CHANGES OF THE RATE OF PHOTOSYNTHESIS AND STOMATAL CONDUCTANCE DURING ONTOGENY OF AMARANTH PLANTS (*AMARANTHUS* SP.)

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The rate of photosynthesis and stomatal conductance in three selected amaranth species: *Amaranthus aureus*, *Amaranthus caudatus* and *Amaranthus cruentes* were studied under field conditions in the years 2000 and 2001. The given physiological indicators were measured gasometrically, by open system, by apparatus LCA-4 in selected growth phases: code 24, code 30, code 39, code 40, code 60, code 65 and code 90. The rate of photosynthesis grew during ontogeny to the period of the formation of apex of main panicle (code 40) and then its values were decreasing, whereas the lowest photosynthesis was in the period of full ripeness (code 90). Statistically significantly higher rate of photosynthesis was found in *Amaranthus caudatus* (7.99 µmol $CO_2.m^{-2}.s^{-1}$) and lower in *Amaranthus cruentus* (6.79 µmol $CO_2.m^{-2}.s^{-1}$). Stomatal conductance was another studied indicator that copied the first part of the curve of photosynthesis, i.e. its growth to the formation of apex of the main panicle, and then the decrease was measured to the beginning of seed formation (code 64). Repeated increase of the values of openness of stomata was monitored in the period of full ripeness, whereas these values were closer to the maximum in the phase of formation of apex of main panicle (code 90).

amaranth; *Amaranthus* sp.; photosynthesis; stomatal conductance

INTRODUCTION

In pre-Colombian America amaranth (*Amaranthus* L.) belonged to important agricultural crops of Incas for whom it was a holy plant. In the period of Spanish colonisers its cultivation was forbidden, but it was kept in unapproachable regions of the Ands. Now it is cultivated almost all over the world.

In view of physiology it is a plant of C4 cycle from that follow demands for environment. As reported by Paredes-López (1994), a temperature between 30 and 40 °C is suitable for growth with high rate of radiation. Under lower rate of incident radiation NAR is decreasing (net assimilation rate [$g.m^{-2}.time^{-1}$]), but LAR (leaf area ratio [$m^2.kg^{-1}$]) is increasing. Productivity of assimilation apparatus of plants is expressed by net assimilation rate. This characteristic can be defined as an increment of dry matter per assimilation area and time unit. Leaf area ratio is a ratio of leaf area to the total weight of dry matter (Šesták, Čatský, 1966). Higher demands for temperature are connected also with adaptation to the drought conditions. Gregorová (1996) in her study confirmed adaptability of amaranth to drought caused by a deficit of precipitation.

Regarding the fact that amaranth is a relatively new crop in Czech conditions, we decided to study in it basic physiological indicators among which photosynthesis plays a primary role.

Photosynthesis as a process is at the beginning of all energy, therefore a great attention is devoted to it, because the rate of photosynthesis is an important factor that affects production and amount of biomass, that is also the yield. Regarding this, photosynthesis is a primary biological basis of productivity of cultural crops (Evans, 1975).

The process of photosynthesis is connected with production and distribution of reserve substances and dry matter. This relationship was studied by e.g. Mokronosov (1978), who reported that in the relationship growth – photosynthesis, co-ordinated bond is applied, under which photosynthetic activity is provided by substances and energy resources for the whole group of growth and morphological processes. Growth activity of plants affects back photosynthesis by consumption and redistribution of produced assimilates on the growth of vegetative and generative organs.

MATERIAL AND METHOD

The trial that studied different physiological indicators and yield formation in three amaranth species: *Amaranthus aureus* (grain), *Amaranthus caudatus* (grain) and *Amaranthus cruentes* (leafy) was established under field conditions in 2000 and 2001. Regarding the different origin and different purpose of growing, the response of these genotypes to the conditions of environment in the Czech Republic was in the centre of attention.

The seeding was done manually on 3 May 2000 and on 11 May 2001 on an experimental plot of the Czech University of Agriculture Prague-Suchdol characterised by loamy soil (luvisol) and sugar-beet growing and wheat production subtype. The area of this experimental

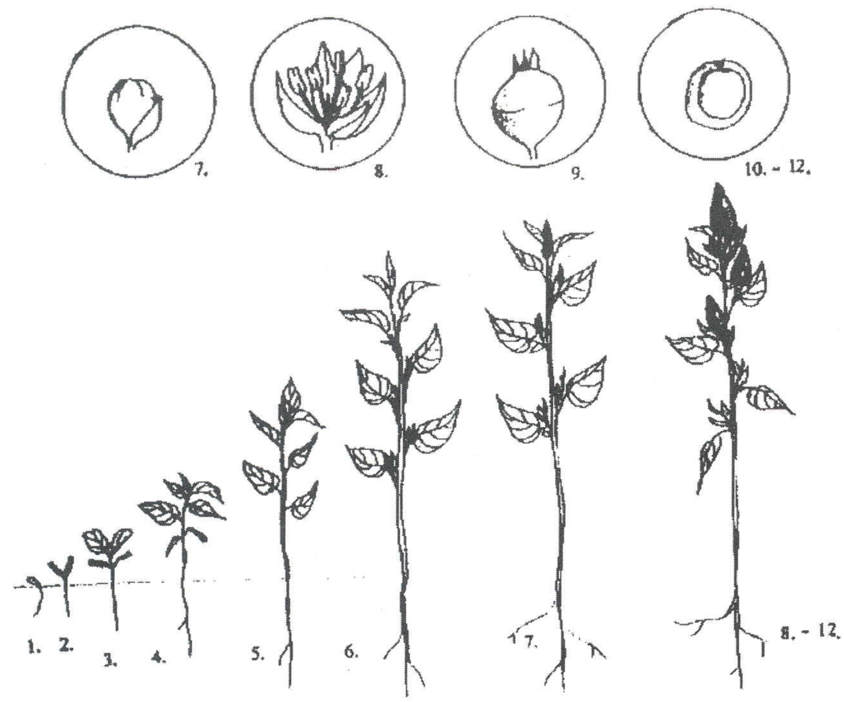

Fig. 1. Developmental phases of amaranth (after Hradecká, Burešová, 1994)

1) emergence (code 10)
2) appearing of cotyledons (code 13)
3) the first two right leaves (code 20)
4) the first four right leaves (code 24)
5) intensive elongation of stomata (code 30)
6) shooting of stems (code 39)
7) formation of the apex of main panicle (code 40)
8) full flowering (code 60)
9) beginning of seed formation (code 61–68)
10) milk ripeness (code 70)
11) wax ripeness (code 80)
12) full ripeness (code 90)

plot was 2 m^2. The plots were fertilised by a dose of fertilisers recommended by Jarošová et al. (2000). Row spacing was 350 mm and the distance of plants per row was 10 cm. Plant samples were taken in the following developmental phase after Hradecká and Burešová (1994): code 24, code 30, code 39, code 40, code 60, code 65 and code 90. Developmental phases of amaranth plants are described in Fig. 1. Immediate rate of photosynthesis and stomatal conductance was measured in different phases of amaranth plants. The experimental year 2000 was marked by strongly warm weather during ontogeny and it was a dry year concerning precipitation. The temperature in 2001 was in the period of main ontogeny of amaranth than given by 30-year normal. This period was poor in precipitation, except September that was very rich in precipitation.

Immediate rate of photosynthesis of amaranth was measured gasometrically in open system by a device LCA-4 under field conditions at the rate of irradiation 490 $\mu mol.m^2.s^{-1}$ and the temperature 25 ± 1 °C. Stomatal conductance together with photosynthesis was measured by a device 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 results obtained were evaluated statistically using the computer programme Statgraphic for Windows on the level of significance $\alpha = 0.05$.

RESULTS AND DISCUSSION

The growth of the rate of photosynthesis of amaranth plants can be recorded from the results obtained from formation of the 4th right leaf (code 24) to the period of forming the apex of main panicle (code 40). In this period in 2000 the rate of photosynthesis rose from an average value 7.99 $\mu mol\ CO_2.m^{-2}.s^{-1}$ to the value 11.99 $\mu mol\ CO_2.m^{-2}.s^{-1}$, in 2001 the measured immediate rate of photosynthesis increased from 5.90 $\mu mol\ CO_2.m^{-2}.s^{-1}$ to 9.35 $\mu mol\ CO_2.m^{-2}.s^{-1}$. Genkel (1969) and Rea, Cale (1991) reported the similar trend in the increase of photosynthesis during ontogeny e.g. in wheat plants. These authors agree that also in wheat the rate of photosynthesis is slowly increasing from emergence to heading, in case of amaranth it is the phase of forming of apex of main panicle.

The obtained results of the rate of photosynthesis were higher than those reported for wheat in laboratory conditions by Hnilička and Novák (2000). The rate of photosynthesis in conditions of complete nutrient solution is ranging between 1.64 (phase 14.DC) and 10.77 $\mu mol\ CO_2.m^{-2}.s^{-1}$ (phase 30.DC) in their study. The rate of photosynthesis of amaranth was also higher in spring barley as documented by Hejnák et al. (1998) in their study. After these authors the rate of photosynthesis of spring barley ranged from 3.50 to 10.47 $\mu mol\ CO_2.m^{-2}.s^{-1}$ in dependence on the rate of nitrogen fertilisation and on soil pH in phase of shooting.

From the phase of formation of apex of main panicle (code 40) only the decrease of the rate of photosynthesis was recorded, whereas the lowest values were at the end of ontogeny, i.e. in full ripeness (code 90). The average rate of photosynthesis in this period in the experimental year 2000 was 4.73 $\mu mol\ CO_2.m^{-2}.s^{-1}$ and 3.53 $\mu mol\ CO_2.m^{-2}.s^{-1}$ in the following year.

The decrease of the values of the rate of photosynthesis of amaranth species in the period of full flowering (code 60) and the beginning of seed formation (code 65) ranged in all studied species in the similar range that was

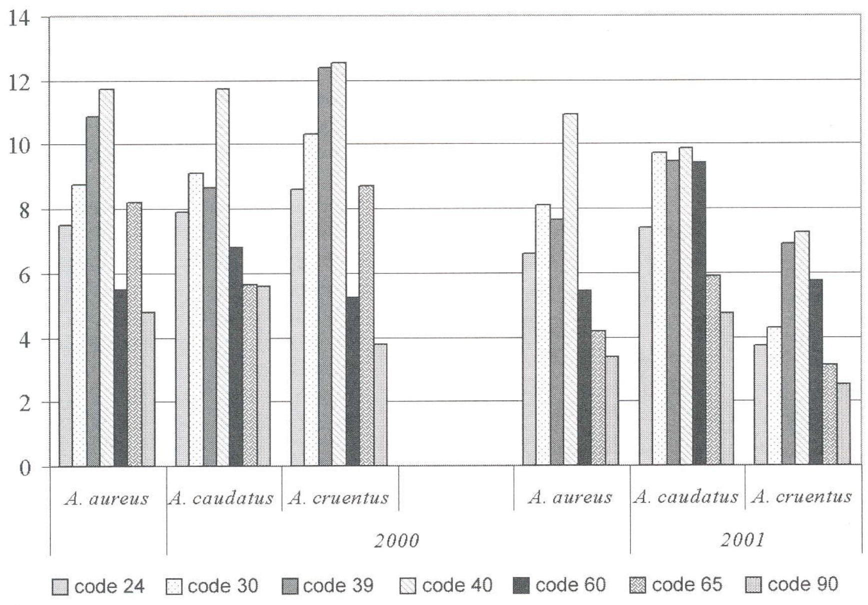

Fig. 2. The rate of photosynthesis (µmol $CO_2.m^{-2}.s^{-1}$) of amaranth plants during ontogeny

x axis: phase of ontogeny
y axis: the rate of photosynthesis (µmol $CO_2.m^{-2}.s^{-1}$)
code 24, code 30, code 39, code 40, code 60, code 65, code 90

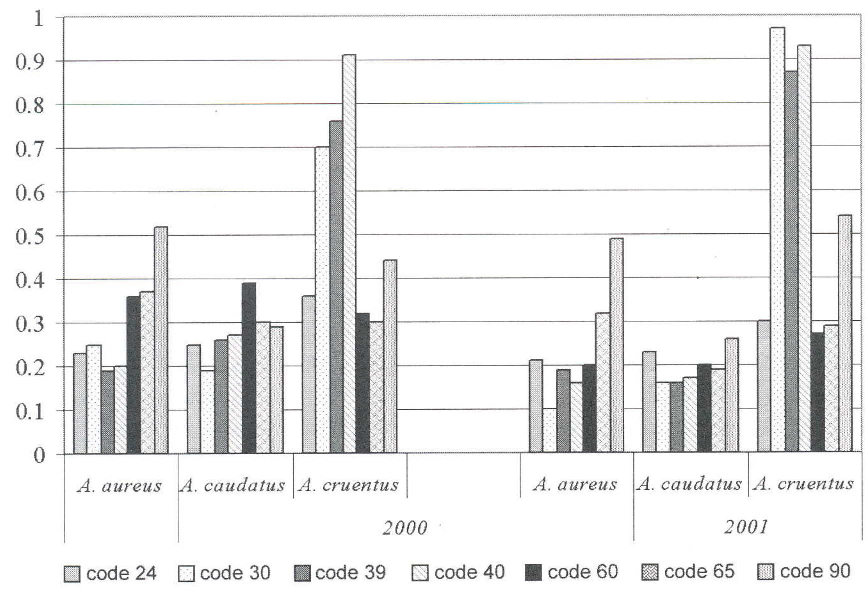

Fig. 3. Stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$) of amaranth plants during ontogeny

x axis: phase of ontogeny
y axis: stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$)

given by Hnilička (1999) for wheat – from 4.09 µmol $CO_2.m^{-2}.s^{-1}$ to 6.99 µmol $CO_2.m^{-2}.s^{-1}$. The only exception was *Amaranthus cruentes* in 2001 that reached lower rate of photosynthesis – 3.13 µmol $CO_2.m^{-2}.s^{-1}$. The rate of photosynthesis in the period of formation of fourth straight leaf (code 24) in 2000 was ranged between the values 7.49 µmol $CO_2.m^{-2}.s^{-1}$ (*Amaranthus aureus* – grain) and 8.60 µmol $CO_2.m^{-2}.s^{-1}$ by *Amaranthus cruentes* (leafy). In 2001 the situation was different because the lowest photosynthesis was recorded at the beginning of ontogeny in leafy *Amaranthus cruentes* – 3.74 µmol $CO_2.m^{-2}.s^{-1}$ and highest in *Amaranthus caudatus* – 7.39 µmol $CO_2.m^{-2}.s^{-1}$ (Fig. 2).

In the period of formation of apex of main panicle (code 40) a marked culmination of the rate of photosynthesis appeared in both years of cultivation. The rate of photosynthesis increased most significantly in 2000 in *Amaranthus aureus.* The rate of photosynthesis in this species increased by 4.24 µmol $CO_2.m^{-2}.s^{-1}$, i.e. by 56.6%. In 2001 the rate of photosynthesis increased the most again in this species, the increase represented 66.49% (4.370 µmol $CO_2.m^{-2}.s^{-1}$). From the beginning of anthesis (code 40) to full ripeness (code 90) a falling tendency was recorded. The measured rate of photosynthesis in the period of full ripeness (code 90) in 2000 ranged between the values 3.79 µmol $CO_2.m^{-2}.s^{-1}$ (*Amaranthus cruentus*) and 5.60 µmol $CO_2.m^{-2}.s^{-1}$ (*Amaranthus caudatus*). In 2001 the values were lower and they ranged between 2.51 µmol $CO_2.m^{-2}.s^{-1}$ (*Amaranthus cruentes*) and 4.73 µmol $CO_2.m^{-2}.s^{-1}$ (*Amaranthus caudatus*). The differences in measured values of the rate of photosynthesis during ontogeny were statistically significant (Table 1). It can be seen from Table 2 that *Amaranthus caudatus* had the highest

Table 1. Differences in the rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$) and in stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$)

Differences in the rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$)			Differences in stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$)		
Phase of organogenesis	average measured values of all measurements	homogenous groups	phase of organogenesis	average measured values of all measurements	homogenous groups
Code 90	4.13	*	code 24	0.26	*
Code 65	4.02	* *	code 60	0.29	* *
Code 24	6.95	* * *	code 65	0.29	* *
Code 60	7.39	* *	code 30	0.39	* * *
Code 30	8.19	* *	code 39	0.41	* *
Code 39	9.52	* *	code 90	0.42	* *
Code 40	10.67	*	code 40	0.44	*

T-method
$\alpha = 0.05$

Table 2. Differences in the rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$) and in stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$) between different amaranth species

Differences in the rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$)			Differences in stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$)		
Amaranth species	average measured values of all measurements	homogenous groups	amaranth species	average measured values of all measurements	homogenous groups
A. cruentus	6.79	*	*A. caudatus*	0.24	*
A. aureus	7.40	* *	*A. aureus*	0.27	*
A. caudatus	7.99	*	*A. cruentus*	0.57	*

T-method
$\alpha = 0.05$

Table 3. Differences in the rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$) and in stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$) in dependence on the year

Differences in the rate of photosynthesis (μmol $CO_2.m^{-2}.s^{-1}$)			Differences in stomatal conductance (mol $H_2O.m^{-2}.s^{-1}$)		
Year	average measured values of all measurements	homogenous groups	year	average measured values of all measurements	homogenous groups
2001	6.49	*	2000	0.37	*
2000	8.30	*	2001	0.34	*

T-method
$\alpha = 0.05$

rate of photosynthesis in the Czech climatic conditions 7.99 μmol $CO_2.m^{-2}.s^{-1}$ and on the contrary, *Amaranthus cruentus* – 6.79 μmol $CO_2.m^{-2}.s^{-1}$. The differences between these species were statistically significant.

The year affected the course of photosynthesis statistically significantly, when in 2001 lower photosynthesis was recorded compared with the year 2000. In 2001 an average rate of photosynthesis was 6.49 μmol $CO_2.m^{-2}.s^{-1}$, but in 2000 it was 8.30 μmol $CO_2.m^{-2}.s^{-1}$, as reported in Table 3.

In addition, the rate of photosynthesis is affected by openness of stomata, i.e. stomatal conductance. Therefore we paid our attention to the study of this physiological characteristic.

The results of measurements of stomatal conductance are summed up in Fig. 3. It follows from the mentioned graph that stomatal conductance grew to the formation of the apex of main panicle (code 40). From this developmental phase the decrease can be recorded from the beginning of seed production (code 65) and this value was again increasing in full ripeness (code 90). At the end of the studied period, i.e. in the period of full ripeness, the measured values of openness of stomata reached almost the maximum in the period of formation of the apex of main panicle. The values of openness of stomata ranged from 0.25 mol $H_2O.m^{-2}.s^{-1}$ (the first four right leaves – code 24, the year 2001) up to 0.46 mol $H_2O.m^{-2}.s^{-1}$ (the formation of apex of main panicle – code 40, the year 2000).

The value of openness of stomata was significantly lowest in the phase of the fourth right leaf (0.26 mol $H_2O.m^{-2}.s^{-1}$) and on the contrary, it was the highest in the phase of formation of the apex of main panicle (0.44 mol $H_2O.m^{-2}.s^{-1}$). The second highest value was found in the period of full ripeness, when it was 0.42 mol $H_2O.m^{-2}.s^{-1}$ (Table 1).

These measured values of stomatal conductance are higher than those given by Zámečníková (2000) in her study for wheat. This author reported the stomatal conductance for wheat in the values ranging from 0.06 to 0.36 mol $H_2O.m^{-2}.s^{-1}$.

The significant difference between different amaranth species can be seen in Table 2. *Amaranthus cruentus* reached significantly highest values of stomatal conductance – 0.57 mol $H_2O.m^{-2}.s^{-1}$ and the lowest openness of stomata was in *Amaranthus caudatus* – 0.24 mol $H_2O.m^{-2}.s^{-1}$ and then in *Amaranthus aureus* – 0.27 mol $H_2O.m^{-2}.s^{-1}$.

The year of cultivation was not manifested significantly in the changes of the values of stomatal conductance, because its values were relatively balanced in both experimental years (0.34 mol $H_2O.m^{-2}.s^{-1}$ – the year 2001, 0.37 mol $H_2O.m^{-2}.s^{-1}$ – the year 2000).

If we compare the values of the rate of photosynthesis and stomatal conductance, it can be said that higher values of the rate of photosynthesis were not reached under higher values of openness of stomata. The only exception is *Amaranthus cruentes* in 2000 at the beginning of studied period. The openness of stomata in this species was 0.76 mol $H_2O.m^{-2}.s^{-1}$ and the rate of photosynthesis was 12.38 μmol $CO_2.m^{-2}.s^{-1}$ (code 39); the stomatal conductance was 0.91 mol $H_2O.m^{-2}.s^{-1}$ the following phase and photosynthesis was 12.52 μmol $CO_2.m^{-2}.s^{-1}$. In congruency with Lawlor et al. (1987) it can be said from their results that the rate of photosynthesis is growing to the certain value of conductance of stomata (0.4 mol $H_2O.m^{-2}.s^{-1}$), but it is not increasing at higher conductance. Except the above-described result in *Amaranthus cruentus*, the result of Karraou and Maranville (1995) was confirmed. In the case of wheat they found that the rate of photosynthesis is relatively higher in some of their genotypes even under decreased conductance of stomata.

In conclusion it can be said that the rate of photosynthesis grew during ontogeny to the period of formation of apex of main panicle (code 40) and then its values were decreasing, whereas the lowest photosynthesis was in full ripeness (code 90). Regarding that these are the plants of the cycle C4, it can be said that the temperatures of summer months were optimum for these plants, therefore the fall of measured values of rates of photosynthesis in both warm years did not occur. Stomatal conductance copied the first part of photosynthesis, i.e. its growth to the formation of apex of main panicle (code 40), and then the decrease was recorded from the beginning of seed formation (code 64). Repeated increase of the values of openness of stomata was monitored in the period of full ripeness, whereas these values were closer to the maximum in the period of formation of apex of main panicle (code 40).

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Změny intenzity fotosyntézy a stomatální vodivosti v průběhu vegetace rostlin laskavce (*Amaranthus* sp.).

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V polních podmínkách byla v letech 2000 a 2001 sledována intenzita fotosyntézy a stomatální vodivost u tří vybraných druhů laskavce: *Amaranthus aureus*, *Amaranthus caudatus* a *Amaranthus cruentus*. Uvedené fyziologické ukazatele byly měřeny gazometricky, otevřeným systémem, přístrojem LCA-4 ve vybraných růstových fázích: kód 24, kód 30, kód 39, kód 40, kód 60, kód 65 a kód 90. V obou pokusných letech byl patrný nárůst intenzity fotosyntézy rostlin laskavce od období prvních čtyř pravých listů (kód 24) do formování vrcholu hlavní laty (kód 40). Intenzita fotosyntézy se zvýšila v tomto období v roce 2000 z průměrné hodnoty 7,99 µmol $CO_2.m^{-2}.s^{-1}$ na hodnotu 11,99 µmol $CO_2.m^{-2}.s^{-1}$, v roce 2001 se naměřená okamžitá intenzita fotosyntézy zvýšila z 5,90 µmol $CO_2.m^{-2}.s^{-1}$ na 9,35 µmol $CO_2.m^{-2}.s^{-1}$. Od fáze formování vrcholu hlavní laty (kód 40) byl již zaznamenán pouze pokles intenzity fotosyntézy, přičemž nejnižší hodnoty byly zaznamenány na konci vegetace, tedy v období plné zralosti (kód 90). V tomto období roku 2000 byla průměrná intenzita fotosyntézy 4,73 µmol $CO_2.m^{-2}.s^{-1}$ a v roce následujícím 3,53 µmol $CO_2.m^{-2}.s^{-1}$. Statisticky průkazně vyšší intenzita fotosyntézy byla zjištěna u *Amaranthus caudatus* (7,99 µmol $CO_2.m^{-2}.s^{-1}$) a nižší u *Amaranthus cruentus* (6,79 µmol $CO_2.m^{-2}.s^{-1}$). Další sledovanou charakteristikou byla stomatální vodivost. Hodnota otevřenosti průduchů byla průkazně nejnižší v období prvních čtyř pravých listů (0,26 mol $H_2O.m^{-2}.s^{-1}$) a naopak nejvyšší ve fázi formování vrcholu hlavní laty (0,44 mol $H_2O.m^{-2}.s^{-1}$). Druhá nejvyšší hodnota byla zjištěna v období plné zralosti, kdy činila 0,42 mol $H_2O.m^{-2}.s^{-1}$.

laskavec; *Amaranthus* sp.; fotosyntéza; stomatální vodivost

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