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Original scientific paper

DIFFERENT ASPECTS OF INHIBITION OF GROWTH AND PHOTOSYNTHESIS OF MAIZE (*Zea mays* L.) BY THE PHOSPHONATE HERBICIDE SULPHOSATE
3. EFFECT OF PLANT AGE

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Effects of the herbicide sulphosate on the growth, accumulation and allocation of dry weight and photosynthesis in maize plants of different age (5, 6 and 7 weeks) were investigated. Dry weight accumulation (ln DW), which ultimately determines growth, was found to correlate highly significantly with root volume (Vr) and stem mass ratio (SMR) in maize plants aged 5 and 7 weeks, while in plants aged 6 weeks a highly significant correlation was found with root mass ratio (RMR) and leaf mass ratio (LMR). Besides, plants aged 6 weeks had a significantly higher content of chlorophyll a (Chl_a) in the youngest fully developed leaves, compared to plants aged 5 and 7 weeks. Based on these findings, we assumed there was also a difference between plants in these age groups in terms of the reaction of their photosynthetic systems to stress caused by the herbicide sulphosate. Regulation of photosynthesis in

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the sulphosate-stressed maize plants aged 5 and 7 weeks is thus most probably independent of photosystem 2 (PS II), which is consistent with literature data on the activity of that herbicide. On the other hand, photosynthesis in the sulphosate-stressed maize plants aged 6 weeks is regulated by non-photochemical quenching of Chl_a fluorescence (whose indicator is NPQ). It is an optimal way through acclimation for regulating photosynthesis under stress. Taking also into consideration the factors that determine dry weight accumulation in maize plants aged 6 weeks, we should not disregard the possibility that photosynthesis in maize plants of that age group may be regulated by changes in the "source-sink" ratios.

INTRODUCTION

Phosphonate herbicides (e.g. glyphosate, sulfosate) primarily induce inhibition of the shikimate biosynthetic pathway as a first assumed mode of action of these herbicides. Geiger et al. (9, 10) investigated the inhibition of photosynthesis and starch synthesis induced by the herbicide glyphosate early (1-2 h) after treatment. We reexamined those findings during inhibition of photosynthesis and growth of different aged maize plants treated with sulphosate.

MATERIALS AND METHODS

Maize (*Zea mays* L.; hyb. *ZPSC 704*) plants were grown in V=5 l pots containing organic compost for 5, 6, and 7 weeks (6, 7 and nearly 8 fully developed leaves, respectively) under field conditions (PARmax> 1500 $\mu mol\ m^{-2}s^{-1}$, variable photoperiod (15/9±1 h), relatively stable temperature and humidity (28/22± 4 ^{0}C, 50/60± 5%) in July and August of 2002. At the beginning of these trials, half of the plants were treated with 10^{-2} mol concentration of the herbicide sulphosate (syn. glyphosate-trimesium; product "*Touchdown*", *Syngenta*, UK, 480 g/l a.i.) until run-off, while the other half (control) was left untreated. Sampling for measurements of growth, dry weight partitioning, relative water content (RWC), content of photosynthetic pigments and root volume was performed on the treatement day and on the 4th and 8th days of the trial. The parameters of growth and dry weight partitioning were calculated according to POORTER AND GARNIER (1996) and DE GROOT ET AL. (2002). In plants aged 6 weeks, dry matter sampling was not performed at the beginning of the trial due to technical difficulties, and the analysis of growth and dry weight partitiong was not done on those plants. Extraction of photosynthetic pigments was performed passively in DMF (–20^0 C), reading the absorbance (A_{664}, A_{647} and A_{480}) directly from extract on the spectrophotometer, and Wellburn's formula (11) was used to calculate contents of Chl_a, Chl_b and total carotenoids (x+c) in leaf extract. Root volume was determined by applying Archimedes' Law. RWC was determined by standard method (NIKOLIĆ, 2007). Chl_a fluorescence, as well as RWC and photosynthetic pigments, were measured 20-25 cm from the tip of the youngest fully formed leaf using a PAM 101/103 fluorometer at the beginning of the 2^{nd}, 4^{th}, 6^{th} and 8^{th} post-treatment days during the first part of the photoperiod after at least 3 h of incubation in the dark. The parameters of Chl_a fluorescence and electron-transport rate (ETR) of photosynthesis were calculated according to MAXWELL AND JOHNSON (2000). Statistical processing began by calculating the means in *M Stat C* software (Michigan State University, USA). Statistical significance was tested using the analysis of variance (LSD test, same software). Statistical significance of differences in the trial was marked by different letters and symbols for 5% statistical threshold. Correlation between different parameters was tested using correlation computation in the same software. Its results are given in tables along with other results. Significant (5%) correlation was marked with a single asterisk symbol (*) and highly significant (1%) with double asterisk (**).

RESULTS AND DISCUSSION

An insignificant dry weight increase was found in control plants aged 5 weeks, compared to treated plants (Fig. 1), which is consist with a general slow growth of the untreated plants and terminated growth of treated ones. On the other hand, considerable change was observed in dry weight allocation. For example, there was a significant decrease in RMR and increase in SMR values, which is especially evident in treated plants (not shown). Consistent with it is a significant decrease in RWC and Vr parameters of treated (compared to control) plants (not shown).

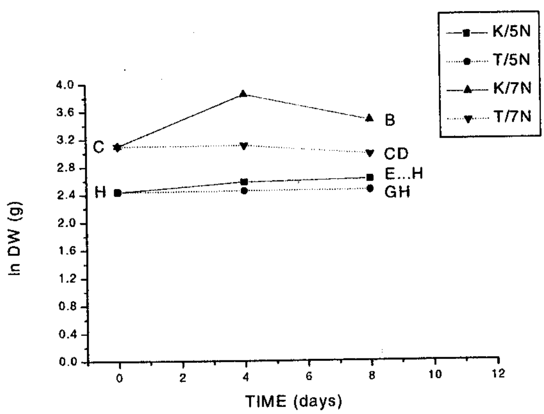

Figure 1. Dry weight accumulation in control and treated (10^{-2} mol sulphosate) plants during the 8-day trial. Plants were grown for 5 and 7 weeks under field conditions. K/5N, K/7N, T/5N, T/7N: control or treated plants aged 5 (RGR_K = 22,62 mg $g^{-1}d^{-1}$; RGR_T = 1,38 mg $g^{-1}d^{-1}$) or 7 weeks (RGR_K = 47,00 mg $g^{-1}d^{-1}$; RGR_T = -13,75 mg $g^{-1}d^{-1}$)

Dry weight accumulation in plants aged 7 weeks was significantly higher in control than in treated plants (Fig. 1). During this trial, a significant redistribution of dry weight occurred among the different maize organs (not shown). In the first half of the trial, root mass ratio (RMR) decreased significantly in both groups, but the decrease proceeded in treated plants, while control plants demonstrated a kind of recovery of this parameter.

On the other hand, stem mass ratio (SMR) was increasing in the initial 4 days of the trial in both groups, but control plants retained the reached level, while it decreased in treated plants to initial values (not shown). Leaf mass ratio (LMR) remained unchanged in the first half of the trial in both groups, but it was significantly lower in control than in treated plants at the end of the trial. The RWC parameter of the 8^{th} leaf of treated plants was significantly lower at the end of the trial than it was in control plants (not shown).

This indicates a considerable dynamic in dry weight accumulation in plants. It is further evidenced by the correlations between different parameters of accumulation and allocation of dry weight in maize plants of the age groups studied (Tab. 1). Dry weight accumulation (and plant growth generally) is highly significantly dependent on root volume (Vr) and SMR, while there is a highly significant negative correlation with LMR. Root volume is highly significantly correlated with RMR and significantly with SMR, while a negative highly significant correlation was found with LMR (Tab. 1). A highly significant negative correlation emerged between SMR and RMR, and the correlation between LMR and all other parameters was also highly significantly negative (Tab. 1). It all shows that root volume (Vr), which is a parameter of functional activity of the root, significantly affects the accumulation and partitioning of dry weight in maize plants of the age groups studied.

Table 1. Correlations between the parameters showing accumulation and partitioning of dry weight, and root volume

	ln DW	RMR	SMR	LMR	Vr
ln DW		-0,063	0,361**	-0,300**	0,701**
RMR			-0,364**	-0,372**	0,339**
SMR				-0,701**	0,208*
LMR					-0,508**
Vr					

The contents of Chl_a (Fig. 2), Chl_b and total Chl, as well as the Chl_a/x+c ratio, were significantly lower in treated than in control plants aged 5 weeks on the 4^{th} day of trial. The content of x+c and Chl_a/Chl_b ratio decreased in treated plants, compared to control plants, but without statistical significance (not shown).

Chl_a (Fig. 2), Chl_b and total Chl contents in the 7^{th} leaf decreased significantly during the trial, but without a significant difference between control and treated plants (age group 6 weeks). The content of x+c and Chl_a/Chl_b ratio in the 7th leaf of those plants did not change significantly during the trial in either group. The Chl_a/x+c ratio decreased, but differences were insignificant throughout the trial. Chl_a content in plants aged 6 weeks was significantly higher than it was in plants aged 5 and 7 weeks (Fig. 2).

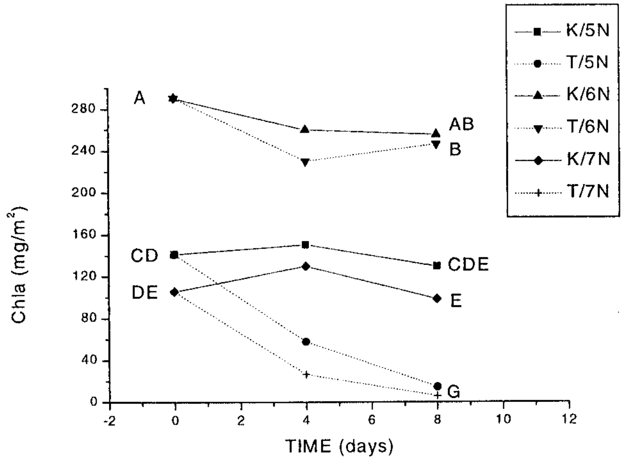

Figure 2. Change in chlorophyll a (Chl_a) contents in the 6th, 7th and 8th leaves of control and treated (10^{-2} mol sulphosate) maize plants during the 8-day trial. The plants were grown for 5, 6 and 7 weeks under field conditions. K/5N, K/6N, K/7N, T/5N, T/6N, T/7N: control or treated plants aged 5, 6 or 7 weeks

The contents of Chl_a (Fig. 2), Chl_b and total Chl in the 8th leaf of treated plants (aged 7 weeks) were significantly lower than they were in control plants on the 4th post-treatment day, while x+c content in the same plants was significantly lower than control at the end of the trial (not shown). The Chl_a/Chl_b ratio was rising in the first half of the trial, but decreased perceptibly by the end of the trial, especially in treated plants. This parameter, however, does not offer a solid basis for any reliable conclusion due to considerable variation. The Chl_a/x+c ratio grew slowly in control plants during the trial, while it was significantly lower in treated plants on the 4th day after treatment (not shown).

Highly significant mutual correlation was detected among all photosynthetic pigments and Chla/x+c (Tab. 2). No correlation appeared between Chl_a/Chl_b and any other parameter (Tab. 2).

Table 2. Correlations between contents and ratios of photosynthetic pigments

	Chl_a	Chl_b	Chl_{a+b}	Chl_a/Chl_b	X+c	Chl_a/x+c
Chl_a		0,968**	0,998**	0,213	0,920**	0,803**
Chl_b			0,981**	0,082	0,865**	0,803**
Chl_{a+b}				0,184	0,913**	0,807**
Chl_a/Chl_b					0,250	0,199
X+c						0,582**
Chl_a/x+c						

The parameters of Chl_a fluorescence and photosynthesis Fv/Fm, Φ PS II, qP and ETR (Fig. 3) reveal an interesting dynamics in the trial. On the 4^{th} day, those parameters were significantly lower in treated plants aged 5 weeks than in control plants. On the 6^{th} day, the differences between control and treated plants were statistically insignificant, but at the end of the trial again they became significant again (not shown). It reflects reparative processes that become overpowered by the phytotoxic activity of sulphosate at the end of the trial. The statistically more sensitive parameter Fv/F_0 (1) showed the beginning of sulphosate-caused inhibition of photosynthesis exactly on the 4^{th} day of the trial (not shown). Changes in the photoprotection parameter NPQ (Tab. 3) and ratios of photosynthetic pigments (Fig. 2, Tab. 2) indicate that antenna changes had no crucial effect on the sulphosate-caused phytotoxicity. The parameters of quantum yield of the reaction centre (RC) of PS II (Fv/Fm, Fv'/Fm') in the 8^{th} leaf of treated plants aged 7 weeks on the 6^{th} day of the trial were significantly lower than they were in control plants (not shown).

However, Fv/F_0 was significantly lower in treated than in control plants as early as on the 2^{nd} day of the trial, and it remained lower until the end of the trial (not shown). The situation is similar regarding the parameters Φ PS II, qP and ETR (Fig. 3). The photoprotection parameter NPQ decreased during the trial without a significant difference between the groups.

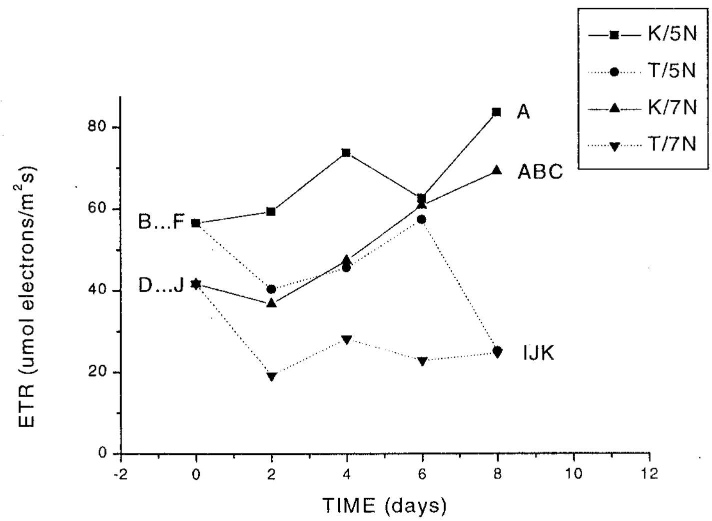

Figure 3. Changes in the ETR parameter of photosynthesis of the 6^{th} and 8^{th} leaves of control and treated (10^{-2} mol sulphosate) maize plants during the 8-day trial. The plants were grown for 5 and 7 weeks under field conditions. K/5N, K/7N, T/5N, T/7N: control or treated plants aged 5 and 7 weeks

Table 3. Correlations between Chl_a fluorescence and photosynthesis parameters

	Fv/Fm	Fv/F_0	Φ PS II	qP	Fv'/Fm'	ETR	NPQ
Fv/Fm		0,909**	0,524**	0,692**	0,441**	0,506**	0,322**
Fv/F_0			0,643**	0,769**	0,517**	0,625**	0,259**
Φ PS II				0,884**	0,905**	0,892**	-0,175
qP					0,747**	0,804**	-0,051
Fv'/Fm'						0,852**	-0,118
ETR							-0,012
NPQ							

What kind of correlation is detectable between the different parameters of Chl_a fluorescence and photosynthesis in maize plants of the age groups investigated? The mutual correlation among ETR, Φ PS II, qP and Fv'/Fm' is highly significant, as well as their correlation with Fv/Fm и Fv/F_0, but the correlation with the NPQ parameter of photoprotection is not significant (Tab. 3). On the other hand, Fv/Fm и Fv/F_0 parameters are highly significantly correlated with NPQ (Tab. 3). Changes in NPQ (Tab. 3) and ratios of photosynthetic pigments (Fig. 2, Tab. 2) showed that the antenna change did not crucially influence phytotoxicity induced by sulphosate. Neither Fv/Fm nor Fv/F_0, as indicators of quantum yield of the RC PS II, had crucial effect (despite being highly significantly correlated with ETR) on the process of photosynthesis in maize plants aged 5 and 7 weeks, regardless of whether the plants had been treated with sulphosate or not. All relevant facts show that sulphosate affected photosynthesis mostly via processes that are independent from the photosystem 2 (PS II), which is consistent with literature (9, 10).

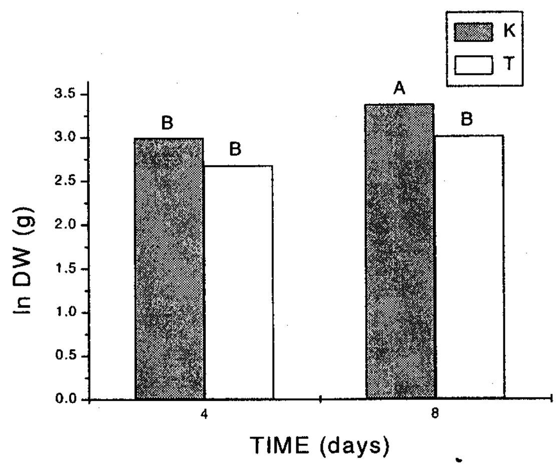

Figure 4. Dry weight accumulation in control and treated (10^{-2} mol sulphosate) maize plants during the 8-day trial. The plants were grown for 6 weeks under field conditions. K, T: control or treated plants

Six-week old plants were not sampled for dry weight measurements at the beginning of the trial due to technical difficulties, so that values for that parameter and RGR are missing. At the end of the trial, dry weight accumulation was significantly higher in control than in treated plants (Fig. 4). Why?

Throughout the trial, the RMR of control plants increased, while that of treated plants stagnated, so that it was significantly higher in control than in treated plants at the end of the trial (not shown). SMR and LMR did not change significantly during the trial and there were no significant differences between control and treated plants. The root volume of control plants increased significantly over the trial period, while that of treated plants stagnated (not shown).

Dry weight accumulation (ln DW) was found to be highly significantly correlated with RMR and significantly with LMR (Tab. 4). LMR had a highly significant negative correlation with RMR and SMR (Tab. 4). This situation is rather different from the findings regarding plants aged 5 and 7 weeks. In 6-week old plants, dry weight accumulation (and growth) did not depend on the functional activity of the root (parameter Vr) or the stem mass ratio (SMR) as it did in plants aged 5 and 7 weeks, but rather on the dry root and leaf mass ratios (RMR and LMR).

Table 4. Correlations between the parameters of accumulation and partitioning of dry weight and root volume in maize plants aged 6 weeks

	ln DW	RMR	SMR	LMR	Vr
Ln DW		0,614**	-0,098	0,412*	0,295
RMR			-0,427*	-0,515**	0,089
SMR				-0,538**	-0,230
LMR					0,144
Vr					

The parameters of Chl_a fluorescence (Fv/Fm, Φ PS II and Fv'/Fm') were significantly higher in 6-week old control plants than treated plants as early as on the 3rd day (not shown). However, Fv/F_0 did not change significantly during the trial, while the parameters qP and ETR (Fig. 5) displayed a difference between control and treated plants on the 3rd and 5th days of the trial. No significant differences were observed between control and treated plants aged 6 weeks at the end of the trial (Fig. 5). The photoprotection parameter NPQ changed in an interesting fashion during the trial. Over the initial 3 days, its values were high, but on the 5th day they were significantly lower in control than in treated plants, and they again levelled at the end of the trial (not shown). All parameters of photosynthesis and Chl_a fluorescence were growing throughout the trial. In control plants, they reached a peak on the 5th day, while in treated plants they climaxed at the end of the trial (not shown).

The parameters of Chl_a fluoresence and photosynthesis ETR, Φ PS II, qP and Fv'/Fm' are highly significantly correlated mutually, but a highly significant negative correlation is observed with the NPQ parameter of photoprotection (Tab. 5). Besides, quantum yield parameters of the PS II (Fv/Fm, Fv/F_0) were highly significantly correlated mutually and with the parameters ETR, Φ PS II and Fv'/Fm', but Fv/F_0 was in significant negative correlation with the NPQ parameter of photoprotection (Tab. 5).

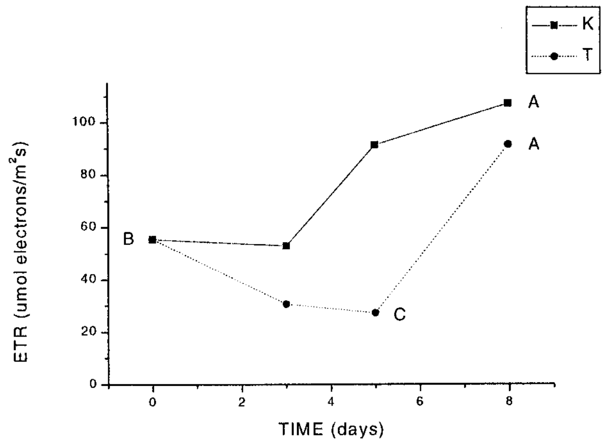

Figure 5. Change in the ETR parameter of photosynthesis of the 7^{th} leaf in control and treated (10^{-2} mol sulphosate) maize plants during the 8-day trial. The plants were grown for 6 weeks under field conditions. K, T: control or treated plants

Table 5. Correlations between the parameters of Chl_a fluorescence and photosynthesis

	Fv/Fm	Fv/F_0	Φ PS II	qP	Fv'/Fm'	ETR	NPQ
Fv/Fm		0,966**	0,518**	0,463	0,516**	0,467*	-0,366
Fv/F_0			0,595**	0,546**	0,579**	0,509**	-0,471*
Φ PS II				0,956**	0,949**	0,921**	-0,943**
qP					0,890**	0,890**	-0,919**
Fv'/Fm'						0,879**	-0,855**
ETR							-0,802**
NPQ							

What is the cause of such a great difference in photosynthetic responses to the sulphosate-caused stress between plants aged 6 weeks and those aged 5 and 7 weeks? It is noteworthy that no significant degradation of chlorophyll a (Chl_a, Fig. 2) was recorded in 6-week old treated plants (in contrast to those aged 5 and 7 weeks), which means that photosynthesis in those plants was not significantly disturbed when stressed by the herbicide sulphosate.

Looking at the dynamics of ETR change in maize plants aged 6 weeks over the trial period, we detected a considerable and statistically significant inhibition of photosynthesis in the first half of that period (Fig. 5). However, a recovery of photosynthesis occurs in the second half of the trial (Fig. 5). What could be the cause of such relatively stable photosynthesis in maize plants aged 6 weeks after being stressed by the herbicide sulphosate? Unlike plants aged 5 and 7 weeks, the 6-week old maize plants were found to have a highly significant negative correlation with the ETR indicator of photosynthesis and NPQ parameter of photoprotection (Tab. 5). It means that plants aged 6 weeks had an active regulation of photosynthesis by non-photochemical quenching of fluorescence (NPQ), which is probably the most optimal way of regulating photosynthesis under stress (DEMMIG-ADAMS AND ADAMS, 1992; LICHTENTHALER, 1996). It is hard to say what is the cause of this characteristic photosynthetic response of maize plants aged 6 weeks to stress caused by the herbicide sulphosate. It is interesting, however, that dry weight accumulation in 6-week old plants (Tab. 4) depends on factors different from those active in 5- and 7-weeks old plants (Tab. 1). As those factors are mostly associated with the mass ratios of different plant organs, we should not reject the possibility of an influence of source-sink relationship on the photosynthesis of 6-week old plant (PAUL AND FOYER, 2001), all the more so as dry weight accumulation in maize plants aged 6 weeks (Fig. 4) is approximately the same as that in 7-week old plants (Fig. 1), so that „tissue dilution" (12), as a method of alleviating herbicide effect, should not be considered a reliable explanation of the phenomenon.

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RAZLIČITI ASPEKTI INHIBICIJE RASTENJA I FOTOSINTEZE KUKURUZA (*Zea mays* L.) UZROKOVANOG HERBICIDOM SULFOSATOM. 3. UTICAJ UZRASTA BILJAKA

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Izvod

U radu je razmatran uticaj herbicida sulfosata na rastenje, akumulaciju i preraspodelu suve mase, kao i fotosintezu biljaka kukuruza različitog uzrasta (5, 6 i 7 nedelja). Zapaženo je da akumulacija suve mase (ln DW), koja u krajnjem određuje rastenje, kod biljaka kukuruza uzrasta 5 i 7 nedelja visoko značajno koreliše sa zapreminom korena (Vr) i udeonom suvom masom stabla (SMR), dok

kod biljaka uzrasta 6 nedelja visoko značajno koreliše sa udeonom suvom masom korena i listova (RMR, LMR). Pored toga biljke uzrasta 6 nedelja imaju statistički značajno veći sadržaj hlorofila a (Chla), u najmlađem potpuno razvijenom listu, u odnosu na biljke uzrasta 5 i 7 nedelja. Na osnovu iznetog možemo pretpostaviti da postoje razlike između biljaka ovih uzrasta i u pogledu reakcije fotosintetskog aparata na stres herbicidom sulfosatom. Tako je, po svemu sudeći, regulacija fotosinteze kod biljaka kukuruza uzrasta 5 i 7 nedelja u uslovima stresa herbicidom sulfosatom nezavisna od fotosistema 2 (PS II), što je u skladu sa literaturnim podacima o dejstvu ovog herbicida. Nasuprot tome, regulacija fotosinteze biljaka kukuruza uzrasta 6 nedelja u uslovima stresa herbicidom sulfosatom regulisana je tzv. nefotohemijskim gašenjem fluorescencije Chla (pokazatelj NPQ).

To je optimalan način regulacije fotosinteze u uslovima stresa i predstavlja aklimacioni odgovor. Uzimajući u obzir i faktore koji određuju akumulaciju suve mase biljaka uzrasta 6 nedelja, ne možemo isključiti pretpostavku da je fotosinteza kod biljaka kukuruza ovog uzrasta regulisana promenama u tzv. „proizvođač-potrošač" odnosima.

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