agreement with the RWC in the first leaf. The reduction in the RWC was observed in the first leaf only after high-temperature treatment at the late stages of wheat seedlings development, in spite of significant inhibition of the first leaf length at all investigated stages. The results suggest that the first leaf had the greater ability to avoid the water stress induced by high temperature (42 °C) than the coleoptile at the early stages of development. These results possibly suggest that the 4-day-old coleoptile showed a better protection mechanism against stressful conditions than the senescent coleoptile.

A significant decrease in the RWC of the stressed coleoptile was observed during the whole period of investigation. Our results are in agreement with those of Ivanov et al. (2001) who report that extreme temperature stresses (45 °C) are closely related to water deficit – due to reduced root water absorption and to a disruption of stomata control of leaf transpiration temperature, stressed plants suffer a strong water shortage. Most of the visible consequences of high temperature action are wilting and chlorosis of treated plants. The increase of the LP content in the coleoptile immediately after high-temperature stress and during the recovery

period is the evidence that the main influence of high temperature is due to the coleoptile at the early stages of seedling development. But the coleoptile getting older it loses the protective properties and the increase of LP in the heat-treated first leaf at the late stages of development was observed. Leakage points may also result from damage of membrane components. A high susceptibility of the wheat coleoptile to high temperature, evidenced by a strong increase in electrolyte leakage after heat treatment, was related with MDA and CD production, which indicate the occurrence of LP. Our data shows that oxidative damages, such as increase of CD production, occur in the coleoptile of wheat seedlings at all investigated stages after heating and that the level of damage increases over 4 days post heating. The MDA content was significantly higher ($p \leq 0.01$) in the coleoptile during the recovery period at the early stages of development compared to control. These results indicated that high-temperature exposure increases LP and EL, which are symptomatic of cellular damage. Similar results were obtained previously in *Arabidopsis* (Larkindale, Knight, 2002) and maize (Gong et al., 1998). Thus, seed germination is the most crucial and sensitive stage of a plant life cycle, particularly in the presence of environmental stresses (Çavusoglu, Kabar, 2010). However, in spite of an increase of oxidative activity in the coleoptile, i. e. increase of membrane permeability, MDA and CD content, a relative stability of the morphological features of the coleoptile (the coleoptile length) was observed. The coleoptile is a senescent organ and its defence systems are reduced, therefore such high susceptibility of wheat coleoptile to high temperature was observed.

As regards EL, although increased permeability occurred in the root of wheat seedlings at the early stages of seedling development submitted to high temperature, these organs presented a return to control values during the recovery period, suggesting the presence of reversible damages mainly resulting from changes in the biophysical properties of the membrane. Cellular membranes are considered the primary site of attack during heat injury (Wahid et al., 2007) and remain functional even in the presence of stress (Raison et al., 1980). Furthermore, no recovery occurred as regards EL in the root at the late stages of development, contrary to what was observed at the early stages. However, no changes as regard MDA content and no statistically significant increase of the CD content were observed in the root at all investigated stages compared to control and such level remained over 4 days post heating. It has been shown in a number of recent studies that long-term exposure to elevated temperatures suggests the ability for root acclimation (Gunn, Farrar, 1999; Atkin et al., 2000). A possible reason of the permanent increase of membrane permeability in the root at the late stages of development is change in the composition and structure of integral membrane proteins. It is a well known fact that high temperature modifies the composition and structure of membranes by weakening the hydrogen bonds and electrostatic interactions between polar groups of proteins within the aqueous phase of the membrane. Thus, integral membrane proteins tend to associate more strongly with the lipid phase. Disruption and damage to membranes alter their permeability and result in loss of electrolytes (Christiansen, 1978). The consensus is that electrolyte leakage reflects damage to cellular membranes and is an important factor in heat tolerance. The structure and stability of various membranes are, therefore, important during high-temperature stress (McDaniel, 1982). However, significant inhibition of the maximum root length was observed after high-temperature exposure.

CONCLUSIONS

In conclusion, obtained results demonstrate that the early seedling development stages in wheat (*Triticum aestivum* L.) are the most crucial and sensitive to high temperature conditions. Wheat organs show symptoms of oxidative stress at elevated temperature (42 °C), as indicated EL and the content of LP products (MDA and CD). The most substantial influence of high temperature was observed in a senescent organ, i. e. the coleoptile. However, no changes as regard the MDA content and no statistically significant increase of the CD content were observed in the heat-treated root in spite of an increase of EL. Our results showed that a relatively long (24 h) high-temperature exposure completely inhibited the growth of wheat seedlings and this effect was also present till the end of the experiment. High temperature results in the desiccation of the plant as well. Our results are in agreement with recent studies, which report that

once the temperature exceeds the maximum up to which growth takes place, plants enter a state of quiescence (Mavi, Tupper, 2004).

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KVIEČIO (*TRITICUM AESTIVUM* L.) DAIGO KAI KURIOS MORFOLOGINĖS, FIZIOLOGINĖS IR BIOCHEMINĖS SAVYBĖS PAVEIKUS AUKŠTA TEMPERATŪRA

S a n t r a u k a

Šiluminis šokas neigiamai veikia augalo augimą bei vystymąsi sukeldamas augalų oksidacinį stresą. Siekiant suprasti aukštos temperatūros šoko poveikį augalo augimui ir vystymuisi, būtina tirti viso augalo ir atskirų jo dalių fiziologiją bei morfologiją. Oksidacinio streso lygmuo buvo įvertintas pagal lipidų peroksidacijos produktų, tokių kaip malono dialdehidas ir konjuguoti alkadienai, pagausėjimą ir ląstelės membranos pralaidumą, kuris vertintas remiantis elektrolitų nutekėjimu skirtingose kviečių (*Triticum aestivum* cv. Harmonija) dalyse po 24 val. poveikio aukšta temperatūra (42 °C). Santykinis vandens kiekis lapų audiniuose buvo matuojamas siekiant įvertinti vandens trūkumą augaluose. Aukšta temperatūra neturėjo įtakos santykiniam vandens kiekiui šaknyje, tačiau vandens sumažėjo visų tirtų daigo vystymosi stadijų diegamakštėse ir vėlyvųjų vystymosi stadijų pirmajame lape ($p \leq 0{,}01$). Aukšta temperatūra per 24 val. visiškai nuslopino pirmojo lapo ir šaknų augimą ($p \leq 0{,}001$) ir sukėlė pirmojo lapelio ir diegamakštės džiūvimą. Akivaizdu, kad kviečių daigų šaknys yra mažiau jautrios šiluminiam šokui nei pirmasis lapelis ir diegamakštės. Aukšta temperatūra reikšmingai padidino lipidų peroksidaciją kviečių daigų diegamakštėse, tačiau šaknyse ši buvo panaši į kontrolę visose tirtose vystymosi stadijose. Reikšmingas lipidų peroksidacijos produktų pagausėjimas ($p \leq 0{,}01$) buvo nustatytas kviečių daigų vystymosi vėlyvųjų stadijų pirmajame lapelyje. Toks aukštesnis lipidų peroksidacijos produktų lygis padidino ląstelių membranos pralaidumą. Tyrimas atskleidė, kad aukštos temperatūros specifinio poveikio šaknims pasekmė yra padidėjęs elektrolitų nuotėkis, tačiau temperatūra beveik nepaveikia lipidų peroksidacijos procesų.

Raktažodžiai: lipidų peroksidacija, elektrolito nuotėkis, santykinis vandens kiekis, šiluminis šokas, oksidacinis stresas, kviečių daigas