THE EFFECT OF ABIOTIC STRESSES ON THE RATE OF PHOTOSYNTHESIS, TRANSPIRATION AND WATER USE EFFICIENCY (WUE) IN WHEAT PLANTS DURING ONTOGENY*

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The rate of photosynthesis, transpiration and water use efficiency was studied in the wheat variety Mironovská in the years 2001 to 2002 in the greenhouse under controlled conditions. Plants were cultivated in four variants of the trial: control, drought, low soil pH and combination of drought and low soil pH. Physiological characteristics were measured gasometrically using the apparatus LCA-4 in the following developmental phases: 22.DC, 30.DC, 50.DC, 61.DC and 83.DC. It is apparent from the results obtained that the rate of photosynthesis in all variants grew during ontogeny to phase 61.DC. The decrease of photosynthesis was recorded after this phase. Statistically significant decrease of photosynthesis appeared in the variant with combination of two stress factors compared with the control variant. The variant drought and low soil pH (DpH) reduced the rate of photosynthesis compared with the control by 45.26%. Immediate rate of transpiration of wheat plants grew in both experimental years to phase 40.DC. Statistically significant decrease of transpiration occurred in phase 50.DC. If we evaluate the effect of variants of the trial as affected the rate of wheat transpiration, it can be said that the rate of transpiration significantly fell in the variant drought and combination of drought and low soil pH in 2001. In 2002 significant decrease on the level of significance $\alpha = 0.05$ can be recorded in all stressed variants compared with the control variant. The WUE values obtained grew to the anthesis and then again a fall could be recorded. The variant drought and low pH in mutual combination decreases the values of water use efficiency (WUE) statistically significantly. In conclusion it can be said that the rate of photosynthesis, transpiration together with water use efficiency are negatively affected by activity of unfavourable physical and chemical properties of environment. The selected abiotic stresses, such as mutual combination of drought and low pH, decreased significantly all studied indicators compared with the control variant.

wheat; *Triticum aestivum*; photosynthesis; transpiration; water use efficiency (WUE)

INTRODUCTION

The present climatic changes bring with them distinct fluctuations of temperature and also relatively unevenly, irregularly and randomly distributed precipitation during growing period of plants. Regarding these facts, even longer drought period cannot be eliminated. The study of adaptation of plants of water deficit is more and more topical, particularly respecting the fact that regular deficit of water occurs at the present time in the period of main vegetation in majority of field crops in our climatic area.

The deficit of water leads to fall of uptake of nutrients, and to limitation of basic physiological processes of plants too. Cornic, Briantais (1991) and Saccardy (1993, 1996) present that photosynthetic apparatus is stable under the conditions of developing water stress. Generally, it can be said that in the case of deepening water deficit the rate of the growth of assimilation of leaf area and limitation of the rate of CO_2 (Cornic et al., 1992; Genty et al., 1990; Lawlor, 1995) fall the first of all.

Except for the deficit of water, lower pH of soil also participates in reduction of plant production. Acid soils are one of serious problems of agricultural production that includes the territory of the central Europe and other continents as well. Decrease of pH values is affected by acid rains, utilisation of physiologically acid fertilisers and lower doses of supplied calciferous fertilisers. The Czech Republic is directly faced to this problem because as reported Vaněk et al. (1995), the percentage of arable land with unfavourable soil reaction amounts to 25%. In many regions of the Czech Republic acidity of soils seriously reduces the growth of plants and their metabolic processes, especially photosynthesis. For example Meyer, Anderson (1952) and Sherman et al. (1919) studied the action of low soil pH as affected the photosynthesis. They reported that the decrease of photosynthesis under low soil pH is caused by lower activity of enzymes.

The effect of abiotic stresses in winter wheat varieties is manifested particularly in the growth of lower weight of plants and in decreased yield. There is a significant effect of different abiotic stresses on basic physiological

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indicators of plant yield production. Negative impact of physical and chemical properties on environment affects above all the exchange of gases in plants, that is photosynthesis followed also by transpiration. Both these factors in their final consequence together with respiration decide with other external factors upon the level and quality of a product obtained. Therefore, we decided in our study to follow the effect of two selected stress factors as affected photosynthesis and transpiration of plants, including effectiveness of water use efficiency during ontogeny of wheat plants.

MATERIAL AND METHODS

In the years 2001 to 2002 selected physiological characteristics in wheat variety Mironovská were studied under controlled conditions in the greenhouse.

Wheat plants were cultivated in pots with homogenised soil and balanced level of nutrients under intensity of irradiation 700 $\mu mol.m^{-2}.s^{-1}$. Average temperature of environment in grain-filling period 23 °C at the day and night was 15 °C under controlled conditions (K). Watering was uniform and was based on 31% volume of soil moisture what represents the value of water soil potential – 0.12 MPa, at pH 7.0.

The second variant of the trial included low soil pH 4.5 (pH). Repeated watering by 0.2% sulphuric acid induced low pH 4.5. The third variant of the trial represented the variant with limited watering – drought (D). Drought was simulated by reduced watering to the level 17% of the volume of soil moisture, i.e. water soil potential – 1.28 MPa. Irrigation in the variant drought was accomplished always after reaching the point of wilting and soil moisture was always lower even after watering. Irrigation was controlled on the basis of the results presented by the apparatus VIRIB. The device VIRIB is manufactured by Litschmann, Czech Republic. The action of drought was monitored from the phase 30.DC to the harvest. The last variant included the combination of the variants of drought and low soil pH (DpH).

Instantaneous rate of photosynthesis and transpiration was measured in wheat plants in selected growth phases: 22.DC, 30.DC, 40.DC, 50.DC, 61.DC and 83.DC.

Instantaneous rate of photosynthesis and transpiration was measured gasometrically in open system by the apparatus LCA-4. The device LCA-4 is manufactured by Analytical Development Company Ltd., Caring for the Environment, Great Britain. The exclusive importer of this device into the Czech Republic is the company Eijkelkamp, Agrisearch from the Netherlands.

The principle of this method consists in detection of the change in concentration of carbon dioxide in the atmosphere surrounding assimilating object (Šesták, Čatský et al., 1966). The calculation of WUE (water use efficiency) is the component of the results. After Boyer (1996) the WUE is a relationship between intake of CO_2 and amount of transpired water. WUE has physical measurement 10^{-3}.

The results obtained were statistically evaluated using the computer programme Statistica version 6.0, statistical analysis ANOVA on the significance level $\alpha = 0.05$.

RESULTS AND DISCUSSION

It can be seen from the results obtained that the rate of photosynthesis in all variants grew during ontogenesis up to the phase 61.DC. The fall of photosynthesis was recorded after this phase. The lowest rate of photosynthesis was measured on the third upper leaf at the beginning of wheat shooting (phase 22.DC), when in 2001 photosynthesis was 4.79 $\mu mol\ CO_2.m^{-2}.s^{-1}$ and in the following year it was 4.92 $\mu mol\ CO_2.m^{-2}.s^{-1}$. The rate of photosynthesis has its maximum during ontogenesis of wheat in phase 61.DC. Average rate of photosynthesis was 13.25 $\mu mol\ CO_2.m^{-2}.s^{-1}$ (2001) in this phase and 10.59 $\mu mol\ CO_2.m^{-2}.s^{-1}$ (2002). In the studied variety Mironovská in this ontogenetic period in 2001 the rate of photosynthesis ranged between 7.65 $\mu mol\ CO_2.m^{-2}.s^{-1}$ (variant DpH) and 15.57 $\mu mol\ CO_2.m^{-2}.s^{-1}$ (control variant). In 2002 the rate of photosynthesis ranged between 7.44 $\mu mol\ CO_2.m^{-2}.s^{-1}$ (variant DpH) and 12.14 $\mu mol\ CO_2.m^{-2}.s^{-1}$ (control variant). From the phase of beginning of anthesis (61.DC) the fall of the rate of photosynthesis was recorded up to the phase of wax maturity (83.DC). In the period of ripening in 2001 average intensity of photosynthesis was 10.52 $\mu mol\ CO_2.m^{-2}.s^{-1}$ and in the following year 9.54 $\mu mol\ CO_2.m^{-2}.s^{-1}$. Statistically increase of the values of the rate of photosynthesis from the beginning of ontogeny to anthesis of both experimental years is in Fig. 3. The results obtained correspond to the conclusions made by Genkel (1969), Rea, Cale (1991) and Hejnák et al. (1998).

A marked increase of the rate of photosynthesis is apparent from the beginning of the studied period (phase 22.DC) to anthesis, then fall follows, as it can be seen from Fig. 1. This trend can be recorded in all studied variants of the trial. The greatest increase of the rate of photosynthesis in the period from phase 22.DC to phase 61.DC can be found in the variant pH (pH) when instantaneous photosynthesis increased by 8.68 $\mu mol\ CO_2.m^{-2}.s^{-1}$ on average of both years. On the contrary, the lowest increase of the rate of photosynthesis was recorded in the variants drought and low pH (DpH). Photosynthesis in this variant increased on average by 4.06 $\mu mol\ CO_2.m^{-2}.s^{-1}$. Relatively lower increase of the rate of photosynthesis in both experimental years recorded in this variant compared with the other variants is evidently given by its low values during the whole ontogeny, when the plants are exposed to two stress factors simultaneously. The period of ontogeny was markedly shortened also in this variant.

If we compare the values of the rate of photosynthesis of wheat during heading with e.g. spring barley; it can be said that the rate of photosynthesis is similar in both crops. This statement can be proved by the study of Hejnák et al. (1998). After these authors the rate of

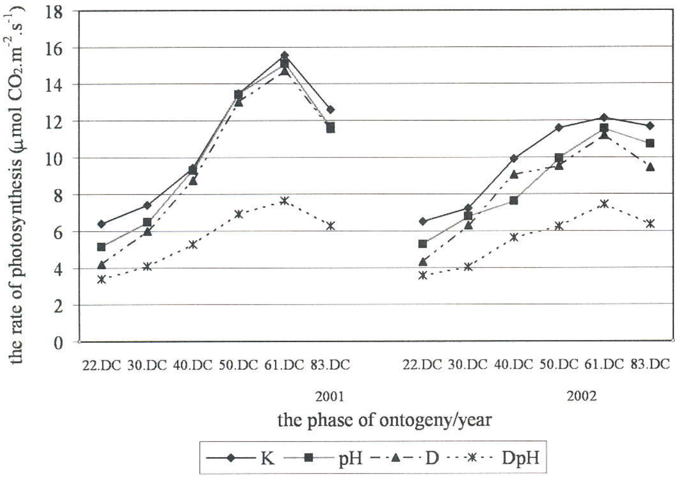

Fig. 1. The rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$) of winter wheat plants during ontogeny

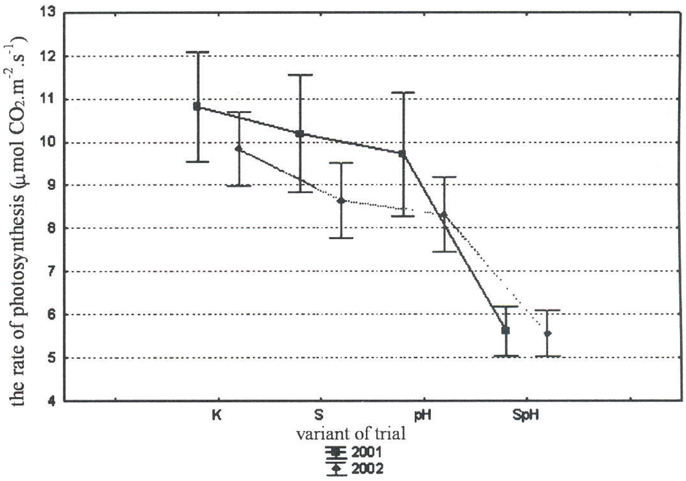

Fig. 2. The graph of average photosynthetic rate, average; terminal: Average – 95 suprange of responsibility, Average + 95 suprange of responsibility

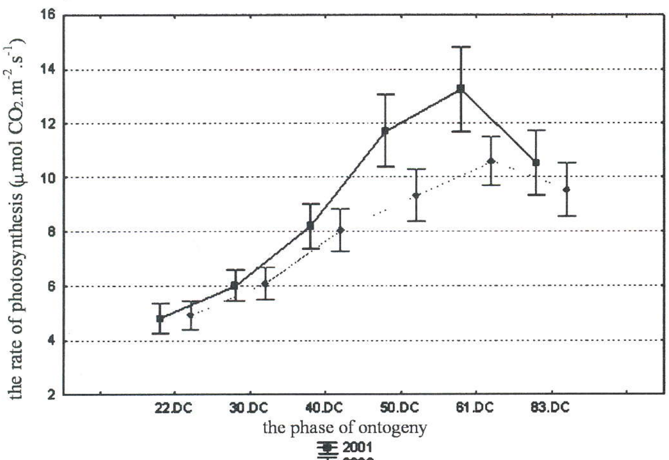

Fig. 3. The graph of average photosynthetic rate, average; terminal: Average – 95 suprange of responsibility, Average + 95 suprange of responsibility

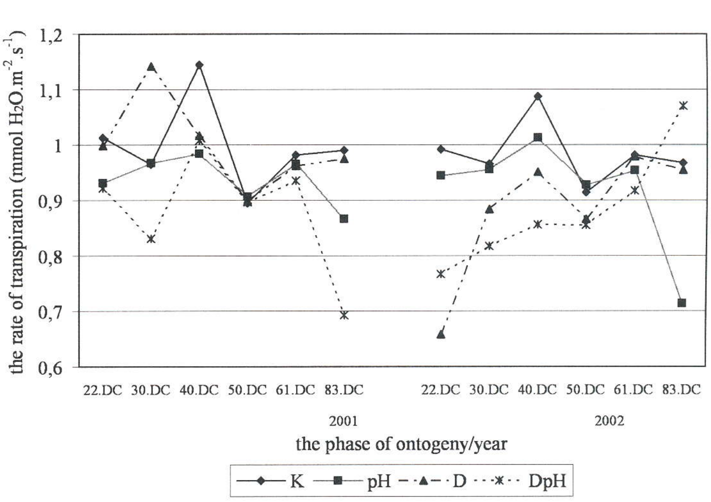

Fig. 4. The rate of transpiration (mmol $H_2O.m^{-2}.s^{-1}$) of winter wheat plants during ontogeny

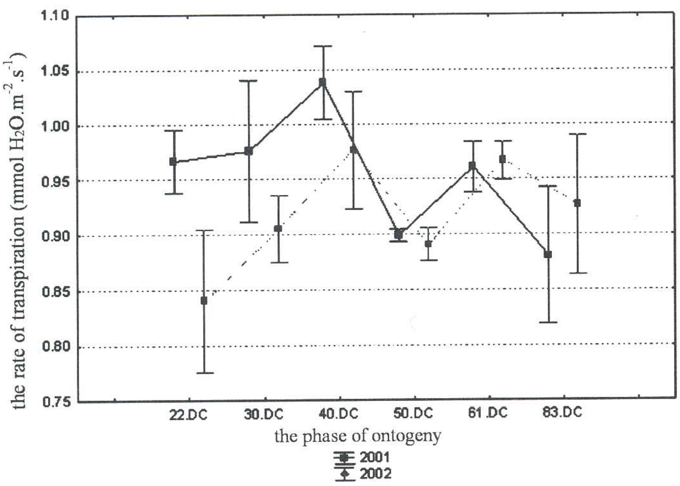

Fig. 5. The graph of average transpiration rate, average; terminal: Average – 95 suprange of responsibility, Average + 95 suprange of responsibility

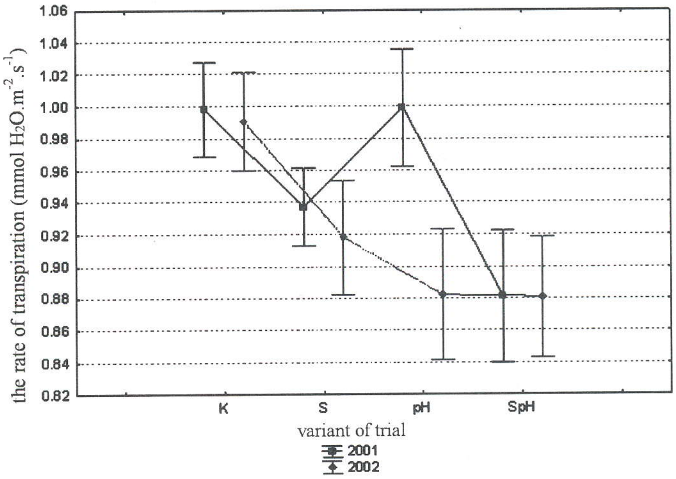

Fig. 6. The graph of average transpiration rate, average; terminal: Average – 95 suprange of responsibility, Average + 95 suprange of responsibility

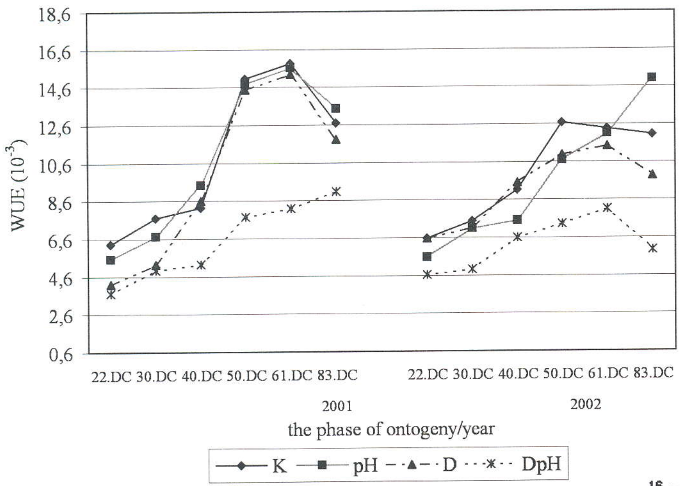

Fig. 7. WUE (10^{-3}) of winter wheat plants during ontogeny

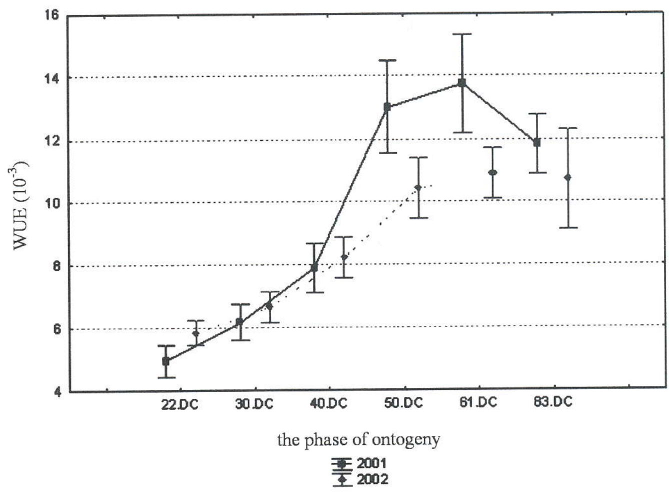

Fig. 8. The graph of average of WUE, average; terminal: Average – 95 suprange of responsibility, Average + 95 suprange of responsibility

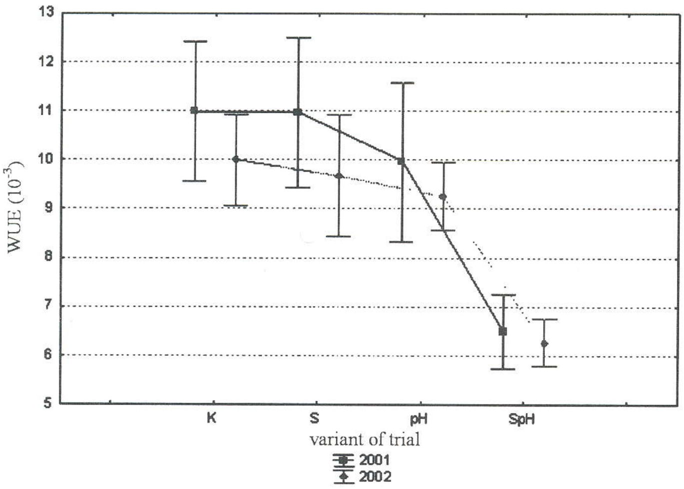

Fig. 9. The graph of average of WUE, average; terminal: Average – 95 suprange of responsibility, Average + 95 suprange of responsibility

photosynthesis of spring barley fluctuated in dependence on the dose of nitrogen fertilisation and soil pH in the phase of shooting between 3.50 and 10.47 μmol $CO_2.m^{-2}.s^{-1}$.

Moreover, statistically significantly decrease of photosynthesis follows from graph 1 in the variant with combination of two stress factors compared with the control variant (Fig. 2). The variants of drought and low soil pH (DpH) reduced the rate of photosynthesis compared with the control by 45.26%. Statistically significantly difference was not recorded in statistical evaluation of remaining variants of stresses, though these variants had lower photosynthesis compared with the control variant. Decrease in the rate of photosynthesis in the variants drought and low pH is apparently given by the fact that stomata are closing under the stress conditions, and therefore CO_2 uptake is falling, as reported Nilsen and Orcutt (1996) or Janáček (1997). Zámečníková (2000) came to the similar result in winter wheat plants cultivated under drought conditions.

The effect of the years on the rate of photosynthesis was confirmed because in 2001 photosynthesis was higher than in 2002. Differences between two years are demonstrated in Figs. 2 and 3. Differences between the years will be probably caused by the length and the rate of falling radiation in the period under study.

The rate of transpiration of the third upper leaf of wheat during ontogeny was another measured characteristics. The taken values of transpiration are given in Fig. 4.

Instantaneous rate of transpiration of wheat plants grew in both experimental years to phase 40.DC, when an average was 1.01 mmol $H_2O.m^{-2}.s^{-1}$. Statistically significantly highest value of the rate of transpiration during the whole ontogenesis was measured in the given phase of organogenesis. Statistically significant decrease of transpiration appeared in phase 50.DC to the average value 0.89 mmol $H_2O.m^{-2}.s^{-1}$, as presented in Fig. 5. Increased transpiration can be recorded to the beginning of anthesis (0.96 mmol $H_2O.m^{-2}.s^{-1}$) and a mild decrease of taken values (0.90 mmol $H_2O.m^{-2}.s^{-1}$) to the period of early wax maturity.

It is interesting that average rate of transpiration was identical at the beginning of tillering and in the period of the beginning of anthesis. The measured values of the rate of wheat transpiration were identical with those reported by Zámečníková (2000) for spring barley. This author in her study recorded higher values for wheat cultivated under the conditions of drought and irrigation than those taken for the variety Mironovská. This difference is apparently caused by different genetic basis of the studied plant material.

In 2001 the values of the rate of transpiration were ranging between 0.69 mmol $H_2O.m^{-2}.s^{-1}$ (variant DpH, phase 83.DC) in the variety Mironovská and 1.14 mmol $H_2O.m^{-2}.s^{-1}$ (control variant, phase 40.DC). In the following year the measured values ranged between 0.71 mmol $H_2O.m^{-2}.s^{-1}$ (variant D, phase 83.DC) and 1.09 mmol $H_2O.m^{-2}.s^{-1}$ (control variant, phase 40.DC). The values taken for the rate of transpiration can be found within the values that are reported by Hnilička (1999).

If we evaluate the effect of variants of wheat transpiration, it can be said that the rate of transpiration decreased significantly in 2001 in the variant drought and the combination of drought and low soil pH (Fig. 6). The rate of transpiration decreased in the variant drought compared with the control variant by 0.06 mmol $H_2O.m^{-2}.s^{-1}$ and by 0.12 mmol $H_2O.m^{-2}.s^{-1}$ in the case of the variants drought and low pH. Significant decrease was recorded in 2002 on the level of significance $\alpha = 0.05$ in all stressed variants compared with the control variant. The rate of transpiration decreased most significantly in the variants drought and low pH (DpH) and the least in the variant drought (D). This decrease in calculation for percentage was in the first mentioned variant 10.56% and in the second variant 6.80%. Spring barley under drought conditions showed lower transpiration in irrigated variant compared with dry variant (Zámečníková, 2000). The variety Mironovská decreased the rate of transpiration identically in drought conditions like e.g. the variety Maris Marksman, that lowered transpiration by 10.3% (Zámečníková, 2000). Compared with the variety Chlumecká 12, the variety Mironovská lowers rate of transpiration less, because the variety Chlumecká 12 in drought conditions reduces transpiration by 18.3 % (Zámečníková, 2000).

Significant effect of the year on the rate of transpiration of wheat plants follow from Figs 5 and 6. An identical pattern of the rate of transpiration during ontogeny in both experimental years can be seen from Fig. 5.

Water use efficiency (WUE) is one of important physiological indicators of adaptability of plants against unfavourable conditions. WUE values were calculated as a ratio of assimilation to transpiration, that is the ratio of taken CO_2 and transpired water. In evaluating of this parameter we started from a prerequisite that was reported – higher the WUE, the better utilisation of water per assimilation unit.

The WUE values obtained are demonstrated in Fig. 7. It is evident from it that during ontogeny of wheat WUE is increasing to the anthesis and then again a decrease can be observed. This trend can be monitored during the both experimental years when phases 50.DC and 61.DC are not significantly different from each other. The pattern of WUE curve during ontogeny is different in both experimental years, when in 2001 the growth between phases 50.DC and 61.DC is steeper than in the same period in 2002 (Fig. 8). From onset of anthesis a mild decrease of calculated WUE values can be recorded. Statistically significantly lowest WUE values were recorded in phase 22.DC, when its average value was $5.39.10^{-3}$ and on the contrary, the highest WUE value was in phase 50.DC – $11.72.10^{-3}$ and in phase 61.DC it was $12.37.10^{-3}$. The values obtained are in congruency with Larcher (1995), who reported that the WUE value was also affected, among other by the developmental stage of plant.

The WUE values ranged between $3.69.10^{-3}$ in 2001, in the variants drought and low pH, in phase 22.DC and $15.85.10^{-3}$ in the control variant and in phase 61.DC. In the following year the WUE values taken were again lowest at the beginning of tillering in the variants drought and low pH ($4.66.10^{-3}$) and the highest in phase 83.DC in the variant low pH ($15.01.10^{-3}$). The WUE values taken are higher than those presented by Zámečníková (2000) in her study. She reports maximum WUE value 10.10^{-3}. This discrepancy is probably given by the fact that the given characteristics was studied during the whole ontogeny of wheat plants, and not only in the selected of development.

If we evaluate the water use efficiency according to the different variants of the trial (Fig. 9), it can be said that statistically significant difference is only between the variants drought and low pH compared with remaining variants of trial. Significant decrease of the value of water use efficiency could be recorded in the both experimental years. A decrease of calculated WUE values can be found in the variants drought and low pH, however, but this decrease is not statistically significant compared with the control variant. It is apparent from the results that stress factors, above all in mutual combination, reduce significantly the water use efficiency compared with the control variant. Therefore, it can be said that the variety Mironovská changes the WUE values statistically significantly after activity of abiotic stresses. The variety Karlík responses in a similar way only under drought as reported Zámečníková (2000) in her study.

In conclusion it can be said that the rate of photosynthesis, transpiration and water use efficiency are negatively affected by unfavourable physical and chemical properties of environment. Selected abiotic stresses, such as mutual combination of drought and low pH, decreased significantly all studied indicators compared with the control variant.

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Vliv vybraných abiotických stresů na intenzitu fotosyntézy, transpirace a účinnost využití vody (WUE) u rostlin pšenice v průběhu vegetace.

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V letech 2001 až 2002 byly ve skleníku v regulovaných podmínkách sledovány intenzita fotosyntézy a transpirace a efektivnost využití vody u odrůdy pšenice seté Mironovská. Rostliny byly pěstovány ve čtyřech variantách pokusu: kontrola, sucho, nízké pH půdy a kombinace sucha a nízkého pH půdy. Fyziologické charakteristiky byly měřeny gazometricky přístrojem LCA-4 v těchto vývojových fázích: 22.DC, 30.DC, 40.DC, 50.DC, 61.DC a 83.DC. Ze získaných výsledků je patrné, že intenzita fotosyntézy u všech variant narůstala v průběhu ontogeneze až do fáze 61.DC. Po této fázi byl již zaznamenán pokles fotosyntézy. Ke statisticky průkaznému snížení fotosyntézy došlo u varianty s kombinací dvou stresových faktorů v porovnání s variantou kontrolní. Varianta sucho a nízké pH půdy (DpH) snížila intenzitu fotosyntézy při porovnání s kontrolou o 45,26 %. Okamžitá intenzita transpirace rostlin pšenice narůstala v obou pokusných letech do fáze 40.DC. Ve fázi 50.DC došlo ke statisticky významnému poklesu transpirace. Jestliže hodnotíme vliv variant pokusu na intenzitu transpirace pšenice, můžeme říci, že k průkaznému snížení intenzity transpirace došlo v roce 2001 u varianty sucho a u kombinace sucha a nízkého pH půdy. V roce 2002 bylo zaznamenáno průkazné snížení na hladině významnosti $\alpha = 0,05$ u všech stresovaných variant ve srovnání s variantou kontrolní. Získané hodnoty WUE narůstaly až do období kvetení a poté byl opět zaznamenán pokles. Statisticky průkazně snižuje hodnoty efektivnosti využití vody (WUE) varianta sucho a nízké pH ve vzájemné kombinaci. Závěrem je možné konstatovat, že intenzita fotosyntézy a transpirace, ale i efektivnost využití vody jsou negativně ovlivňovány působením nepříznivých fyzikálně-chemických vlastností vnějšího prostředí. Vybrané abiotické stresy, jako je vzájemná kombinace sucha a nízkého pH, průkazně snížily v porovnání s kontrolní variantou hodnoty všech sledovaných ukazatelů.

pšenice; *Triticum aestivum*; fotosyntéza; transpirace; účinnost využití vody; WUE

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