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RESEARCH ARTICLE

Functionality of photosystem II in barley leaves under different supply with Mn^{2+}

Eugene M. Lisitsyn*, Svetlana A. Churakova
Federal Agricultural Research Center of the North-East named N.V. Rudnitsky, 166a Lenin Street, Kirov, 610007, Russian Federation; *edaphic@mail.ru

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Abstract

Estimation of parameters of chlorophyll a fluorescence measurements were carried out on six barley (*Hordeum vulgare* L.) cultivars at 14 days after treatment with 0 mmol, 0.5 mmol, 1.0 mmol, 1.5 mmol manganese to investigate changes in some parameters of OJIP-test and reveal similarities or dissimilarities between cultivars in this respect. It is revealed that the sensitivity of different parts of the PSII units varies, and this response is the different for different Mn concentration and is cultivar-dependent. At the same time, none of the varieties, in any of the manganese exposure variant showed deviations of the maximum photochemical efficiency PSII from the physiological norm-the minimum value was noted in 1.0 mM Mn in the cv. Boyarin and amounted to 0.783 units. It was assumed that the change in the integral index of effective photosynthesis occurs in different cultivars due to different functional changes, while the level of stress factor also plays an important role. This indicates, firstly, the need for targeted breeding (to a specific level of the acting factor); secondly, the possibility of pyramidizing the integral level of resistance to stress by selecting parents differing in the level of change in individual functional reactions of photosynthesis.

Keywords: OJIP-test, chlorophyll fluorescence, manganese, absorption, trapping, dissipation, performance index.

Introduction

The level of photosynthetic reactions is a good measure of the total plant productivity. Therefore, evaluating the operation of the photosynthetic apparatus can significantly simplify and accelerate the process of plant's phenotyping. Today, the fastest and most economical method of measuring the photosynthetic processes of plants is the method of assessing the fluorescence of chlorophyll (Chl). Chlorophyll a fluorescence is a measure of the energy of absorbed light quants that have not been used during photosynthesis or dissipated as heat (Strasser et al. 2000). At normal and effective operation of photosystem II (PSII), the intensity of chlorophyll a fluorescence remains low, and any disruption to the photosynthesis process leads to a its significant increase (Lichtenthaler & Rinderle 1988).

Measurement of parameters of Chl a rapid fluorescence gives a very large amount of information about the functionality of the PSII in a relatively short time (several minutes). In recent years, the measurement of Chl fluorescence, in particular the OJIP test, has become a popular method for assessing the stability of photosynthesis under the influence of various stress factors of both abiotic and biotic nature (Dorsaf et al. 2018; Kalaji et al. 2018; Rapacz et al. 2019). The authors confirmed the suitability of some fluorescence parameters as biomarkers for screening plants resistant to these stressors.

Both manganese (Mn) deficiency (Schmidt et al. 2016) and excess (Liu et al. 2021) represents a major abiotic stress for plant growth. One proposed mechanisms behind Mn efficiency linked to the functionality of the oxygen evolving complex (OEC) of PSII (Schmidt et al. 2015; de Bang et al. 2015). Effect of Mn deficiency (concentration equal to some nM or μM) is studied mainly on agricultural crops (legumes, cereals, etc.) (Husted et al. 2009; Schmidt et al. 2016) whereas Mn excess (concentration equal to some mM)-on woody crops (Liang et al. 2019; Liu et al. 2021). But agricultural soil in European North-east are mainly podzolic and sod-podzolic with low natural pH and high content of mobile and total manganese up to 233 mg/kg-486 mg/kg of soil (Shikhova & Egoshina 2004; Zubkova 2015) that is equal to 1.5 mM-3.5 mM Mn. Genotypic differences of barley with respect to activity of photosynthetic apparatus under Mn deficiency have been reported earlier (Husted et al. 2009).

The aim of the present article was to investigate changes in some parameters of OJIP-test in six spring barley cultivars under condition of excess manganese in growth media and reveal similarities or dissimilarities between cultivars in this respect.

Materials and Methods

The object of the study was six barley cultivars: Belgorodsky 100, Bionic, Boyarin, Dobryak, Farmer and Forward. Thirty-five grains of each cultivar were placed in rolls of filter paper in 3 times repetition. Plants were grown for 2 weeks on a full nutrient mixture at a photoperiod of 16/8 hours (day/night) and room temperature. Manganese was added to the nutrient medium as a $MnSO_4 \times H_2O$ salt at a concentration of 0.5 mM, 1.0 mM and 1.5 mM Mn; control (zero) variant-without manganese addition. Chl A fluorescence was recorded on dark-adapted (20 minutes) seedlings using a Fluor Pen FP 110/S fluorometer (Photon Systems Instruments, Czech Republic) according to the manufacturer's guidelines. Induction of fluorescence curves of Chl A were initiated with red light (=650 nm) at an intensity of 3,000 μmol $m^{-2}s^{-1}$. The following Chl A fluorescence kinetics parameters were evaluated and calculated: Fo (minimal fluorescence when all PSII reaction centers are assumed to be open); Fm (maximal fluorescence when all reaction centers of PSII are closed); Fv (maximal variable fluorescence); Fv/Fm (maximal quantum yield of PSII); Fv/Fo (ability of antenna complexes to capture excitation energy); (efficiency of electron transfer from QA to QB); δRE (efficiency of electron transfer from QB until PSI acceptor); δRE (summering efficiency of electron transfer from PSII until PSI acceptor); specific energy fluxes per one reaction center of PSII (ABS/RC–light energy absorption flux; TRo/RC–maximum trapped exiton flux; ETo/RC–electron transport flux from QA to QB; DIo/RC–energy dissipation flux); performance index for energy conservation from absorbed photons to the reduction of QB (PIABS) or of PSI acceptors (PIABS_total).

The obtained data were processed using descriptive statistics with Microsoft Office Excel 2007 software packages. The tables show the average data of threefold replication; the significance of the differences between the variants for each cultivar was assessed by the Duncan criterion at p≤0.05.

Results and Discussion

The data in (Tab. 1) show the effect of exogenous manganese ions on the energy capture and conversion efficiency of the PSII of spring barley leaves.

Table 1. Indexes of PSII functionality on photon capture and efficiency of electron transferring within PSII

Cultivar	Mn	Fv/Fm	Fv/Fo	ψo	δRE	ψRE
Forward	0	0.799 a	3.98 a	0.608 b	0.335 a	0.203 b
	0.5	0.813 b	4.35 b	0.640 b	0.364 b	0.233 c
	1	0.803 a	4.08 a	0.562 a	0.328 a	0.184 a
	1.5	0.803 ab	4.10 ab	0.609 b	0.360 ab	0.221 bc
Farmer	0	0.790 ab	3.78 ab	0.595 bc	0.300 b	0.179 b
	0.5	0.796 b	3.91 b	0.602 c	0.291 b	0.175 b
	1	0.797 b	3.93 b	0.579 ab	0.263 a	0.152 a
	1.5	0.787 a	3.69 a	0.566 a	0.266 a	0.151 a
Belgorodsky 100	0	0.801 a	4.04 a	0.667 c	0.339 b	0.228 b
	0.5	0.795 a	3.89 a	0.614 a	0.245 a	0.151 a
	1	0.802 a	4.05 a	0.643 b	0.237 a	0.152 a
	1.5	0.801 a	4.02 a	0.638 b	0.259 a	0.165 a
Bionic	0	0.795 a	3.89 a	0.623 a	0.304 a	0.189 a
	0.5	0.804 b	4.12 b	0.629 a	0.318 a	0.200 a
	1	0.801 ab	4.02 ab	0.609 a	0.312 a	0.191 a
	1.5	0.807 b	4.19 b	0.610 a	0.347 b	0.212 b
Boyarin	0	0.795 b	3.89 b	0.574 ab	0.322 b	0.185 b
	0.5	0.784 a	3.62 a	0.586 b	0.259 a	0.152 a
	1	0.783 a	3.61 a	0.554 a	0.253 a	0.140 a
	1.5	0.796 b	3.91 b	0.586 b	0.293 b	0.171 b
Dobryak	0	0.796 a	3.90 a	0.571 a	0.321 b	0.184 a
	0.5	0.800 a	3.99 a	0.644 c	0.309 a	0.199 a
	1	0.802 a	4.04 a	0.612 b	0.336 bc	0.206 ab
	1.5	0.807 b	4.19 b	0.634 bc	0.362 c	0.231 b

Note: for each cultivar values followed with the same letter don' t differed statistically according to the Duncan criterion at p≤0.05

Index of the maximum photochemical efficiency of PSII (Fv/Fm), which normally should not be lower than 0.740 (Goltsev et al. 2016), is earlier proposed as a powerful tool to accurately diagnose even latent Mn deficiency (Leplat et al. 2016). According to our data, none of the cultivars, in any of the manganese concentration, showed deviations of the parameter from the physiological norm-the minimum value was noted in variant 1.0 mM Mn for the cv. Boyarin and amounted to 0.783 arbitrary units. In corn plants, (Doncheva et al. 2009) noted the significant effect of manganese on this parameter in the Mn-sensitive cv. Kneja 605 but the absence of an effect in the Mn-resistant cv. Kneja 434.

All cultivars tested showed a qualitatively similar reaction of the parameters Fv/Fm (maximum quantum field of PSII) and Fv/Fo (ability of antenna complexes PSII to capture excitation energy) to change in Mn concentration. At the same time, the cv. Farmer and Belgorodsky 100 did not show statistically significant differences from the zero variant. Cv. Forward raised the level of the parameters when exposed to 0.5 mM Mn (by 1.8% and 9.3%, respectively); cv Dobryak-at 1.5 mM Mn (by 1.4% and 7.4%); cv Bionic-at 0.5 (by 1.1% and 5.9%) and 1.5 mM Mn (by 1.5% and 7.7%). The cv Boyarin was fundamentally distinguished by the fact that, under the influence of 0.5 and 1.0 mM Mn, it reduced the efficiency of capturing and converting light energy (by 1.4%-1.5% and 7.0%-7.2%).

The Fv/Fo parameter is used to evaluate the ability of PSII antenna complexes of leaf chloroplasts to capture excitation energy (photons) (Strasser et al. 2000). Based on the data of (Tab. 1), the variability of the index in the study set of cultivars varied slightly-from 2.3% (at 0 mM Mn) to 6.1% (at 0.5 mM Mn). At the same time, the antenna chlorophylls of cv. Boyarin leaves were the least capable of capturing photons (the average parameter value is 3.758 arbitrary units), and the cv Forward is the most capable of capturing photons (the average parameter value is 4.128 arbitrary units).

The efficiency of electron transfer from the primary (quinone QA) to the secondary (quinone QB) acceptor of PSII (index) statistically significantly decreased under the influence of manganese in the cv Belgorodsky 100 (maximum-in the 0.5 mM Mn variant-by 8%). In the cv Forward, a decrease was noted in variant 1.0 mM Mn (7.5%), in the cv Farmer variety-in variants 1.0 and 1.5 mM Mn (2.7% and 4.9%). The cv. Dobryak, on the contrary, increased the efficiency of this process by 7.2%-12.8%. For the cv Bionic and Boyarin, no statistically significant differences were noted between different manganese concentration in growing media.

For the cv Farmer and Belgorodsky 100, changes in the level of efficiency of electrons transfer from the secondary acceptor PSII and in general from the PSII to the primary acceptors PSI (parameters RE and RE) coincided in the direction with the change of the parameter, but were significantly large in size: the parameter RE decreased in the cv Farmer by 11.4%-12.3%, the parameter RE-by 15.1%-15.7%. For the cv Belgorodsky 100, the decrease was 23.6%-30.1% and 27.7%-33.8%, respectively. A significant decrease in the efficiency of electron transfer to PS1 was noted in the cv Boyarin in variants 0.5 mM and 1.0 mM Mn respectively 20.5%-21.5% and 17.8%-24.3%. However, 0.5 mM manganese increased the efficiency of electron transfer to PS1 in cv Forward by 8.6% (from the secondary acceptor) and 14.7% (in general from PSII). A similar increase was noted in variant 1.5 mM Mn in the cv. Bionic (by 14.1% and 12.6%) and Dobryak (by 12.7% and 25.5%). At the same time, for the cv. Dobryak, a decrease in the δRE parameter in variant 0.5 mM Mn (by 3.8%) was noted compared to the zero variant.

Processes characterizing the photosynthetic activity of PSII can be described in terms of specific energy flows calculated per active reaction center (Tab. 2).

Table 2. Specific energy flows calculated per one active reaction center of PSII.

Cultivar	Mn	ABS/RC	TRo/RC	ETo/RC	DIo/RC
Forward	0	2.082 b	1.664 b	1.012 bc	0.418 b
	0.5	1.809 a	1.470 a	0.938 ab	0.339 a
	1	2.068 b	1.660 b	0.932 a	0.407 b
	1.5	2.155 b	1.729 b	1.046 c	0.426 b
Farmer	0	2.044 a	1.632 a	0.970 a	0.412 a
	0.5	2.189 a	1.743 a	1.049 b	0.446 a
	1	2.367 b	1.887 b	1.092 c	0.480 b
	1.5	2.373 b	1.866 b	1.055 bc	0.507 c
Belgorodsky 100	0	2.170 a	1.736 a	1.148 a	0.435 a
	0.5	2.341 a	1.861 a	1.143 a	0.480 a
	1	2.284 a	1.831 a	1.177 a	0.453 a
	1.5	2.289 a	1.833 a	1.168 a	0.456 a
Bionic	0	2.158 b	1.716 b	1.070 b	0.442 b
	0.5	2.268 b	1.824 c	1.147 c	0.443 b
	1	1.986 a	1.599 a	1.039 ab	0.428 b
	1.5	2.013 a	1.625 a	0.991 a	0.388 a
Boyarin	0	2.241 a	1.781 a	1.019 a	0.460 a
	0.5	2.418 b	1.895 b	1.110 b	0.523 b
	1	2.556 b	2.001 b	1.108 b	0.555 b
	1.5	2.202 a	1.753 a	1.029 ab	0.449 a
Dobryak	0	2.113 b	1.681 b	0.958 a	0.432 b
	0.5	1.910 a	1.640 b	1.056 b	0.411 b
	1	2.177 b	1.643 b	1.006 ab	0.433 b
	1.5	1.922 a	1.551 a	0.979 a	0.371 a

Note: see Tab. 1

The cv. Belgorodsky 100 turned out to be the only one of the studied cultivars in which the manganese concentrations used did not lead to a statistically significant change in any of the parameters of specific energy flows.

The energy flow absorbed by one reaction center (ABS/RC) simultaneously serves as an indicator of the size of the antenna complexes. Growing barley plants in the presence of 0.5 mM manganese led to a decrease in the size of antenna complexes in the cv Forward (by 13.1%) and Dobryak (by 9.7%), but to an increase in it in the cv. Boyarin (by 7.9%). An increase in manganese concentration to 1.0 mM increased the index for the cv. Farmer (by 15.8%) and Boyarin (by 14.1%), reducing it for the cv. Bionic (by 8.0%). The maximum concentration of manganese (1.5 mM) reduced the level of absorption of energy flow by antenna complexes of leaves in the cv. Bionic (by 6.8%) and Dobryak (by 9.0%), but increased in the cv Farmer (by 16.1%).

Non-productive energy consumption (for radiation in the form of heat and fluorescence-DIo/RC parameter) increased in the cv. Farmer (in variant 1.0 mM mn-by 16.5%, in variant 1.5 mM Mn-by 23.1%) and Boyarin (in variant 0.5 mM Mn-by 13.7%, in variant 1.0 mM Mn-by 20.7%). At the same time, there was a decrease in these costs under the influence of manganese in the cv Forward in variant 0.5 mM Mn (by 18.9%), the cv Bionic and Dobryak in variant 1.5 mM Mn (by 12.2 and 14.1%).

The flow of energy stored in the primary photochemical reactions, designated as TRo/RC, in plants grown at 0.5 mM manganese, increased in the cv Bionic and Boyarin (by 6.3% and 6.4%), but decreased in the cv. Forward (by 11.7%) relative to the manganese-free variant. A further increase in manganese content in the growth medium to 1.0 mM led to an increase in the parameter in the cv Farmer and Boyarin (by 15.6% and 12.4%), but a decrease in the cv. Bionic (by 6.8%). In variant 1.5 mM Mn, the cv Farmer has an increase of 14.3%, and the cv Bionic and Dobryak, on the contrary, have a decrease in this flow (by 5.3% and 7.7%).

The energy trapped as the TRo/RC flow is then transferred to the reaction centers and converted there to redox energy by oxidation of the primary acceptor QA, which is then re-oxidized into the initial form, thus creating an electronic transport ETo/RC, resulting in CO_2 fixation (Matorin & Rubin 2012). In the test set of barley cultivars, the presence of 0.5 mM manganese had the greatest effect on this flow. With this effect, the parameter under consideration increased in four cultivars: Farmer, Bionic, Boyarin and Dobryak (by 7.2%-10.2%). An increase in manganese concentration to 1.0 mM was reflected in three cultivars, but while in the cv Farmer and Boyarin there was an increase in the parameter (by 12.6% and 8.7%), then in the cv Forward-a decrease of 7.9%. The variant 1.5 mM Mn affected only two cultivars, while in the cv Farmer the studied flow increased by 8.8%, and in the cv Bionic it decreased by 7.4%.

(Liang et al. 2019) indicates that absorption ABS/RC, trapping TRo/RC, and dissipation DIo/RC were increased in Ligustrum lucidum in a Mn-concentration dependent manner. It is possible that in woody plants these processes go a little differently than in spring barley. The authors also note that all OJIP-test parameters significantly varied with the Mn levels.

For a general characteristic of photosynthetic activity of PSII it is offered to use in practice of Tolerance Index (TI) (Gururani et al. 2015), summarizing the main processes coming at adsorption of photons from antenna complexes to a secondary acceptor of electrons of PSII (plastoquinone QB)-efficiency of absorption of photons (i.e. the ABS parameter), efficiency of capture of excitation energy (TR parameter) and efficiency of use of energy in an Electron Transport chain (ET). In(Giorio & Sellami 2021), this index is designated as the Performance Index (PIABS) and its modification is proposed, taking into account the efficiency of energy transfer to PSI (PIABS_total). The results of the calculation of both indices for the studied barley cultivars are shown in (Tab. 3).

Table 3. Performance Indices of PSII functionality in barley cultivars

Cultivar	Mn	PIABS	PIABS_total
Forward	0	3.011 a	1.508 b
	0.5	3.829 b	2.193 c
	1.0	2.551 a	1.244 a
	1.5	2.384 a	1.260 ab
Farmer	0	2.085 ab	0.846 a
	0.5	2.714 c	1.117 b
	1.0	2.279 b	0.816 a
	1.5	2.040 a	0.744 a
Belgorodsky 100	0	2.961 ab	1.335 c
	0.5	2.677 a	0.685 a
	1.0	3.213 b	0.912 b
	1.5	3.121 ab	0.965 bc
Bionic	0	2.736 a	1.219 a
	0.5	3.315 b	1.668 bc
	1.0	3.417 b	1.686 c
	1.5	2.873 a	1.547 b
Boyarin	0	2.729 c	1.386 c
	0.5	2.134 b	0.753 a
	1.0	1.758 a	0.599 a
	1.5	2.513 c	1.040 b
Dobryak	0	2.859 a	1.441 a
	0.5	3.880 b	1.732 b
	1.0	2.970 a	1.379 a
	1.5	4.516 c	2.814 c

According to the data of the (Tab. 3), it can be concluded that the cultivar reactions to manganese ions are significantly different in terms of energy conservation efficiency when transferred within PSII (PIABS) and beyond (PIABS_total). At the same time, the highest concentration of manganese in the growth medium (1.5 mM) led to a change in the first parameter (PIABS) only in the cv Dobryak, increasing it by 58%. The concentration of 1.0 mM Mn affected four out of six cultivars slightly increasing it in the cv Farmer and Belgorodsky 100 (by 9.3% and 8.5%), significantly increasing it in the cv Bionic (by 24.9%) and reducing it very much in the cv Boyarin (by 35.6%). At the same time, the presence of 0.5 mM manganese was reflected at the level of the PIABS parameter in all cultivars: the cv Forward, Farmer, Bionic and Dobryak increased the parameter by 21.2%-35.7%, and the cv Belgorodsky 100 and Boyarin, on the contrary, decreased by 9.6% and 21.8%.

The PIABS_total index at the cv. Forward increased in variant 0.5 mM Mn (by 45.4%), but decreased in variant 1.0 mM Mn (by 17.5%). In the cv Belgorodsky 100, the index decreased with 0.5 mM and 1.0 mM of manganese by 48.7% and 31.7%, respectively. An increase in the index was noted in the cv Farmer only at 0.5 mM Mn (by 32%). In the cv Bionic, an increase in the index in all variants of manganese exposure by 26.9%-38.3% was noted, while in the cv Boyarin, on the contrary, it decreases by 25.0%-

56.8%. 0.5 mM manganese increased PIABS_total index in the cv Dobryak by 20.2%, and 1.5 mM Mn-by 95.2%. At the same time, variant 1.0 mM Mn did not lead to a deviation from the zero variant.

Thus, the sensitivity of different parts of the PSII units varies, and this response is the different for different Mn concentration and is cultivar-dependent.he calculation of both indices for the studied barley cultivars are shown in Tab. 3.

Conclusions

None of the varieties, in any of the manganese exposure variant showed deviations of the maximum photochemical efficiency PSII from the physiological norm- the minimum value was noted in 1.0 mM Mn in the cv. Boyarin and amounted to 0.783 units. Antenna chlorophylls of cv. Boyarin were least capable of photon capture (average parameter value 3.758 arbitrary units), and in Forward-to the greatest extent (average parameter value 4.128 arbitrary units).

There are no regular changes of all estimated parameters from manganese concentration in the growth medium. For example, the ability of antenna complexes of PSII to capture excitation energy increased in the cv. Forward (0.5 mM Mn-by 9.3%); Dobryak (1.5 mM Mn-by 7.4%); Bionic-at 0.5 (by 5.9%) and 1.5 mM Mn (by 7.7%), but decreased in cv. Boyarin under the influence of 0.5 and 1.0 mM Mn (by 7.0%-7.2%). Reduction of electron transfer efficiency from primary (quinone QA) to secondary (quinone QB) acceptor PSII (parameter) decreased in cv. Belgorodsky 100 (maximum in 0.5 mM Mn by 8%). In the cv. Forward, a decrease was noted in 1.0 mM Mn (-7.5%), in the cv. Farmer in 1.0 and 1.5 mM Mn (-2.7% and -4.9%). The cv. Dobryak, on the contrary, increased the efficiency of this process by 7.2%-12.8%. For cv. Bionic and Boyarin, no statistically significant differences were noted between manganese exposure options. The flow of energy stored in primary photochemical reactions, designated as TRo/RC, in plants grown at 0.5 mM Mn, increased in the cv. Bionic and Boyarin (by 6.3% and 6.4%), but decreased in the cv. Forward (by 11.7%) relative to the manganese-free variant. Electron transport ETo/RC, which ultimately leads to fixation of CO_2 in the studied set of barley cultivars most changed under the influence of manganese at a concentration of 0.5 mM. With this effect, the parameter under consideration increased in four cultivars: Farmer, Bionic, Boyarin and Dobryak (by 7.2%-10.2%). An increase in manganese concentration to 1.0 mM was reflected in three cultivars, while in the cv. Farmer and Boyarin there was an increase in the parameter (by 12.6% and 8.7%), and in the cv. Forward-a decrease of 7.9%. The concentration of manganese 1.5 mM affected only two cultivars, while in the cv. Farmer the studied flow increased by 8.8%, and in the cv. Bionic decreased by 7.4%. Cultivar reactions to manganese ions are also significantly different in terms of energy conservation efficiency when transferred within PSII (PIABS) and beyond (PIABS_total). At the same time, the highest concentration of manganese in the growth medium (1.5 mM) led to a change in the first parameter only in the cv. Dobryak (+58%). The concentration of 1.0 mM affected four out of six cultivars, slightly increasing it in the cv. Farmer and Belgorodsky 100 (by 9.3 and 8.5%), significantly increasing it in the cv. Bionic (by 24.9%) and reducing it very much in the cv. Boyarin (by 35.6%). The PIABS_total index at the cv. Forward increased in 0.5 mM Mn (by 45.4%), but decreased in 1.0 mM Mn (by 17.5%). In the cv. Belgorodsky 100, the index decreased with 0.5 and 1.0 mM Mn by 48.7 and 31.7%, respectively. In the cv. Bionic, an increase in the index in all variants of manganese exposure by 26.9%-38.3% was noted, while in the cv. Boyarin, on the contrary, a decrease in it by 25.0%-56.8%. The cv. Belgorodsky 100 turned out to be the only one of the studied cultivars in which the manganese concentrations used did not lead to a statistically significant change in any of the parameters of specific energy flows.

Based on the above, it can be assumed that the change in the integral index of effective photosynthesis occurs in different cultivars due to different functional changes, while the level of stress factor also plays an important role

This indicates, firstly, the need for targeted breeding (to a specific level of the acting factor); secondly, the possibility of pyramidizing the integral level of resistance to stress by selecting parents differing in the level of change in individual functional reactions of photosynthesis.

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