THE EFFECT OF ABIOTIC STRESSES ON RATE OF PHOTOSYNTHESIS AND FORMATION OF DRY MATTER IN WINTER WHEAT PLANTS*

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The rate of photosynthesis and dry matter was studied in the wheat varieties Estica, Ebi and Mironovská 808 in the greenhouse under controlled conditions. Plants were cultivated in four treatments of the trial: control, drought, low pH and combination of drought and soil pH. The photosynthesis and accumulation of dry matter are negatively affected by abiotic stresses. The variety Ebi had the lowest photosynthesis (9.13 μmol $CO_2.m^{-2}.s^{-1}$) and variety Estica had the highest value (9.40 μmol $CO_2.m^{-2}.s^{-1}$). The average weight of root and shoot in Mironovská 808 was the highest (0.92 g and 5.73 g) and in the variety Estica was the lowest (0.87 g and 5.58 g).

abiotic stresses; wheat; *Triticum aestivum* L.; rate of photosynthesis; dry matter

INTRODUCTION

The development of a mature plant from a single fertilized egg requires a precise and highly ordered succession of events. The fertilized egg cell, or zygote, divides, grows, and differentiates into increasingly complex tissues and organs. At the end, these events give rise to the complex organization of a mature plant that flowers, bears fruit, senesces, and eventually dies. Development is an umbrella term, referring to the sum of all of the changes that an organism goes through in its life cycle – from germination of the seed through growth, maturation, flowering, seed formation, and senescence. Development is most readily manifested in changes of form of the organism or organ, such as the transition from the vegetative to flowering condition or from leaf primordium to fully expanded leaf. Development may also be manifested at the subcellular and biochemical levels, such as when chloroplasts appear in leaf cells brought into the light and the enzymes of photosynthesis are activated. Growth is a quantitative term, related to changes in size and mass (Hopkins, Hüner, 2004).

The rate of photosynthesis is of great importance for plants, because it influences production and quantity of biomass, as well as the yield.

Mokronosov (1978) has reported that there has been co-ordinated bond between growth – photosynthesis. The photosynthesis safeguards matters and energy sources for the whole set of growth and morphological processes and changes. The activity of plant growth has return effects on photosynthesis, because the growth needs product of photosynthesis and its redistribution to the vegetative and generative organs.

The accumulation and distribution of dry matter to the single organs of plants is linked to the rate of photosynthesis, but dry weight can be misleading as a measure of growth in some situations. The quantity of produced dry matter is dependent on biological characteristics of grown plants and on optimisation of conditions of its vegetation, too. The optimisation of conditions for plant vegetation is achieved by technological means (e.g. purpose amount incurred and excessive energy) by Čislák (1983) and Bláha et al. (2003).

The accumulation of dry matter and translocation of product of photosynthesis into the organs of plant is influenced by its ontogeny. The highest content of dry matter is identified in a spike of wheat at complete ripeness stage. The content of dry matter in a spike is the highest at the stage of grain filling compared with the other organs of plants (Přikryl, Flašarová, 1985).

Nátr (1975, 1980, 1995), Hodaňová (1977) and Přikryl (1982) dealt with the rate of accumulation and production of dry matter. The authors claim that this rate for cereals is proportional to the quantity of absorbed solar radiation. The contents of photosynthesis products are dependent on the size of assimilation area of growth (LAI) and the activity of photosynthesis of leaf apparatus.

Growth can be assessed by a variety of quantitative measures, depending on the conditions of environment (Petr et al., 1977).

The influence of environmental conditions firstly means distinct fluctuations of temperature and also rela-

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tively unevenly, irregularly and randomly distributed precipitation during the growing season of plants. Regarding these facts, even longer drought period cannot be eliminated. The study of adaptation of plants to water deficit is becoming increasingly relevant, particularly respecting the fact that regular deficit of water occurs at the present time during the main growing period in the majority of field crops in our climatic area.

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

Except for the deficit of water, lower pH of soil also participates in the reduction of plant productivity. Acid soils are one of the serious problems of agricultural production that includes the territory of Central Europe and other continents as well. The decrease in pH values is affected by acid rains, utilisation of physiologically acid fertilisers and lower doses of supplied calciferous fertilisers. The Czech Republic faces directly this problem because 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 and Anderson (1952) studied the action of low soil pH as affected by 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 formation of lower weight of plants and in decreased yield. There is a significant effect of different abiotic stresses on the basic physiological indicators of plant yield production. Negative impact of physical and chemical properties on the 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 and with other external factors decide upon the level and quality of a product obtained.

The aim of the present study is to investigate the effect of abiotic stresses (drought, low pH of soil, combination of drought and low pH) on the rate of photosynthesis and accumulation of dry matter in vegetative and generative plant organs in the three winter wheat varieties (*Triticum aestivum* L.) and development of their growth.

MATERIALS AND METHODS

In the years 2001 to 2003 selected physiological characteristics in wheat varieties Mironovská 808, Estica and Ebi were studied under controlled conditions in the greenhouse.

Wheat plants were cultivated in Mitcherlich pots with homogenised soil and balanced level of nutrients. Plants were cultivated in controlled light conditions of greenhouse at the light regime of 16 hours light with irradiation intensity of 700 $\mu mol.m^{-2}.s^{-1}$ and 8 hours of dark. Average temperature of environment at grain-filling period during the day and night was 15 °C under controlled conditions (C). Watering was uniform and was based on 31% volume of soil moisture, which represents the value of water soil potential – 0.12 MPa, at pH 7.0.

The second treatment of the trial included low soil pH 4.5 (pH). The soil with low pH 4.5 was obtained from field conditions from Chomutov area. The reaction of soil was expressed as pH_{KCl}, i.e. potential exchange reaction. The pH of soil was measured with a pH metre. A pH metre has two electrodes – glass and calomel electrode (i.e. filling chloride mercurous). A pH meter extends at appropriate outside temperature. Then it makes accurate calibration with using at least two suppressor solutions exact pH (ISO/DIS 10390, 1992). Soil acidity was measured at a monthly interval. Modification of pH was provided by 0.01% solution of sulphuric acids and next the soil was watered by deionised water. The third treatment of the trial represented the treatment 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 treatment drought was always accomplished after reaching the point of wilting and soil moisture was always lower even after watering. Watering 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 stage 30DC to the harvest. The irrigation was always lower in these treatments compared with the control conditions. The last treatment included a combination of the treatments of drought and low soil pH (DpH).

Immediate rate of photosynthesis and weight of dry matter were measured in wheat plants at the chosen growth stages: 25DC – full tillering, 30DC – start of shooting, 40DC – flag leaf ligule and auricles visible, 50DC – start of heading, 61DC – start of anthesis, 83DC – precocious of wax maturity and 91DC – complete ripeness. Growth stages are according to Zadoks et al. (1974).

Immediate rate of photosynthesis was measured gasometrically in the open system by the apparatus LCA-4. The device LCA-4 is manufactured by the Analytical Development Company Ltd. in 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 is detection of the change in carbon dioxide concentration in the atmosphere surrounding assimilating object (Šesták, Čatský, 1966).

The obtained results were statistically evaluated using the computer programme Statistica versions 6.0 and 6.1 Cz, statistical analysis ANOVA at the significance level $\alpha = 0.05$.

RESULTS AND DISCUSSION

From the obtained results it is evident that the rate of photosynthesis during ontogenesis manifested the increasing tendency because the lowest photosynthesis was identified at the end of shooting, and it reached its maximum at the beginning of flowering. The decrease of photosynthesis was recorded only after this stage. This trend can be recorded in all studied treatments and varieties of the trial.

The lowest rate of photosynthesis was measured on the third upper leaf at the end of wheat shooting (stage 25DC), when photosynthesis was from 3.76 μmol $CO_2.m^{-2}.s^{-1}$ (Mironovská 808, treatment DpH) to 7.99 μmol $CO_2.m^{-2}.s^{-1}$ (Ebi, treatment pH). The values of photosynthesis are provided in Fig. 1.

A marked increase in the rate of photosynthesis is apparent from the beginning of flowering (stage 61DC), as it can be seen from Fig. 1. At the beginning of flowering the lowest rate of photosynthesis was found in the treatment with a combination of drought and low pH, in which the photosynthesis was measured, amounting to 12.48 μmol $CO_2.m^{-2}.s^{-1}$ (Ebi). On the contrary, the highest rate of photosynthesis was in the control treatment for the variety Estica (14.53 μmol $CO_2.m^{-2}.s^{-1}$). The decrease of the rate of photosynthesis was recorded at the stage of wax ripeness (stage 83DC). The rate of photosynthesis was from 9.28 μmol $CO_2.m^{-2}.s^{-1}$ (Mironovská 808, DpH) to 12.67 μmol $CO_2.m^{-2}.s^{-1}$ (Ebi, pH) during the period of ripening. The obtained results correspond to the conclusions made by Genkel (1969), Rea, Cale (1991) and Hnilička, Petr (2003).

The effect of the treatments of the trial on the rate of photosynthesis was confirmed (see Fig. 1). The highest increase in the rate of photosynthesis was recorded in the control treatment in which the average value of photosynthesis increased from 6.37 μmol $CO_2.m^{-2}.s^{-1}$ (stage 25DC) to 13.53 μmol $CO_2.m^{-2}.s^{-1}$ (stage 61DC). In the treatment with drought and low pH (DpH) the rate of photosynthesis increased, too. The rate of photosynthesis for this treatment was the lowest compared with the other treatments. The average value of photosynthesis ranged between 5.09 μmol $CO_2.m^{-2}.s^{-1}$ (stage 25DC) and 9.95 μmol $CO_2.m^{-2}.s^{-1}$ (stage 61DC) in the treatment with drought and low pH.

Moreover, a statistically significant decrease of photosynthesis follows from Fig. 2 in the treatment with combination of two stress factors compared with the control treatment. The treatment of drought and low soil pH (DpH) reduced the rate of photosynthesis compared with the control by 11.31%. The current effect was F (6.30) = 0.99659, p = 0.44561.

Statistically significant difference was recorded in statistical evaluation of treatment with drought, too, when at stage 25DC photosynthesis was 5.61 μmol $CO_2.m^{-2}.s^{-1}$ and at the stage 61DC it was 12.83 μmol $CO_2.m^{-2}.s^{-1}$. The treatment of drought (D) reduced the rate of photosynthesis compared with the control by 94.60%.

Decrease in the rate of photosynthesis in the treatments of drought and low pH, drought is apparently given by the fact that stomata are closing under the stress conditions, and therefore CO_2 uptake is decreasing, as reported Nilsen, Orcutt (1996), Janáček (1997) or Brestič, Olšovská (2001). Zámečníková (2000) and Hnilička, Petr (2003) came to the similar conclusion in winter wheat plants cultivated under drought conditions.

It can be said that the rate of photosynthesis was not influenced by the varieties. Nevertheless, it can be said

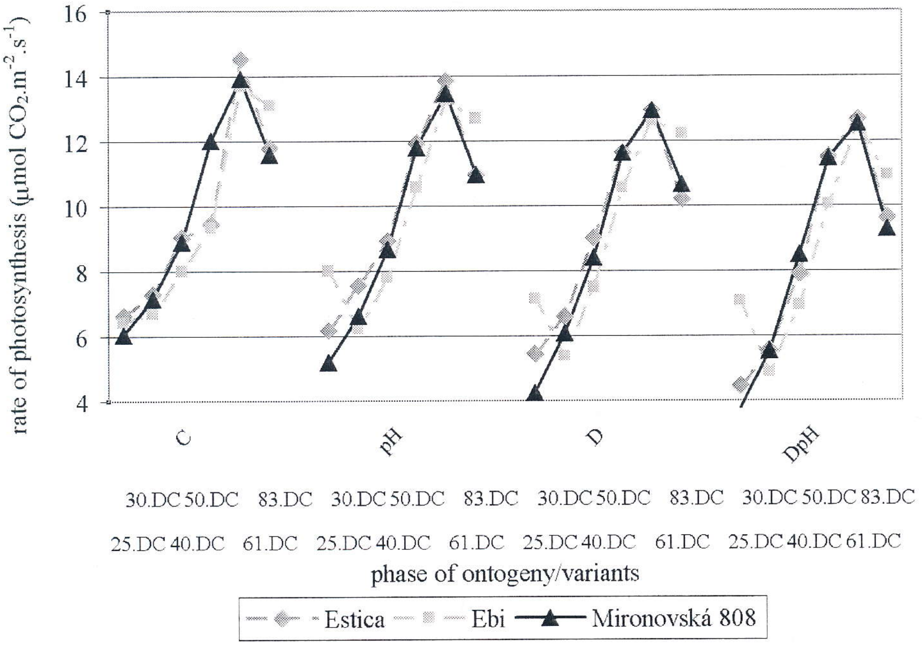

Fig. 1. The rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$)

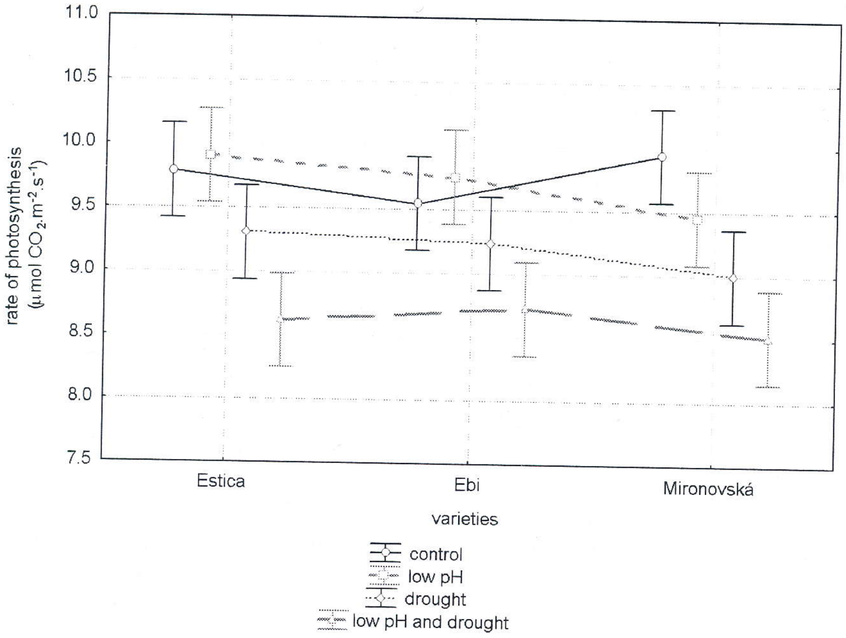

Fig. 2. The interaction between varieties and variants on photosynthesis (vertical columns denote 0.95 intervals of reliability)

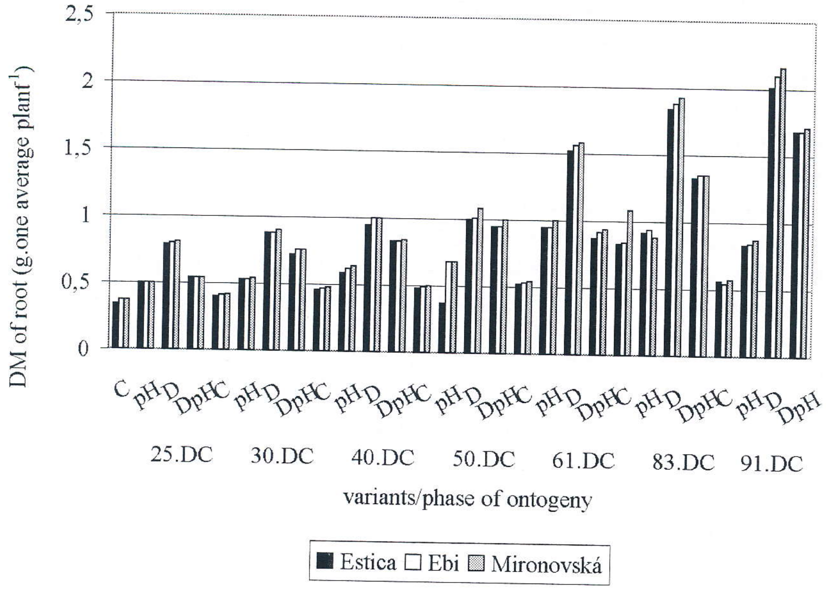

Fig. 3. Weight of dry matter in roots (g)

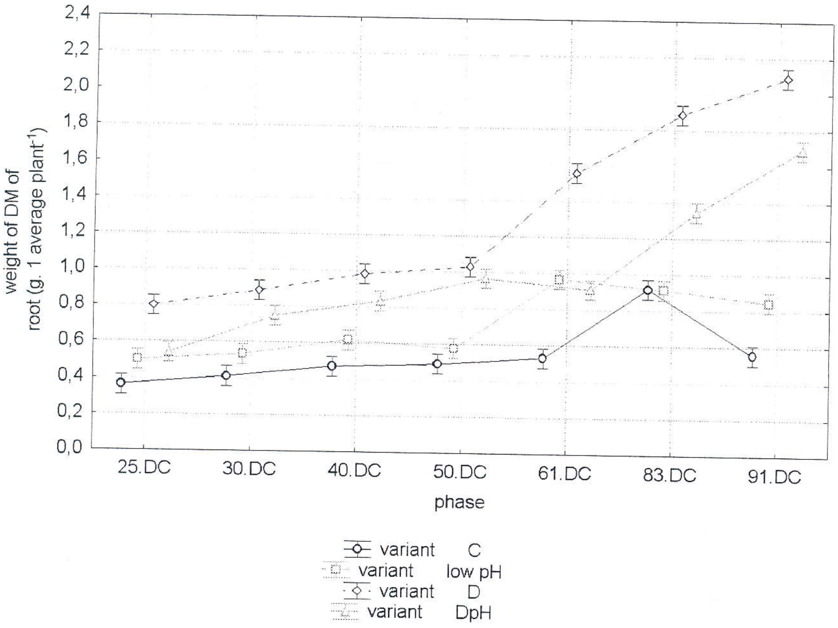

Fig. 4. The interaction between stage and variants on weight of DM in root (vertical columns denote 0.95 intervals of reliability)

that the variety Ebi had the lowest rate of photosynthesis (9.13 μmol $CO_2.m^{-2}.s^{-1}$) and the variety Estica had the highest value (9.40 μmol $CO_2.m^{-2}.s^{-1}$) (see Table 1).

The production of photosynthesis products and their translocation into dry matter correlate with the rate of photosynthesis. This conclusion was also confirmed by the calculated correlation coefficient $r = 0.78$ (dry matter is a dependent variable and rate of photosynthesis is an independent variable: $y = -3.1734 + 0.8503\ x$).

As can be seen from the obtained results, the amount of dry matter in roots in the experimental treatments (Fig. 3) grew gradually from the lowest values at the stage 25DC (from 0.34 g for the variety Estica, control conditions to 0.81 g for the variety Mironovská 808, drought) to the highest values at the stage 91DC (from 0.54 g for the variety Ebi, control conditions to 2.16 g for the variety Mironovská 808, drought). A similar trend was also recorded with the shoot (Fig. 5), when dry matter of leaves and stems was the lowest at the stage of end of shooting (fluctuating from 0.95 g for the variety Mironovská 808, treatment with drought and low pH to 1.82 g for the variety Ebi, control conditions) and it was the highest at the onset of cropping maturity (ranging from 9.68 g for the variety Estica, treatment with drought and low pH to 14.03 g for the variety Mironovská 808, control conditions).

The formation of dry matter and translocation of products of photosynthesis were not affected only by the development of plant, when dry matter in roots and shoot was the highest at the stage 91DC, but also by the varieties and treatments of trial.

It can be seen from Fig. 3 that the weight of roots increasing in all treatments during ontogenesis up to the stage 91DC, because the number of adventitious roots and the length of roots increased. The treatments with stress conditions had higher weight of roots compared with the control treatment (see Fig. 4).

The weight of roots ranged between value 0.34 g (variety Estica, control treatment) and 0.81 g (variety Mironovská 808, treatment with drought) at the end of wheat shooting (stage 25DC). The values of root weight are given in Fig. 2. The root weight was the highest at the stage 91DC. The average root weight was 1.30 g at this stage. The weight was the lowest for the variety Ebi, control conditions, and the highest for the variety Mironovská 808 (control conditions). The root weight ranges between 0.54 g and 2.16 g.

The highest root weight was found for the variety Mironovská 808 and the lowest for the variety Estica. The statistical difference was found between the varieties Mironovská 808 and Estica. The average root weight for Mironovská 808 was 0.92 g and for the variety Estica 0.87 g (see Table 2).

Another factor influencing the production of dry matter of roots was the treatment of the trial. It can be said that higher amount of dry matter in the shoot than in roots was produced in all treatments with stresses. These results are in agreement with the observations made by Černý, Ferik (1977) and Greef, Kullmann (1992) for nitrogen concentration in solution.

The most rapid and dynamic root dry matter growth was surprisingly recorded in the treatment drought,

Table 1. Repeated measures analysis of variance (*F*-test). Values of *F*-test are introduced for rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$)

Effect	SS	Degree of freedom	MS	*F*	*p*
Intercept	6246.464	1	6246.464	31936.93	0.000
Stage	522.893	5	104.579	534.69	0.000
Variants	15.296	3	5.099	26.07	0.000
Varieties	0.384	2	0.192	0.98	0.386
Stage x variants	9.666	15	0.644	3.29	0.003
Stage x varieties	28.596	10	2.860	14.62	0.000
Variants x varieties	1.170	6	0.195	1.00	0.446
Error	5.868	30	0.196		

Table 2. Repeated measures analysis of variance (*F*-test). Values of *F*-test are introduced for DM in root (g.average $plant^{-1}$)

Effect	SS	Degree of freedom	MS	*F*	*p*
Intercept	66.661	1	66.661	30868.41	0.000
Stage	6.397	6	1.066	493.72	0.000
Variants	7.493	3	2.498	1156.54	0.000
Varieties	0.039	2	0.020	9.07	0.001
Stage x variants	2.462	18	0.137	63.35	0.000
Stage x varieties	0.0180	12	0.001	0.69	0.746
Variants x varieties	0.006	6	0.001	0.49	0.809
Error	0.078	36	0.002		

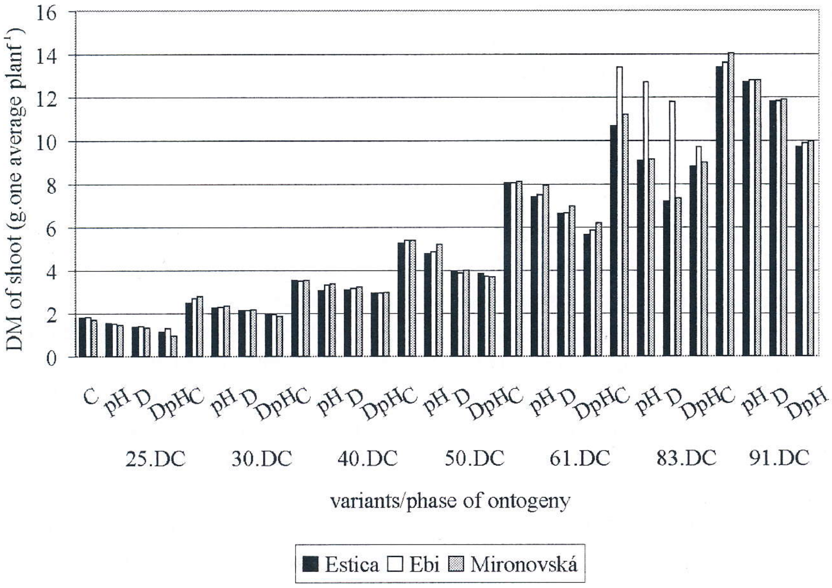

Fig. 5. Weight of dry matter in the aboveground biomass (g)

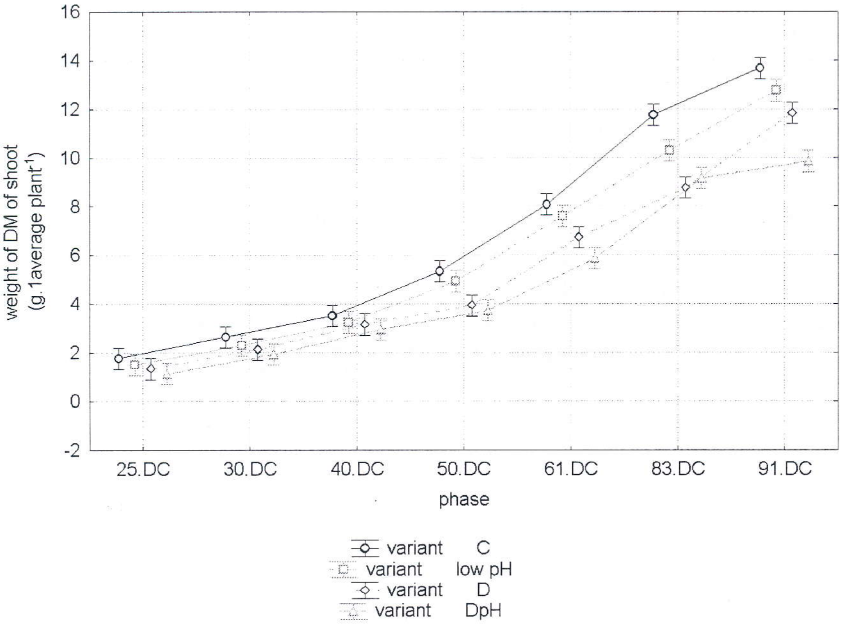

Fig. 6. The interaction between stage and variants on weight of DM in shoot (vertical columns denote 0.95 intervals of reliability)

which was statistically significant in comparison to the remaining treatments of the trial. The weight of root dry matter had average value 1.32 g. This value is 151.33% higher than for the control treatments. In the other treatments of the trial the weight of dry matter of root was as follows: control treatments (0.52 g), low pH (0.73 g) and treatment with drought and low pH (1.00 g). The statistical difference was found between treatments of trial (see Table 2).

From Fig. 5 it is evident that the lowest shoot dry matter of an average plant (stems, leaves and spikes) was at the end of wheat shooting (25DC). The average value of dry matter of shoot was for the variety Mironovská 808, growing in the treatment with combination drought and low pH (DpH) – 0.95 g at this stage. On the other hand, the highest value of dry matter was for the variety Ebi that was growing in control conditions – 1.82 g. The weight of shoot was made first of all by leaves and stems up to the beginning of formation of spikes. The ratio of weight of spike with grains on total weight of dry matter started to increase from phase of topping of grains to the term of harvest. The ratio weight of spikes on total weight of dry matter of shoot was highest at the stage 91DC. These results are in agreement with the observation made by Přikryl and Flašarová (1985).

The total weight of dry matter of shoot was highest at the stage 91DC. The average weight of shoot was 12.03 g at this stage. The lowest dry matter weight was identified for the variety Estica growing in the treatment with combination of drought and low pH (DpH) – 9.68 g and the highest value was for the variety Mironovská 808 growing in the control treatment – 14.03 g. The increment of dry weight of shoot organs during ontogenetic development was given by their gradual senescence and losses of water during the period of maturing (see Fig. 6). The current effect was *F* (18.36) = 7.7881, *p* =

Table 3. Repeated measures analysis of variance (*F*-test). Values of *F*-test are introduced for DM in shoot (g.average plant^{-1})

Effect	SS	Degree of freedom	MS	*F*	*p*
Intercept	2811.892	1	2811.892	20006.54	0.000
Stage	1173.530	6	195.588	1391.61	0.000
Variants	36.328	3	12.109	86.16	0.000
Varieties	3.314	2	1.657	11.79	0.001
Stage x variants	19.703	18	1.095	7.79	0.000
Stage x varieties	18.838	12	1.570	11.17	0.000
Variants x varieties	0.629	6	0.105	0.75	0.617
Error	5.060	36	0.141		

0.0000. These results are in agreement with the observation made by Hnilička (1999) and Marek (2000).

It can be said that the weight of the shoot was not influenced by the varieties. Nevertheless it can be said that the variety Mironovská 808 had the highest weight of stems and leaves of one average plant (5.73 g) and the variety Estica had the lowest value (5.58 g). This difference is given by general appearance of plant, because the variety Mironovská 808 had longer shoot in comparison with the varieties Ebi and Estica. Petr et al. (1977) came to the similar conclusion in winter wheat plants cultivated under drought conditions.

The statistically significant decrease of weight of average plants was recorded for the treatments with stress conditions compared with the control treatment. The lowest dry matter weight was recorded for the treatment with combination of two stress factors (DpH). In this treatment dry matter weight decreased by about 25.23% compared with the control treatment. The plant growing in the condition of drought decreased by about 1.36 g compared with the control treatment. The average weight of plants was 5.20 g in this treatment (see Table 3).

The shoot : root ratio calculated on dry matter weight basis was significantly affected by treatments. The highest ratio from all samplings was in the treatment with low pH (0.44). In the other treatments of the trial the ratio of roots and shoot was as follows: control treatments (0.08), drought (0.26) and treatment with drought and low pH (0.21). From the results it is evident that abiotic stresses (e.g. drought, mineral nutrient, low pH of soil...) leads to the narrowing of the ratio between the shoot and roots. Similar results were obtained by Novák et al. (1988), Luo et al. (1994) and Marek (2000) in spring barley and forest wood species. Spring barley was grown in the treatments with different nitrogen concentrations in the nutrient solution (1 N, 0.1 N and 2 N). Hnilička et al. (2002) and Procházka et al. (1998) came to the similar conclusions.

The rate of photosynthesis and accumulation of dry matter are negatively affected by unfavourable physical and chemical factors of the environment. The selected abiotic stresses, such as combination of drought and low pH, significantly decreased all studied indicators compare to the control treatment. The rate of photosynthesis during ontogenesis manifested the tendency of growth because the lowest photosynthesis was identified at the end of shooting, and it reached its maximum at the beginning of flowering. The variety Ebi had the lowest rate of photosynthesis (9.13 μmol $CO_2.m^{-2}.s^{-1}$) and the variety Estica had the highest value (9.40 μmol $CO_2.m^{-2}.s^{-1}$). The dry matter weight in roots and the shoot was the highest at the stage 91DC compared to the stage 25.DC. The average root weight for Mironovská 808 was 0.92 g and for Estica 0.87 g. The variety Mironovská 808 had the highest weight of stems and leaves per average plant (5.73 g) while the variety Estica had the lowest value (5.58 g).

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Vliv abiotických stresorů na rychlost fotosyntézy a tvorbu sušiny pšenice ozimé.

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V řízených skleníkových podmínkách byla měřena rychlost fotosyntézy a tvorba sušiny u vybraných odrůd ozimé pšenice. Do pokusu byly zařazeny odrůdy Ebi, Estica a Mironovská 808, které byly pěstovány ve čtyřech variantách pokusu. Schéma pokusu zahrnovalo variantu kontrolní, variantu s nízkým pH půdy (pH 4,5), variantu s vodním stresem (sucho) a kombinaci sucha a nízkého pH. Z naměřených hodnot vyplývá, že rychlost fotosyntézy a akumulace sušiny jsou negativně ovlivněné abiotickými stresory. Vybrané abiotické stresory, především kombinace sucha a nízkého pH, významně snížily hodnoty sledovaných charakteristik v porovnání s variantou kontrolní. Rozdíly byly také nalezeny mezi sledovanými odrůdami, kdy odrůda Ebi měla nejnižší průměrnou rychlost fotosyntézy (9,13 μmol $CO_2.m^{-2}.s^{-1}$) a naopak odrůda Estica nejvyšší (9,40 μmol $CO_2.m^{-2}.s^{-1}$). Průměrná hmotnost kořenů odrůdy Mironovská 808 byla 0,92 g a odrůdy Estica 0,87 g. Odrůda Mironovská 808 měla také nejvyšší hmotnost nadzemní biomasy jedné průměrné rostliny (5,73 g). Naopak rostliny odrůdy Estica měly nejnižší hmotnost nadzemních orgánů (5,58 g).

abiotické stresory; pšenice; *Triticum aestivum* L.; rychlost fotosyntézy; sušina

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