https://doi.org/10.26898/0370-8799-2022-6-2 Тип статьи: оригинальная
УДК: 632.4.01/.08:535.37 Type of article: original

ФЛУОРЕСЦЕНЦИЯ ХЛОРОФИЛЛА ЛИСТЬЕВ ПШЕНИЦЫ ПРИ ИНФИЦИРОВАНИИ *BIPOLARIS SOROKINIANA*, ХЛОРИДНОМ ЗАСОЛЕНИИ И ГИПЕРТЕРМИИ СЕМЯН

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Представлены результаты измерения и сравнение информативности параметров флуоресценции хлорофилла (ФлХ) 10-суточных проростков яровой пшеницы в лабораторных условиях при раздельном и совместном действии стрессоров. Исследования проводили в 2020, 2021 гг. Установлено, что раздельное и совместное действие хлоридного засоления (1,3%), инфицирования возбудителем корневой гнили злаков *Bipolaris sorokiniana* Shoem. (5000 конидий на зерно) подавляло световые и темновые реакции фотосинтеза. Обнаружено достоверное снижение эффективного квантового выхода *Y*(II), коэффициента фотохимического тушения *qP* и скорости электронного транспорта *ETR* у обоих сортов, наибольшее – в варианте совместного действия стрессоров (до 62,7%). Максимальный фотохимический квантовый выход ФС II *Fv / Fm* оказался менее информативным, достоверных изменений параметра не обнаружено. Ингибирование светозависимых реакций сопровождалось достоверным увеличением значений параметров нефотохимического тушения ФлХ – коэффициента *qN* и квантового выхода регулируемого нефотохимического тушения ФлХ *Y*(*NPQ*) от 24,1 до 72,1% у обоих сортов, наиболее выраженным у сорта Сибирская 12. Параметр *Y*(*NO*) – квантовый выход нерегулируемого нефотохимического тушения ФлХ – изменялся недостоверно относительно контроля у обоих сортов. Выявлен положительный эффект предварительной гипертермии семян (43 °C) на функциональную активность фотосинтетического аппарата проростков – достоверное ($p \leq 0{,}05$) увеличение значений параметров *Y*(II), *qP, ETR* (на 18,0–59,0%) и снижение значений параметров *Y*(*NPQ*), *Y*(*NO*) и *qN* (на 18,8–35,1%) при последующем действии инфицирования и хлоридного засоления у обоих сортов, преимущественно у сорта Омская 18. Установлена информативность параметров ФлХ для оценки стрессоустойчивости сортов. Достоверные межсортовые различия (от 1,2–6,2 раза) выявлены практически по всем параметрам (кроме *Fv / Fm, Y*(*NO*), *Fv*) по всем вариантам опыта. Установлена сортоспецифичность – наименьшие изменения параметров ФлХ относительно контроля были у устойчивого сорта Омская 18 во всех вариантах опыта. Предложенный подход позволит разработать неинвазивный метод ранней диагностики стрессоустойчивости (фенотипирования) новых генотипов пшеницы к действию биотических и абиотических стрессоров.

Ключевые слова: пшеница, сорт, устойчивость, стрессоры, фотосинтез, параметры флуоресценции хлорофилла

CHLOROPHYLL FLUORESCENCE OF WHEAT LEAVES WHEN INFECTED WITH *BIPOLARIS SOROKINIANA*, CHLORIDE SALINITY AND SEED HYPERTHERMIA

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Results of chlorophyll fluorescence parameters (ChlF) informativity measurement and comparison of 10-d-old spring wheat seedlings under laboratory conditions under separate and combined stressors action are presented. It was found that separate and combined action of chloride salinity (1,3%), infection with cereal root rot pathogen *Bipolaris sorokiniana* Shoem. (5000 conidia per grain) suppressed light and dark reactions of photosynthesis. The effective quantum yield *Y*(II), photochemical quenching *qP* and electron transport *ETR* decreased significantly in both cultivars, most significantly in the co-activated version (up to 62,7%). The maximum photochemical quantum yield of FS II *Fv / Fm* was less informative, no significant changes in the parameter were found. Inhibition of light-dependent reactions was accompanied by a significant increase in the values of the parameters of non-photochemical quenching ChlF - coefficient qN and quantum yield of regulated non-photochemical quenching ChlF *Y* (*NPQ*) from 24.1 to 72.1% in both varieties, most pronounced in the variety Sibirskaya 12. The parameter *Y*(*NO*)*,* the quantum yield of unregulated non-photochemical quenching of ChlF, changed insignificantly relative to the control in both varieties. The positive effect of seed pre-heating (43 °C) on the functional activity of photosynthetic apparatus of seedlings - the reliable ($p \leq 0{,}05$) increase of the parameter *Y(II)*, *qP*, *ETR* (by 18,0-59,0%) and decrease of the parameter *Y*(*NPQ*)*, Y*(*NO*) and *qN* (by 18,8-35,1%) at further infection and chloride salinization in both sorts, mainly in the variety Omskaya 18 was revealed. The informativeness of the parameters ChlF for assessment of varieties stress tolerance was established. Significant inter-variety differences (from 1.2-6.2 times) were revealed for almost all parameters (except for *Fv / Fm, Y(NO), Fv*) for all variants of experiment. The varietal specificity was established - the least changes in ChlF parameters relative to the control were in the stable variety Omskaya 18 in all variants of the experiment. The proposed approach will make it possible to develop a non-invasive method for early diagnosis of stress tolerance (phenotyping) of new wheat genotypes to biotic and abiotic stressors.

Keywords: wheat, variety, resistance, stressors, photosynthesis, chlorophyll fluorescence parameters

Для цитирования: *Гурова Т.А., Чесноченко Н.Е.* Флуоресценция хлорофилла листьев пшеницы при инфицировании *Bipolaris sorokiniana,* хлоридном засолении и гипертермии семян // Сибирский вестник сельскохозяйственной науки. 2022. Т. 52. № 6. С. 12–28. https://doi.org/10.26898/0370-8799-2022-6-2

For citation: Gurova T.A., Chesnochenko N.E. Chlorophyll fluorescence of wheat leaves when infected with *Bipolaris sorokiniana,* chloride salinity and seed hyperthermia. *Sibirskii vestnik sel'skokhozyaistvennoi nauki = Siberian Herald of Agricultural Science*, 2022, vol. 52, no. 6, pp. 12–28. https://doi.org/10.26898/0370-8799-2022-6-2

Конфликт интересов
Авторы заявляют об отсутствии конфликта интересов.
Conflict of interest
The author declares no conflict of interest.

INTRODUCTION

Adverse environmental conditions, soil salinity, pathogens lead to stressful conditions of plants, which limits the agricultural production of wheat worldwide. According to current projections, stress interactions between abiotic and biotic environmental factors will become even more prevalent due to observed and projected climate change [1, 2]. One of the ways to reduce the negative effects of the complex of stressors and to obtain high and stable yields of spring wheat grain is a reasonable choice of stress-resistant varieties [3, 4]. In this regard, the development of selection methods to accelerate the screening of stress-resistant genotypes at the early stages of plant development plays an important role in the programs to develop stress-resistant crop varieties. Biophysical diagnostic methods meet such requirements. In this case, integral indices of plant organism state, such as energy status (photosynthesis intensity, oxidative phosphorylation), cell membrane stability (permeability), electrical parameters (action potential), spectral characteristics, etc., are used as diagnostic indicators. [5-7].

Photosynthesis is one of the stress-sensitive processes of plant cells [8, 9]. During photosynthesis, all the light energy absorbed by chlorophyll molecules is spent on photochemical reactions (photochemical quenching), thermal dissipation (non-photochemical quenching) and fluorescence, processes competing in the deactivation of excited states of photosystem II (PS II) pigments [10]. A change in the efficiency of one of them leads to an oppositely directed change in the other two. Disruption of photosynthetic activity of plants can be assessed by chlorophyll fluorescence registration (ChlF), which allows to determine the overall bioenergetic status of a plant organism, i.e. its ability to photosynthetically transform energy [11, 12]. ChlF is a secondary emission of light energy absorbed by a chlorophyll molecule, a measure of the energy of light quanta that were not used in photosynthesis. ChlF is emitted mainly by chlorophyll α molecules in FS II antenna complexes and is associated not only with processes in the pigment matrix and reaction centers (RC) of photosystem II (PS II), but also with redox reactions on the donor and acceptor sides and even in the entire electron transfer chain. It is determined in the mode of recording dark induction curves with pulse time saturation analysis [13]. By measuring the characteristics of ChlF, it is possible to estimate the photosynthetic apparatus performance, including the fraction of energy used in photochemistry [14].

The use of ChlF measurements in the study of photosynthetic characteristics and stress in plants is currently widespread in physiological and ecophysiological studies. This is due to the development of understanding of the relationship between the parameters of ChlF and the processes of photosynthetic electron transport in the electron transport chain (ETC), which determine the change in fluorescence intensity, as well as the commercial availability of a number of fluorimeters [15, 16].

The method is non-destructive, highly sensitive and allows us to obtain information on photosynthetic efficiency and integrity of photosynthetic apparatus at the earliest stages of stress development [13, 17]. In particular, it is used to assess the resistance of wheat to temperature stress, drought, increased acidity, salinity and herbicides [7, 18- 20], apple varieties and forms to pesticides [21], garden strawberry to diseases and pests [22, 23], and for diagnostics of mineral nutrition [24, 25].

ChlF is registered by means of sensitive photodiodes used separately or as a part of fluorimeters. The most promising and widespread are PAM fluorimeters, which measure ChlF by pulse-amplitude-modulation method (Pulse-Amplitude-Modulation). By modulating the amplitude of the measuring light beam (microsecond pulse range) and parallel detection of the excited ChlF, the relative photochemical yield can be determined[1] [14]. Registration of ChlF is performed *in vivo*, does not require sample preparation of the objects under study, and takes place in the presence of light with any spectral composition, as well as sunlight under field conditions [16].

[1]Product catalog of the German company “Heinz Walz GmbH”. http://www.heinzwalz.ru/

Our study was aimed at evaluation of photosynthetic activity of wheat seedlings under separate and combined action of salt stress, infection with cereal root rot pathogen *Bipolaris sorokiniana* Shoem. and elevated temperature (seed heating). These stressors are among the factors negatively affecting the growth and development of wheat in the major grain-growing areas of the world, including the West Siberian region[2] [26, 27]. These factors can disrupt normal metabolism of wheat plants, negatively affecting key physiological processes, including photosynthesis [6, 28].

The purpose of the work is to study the effect of separate and combined action of chloride salinity, common root rot and elevated temperature (seed heating) on ChlF parameters of soft spring wheat seedlings to identify informative parameters for assessing stress tolerance of varieties.

MATERIAL AND METHODS

Experimental work was carried out in the laboratory for the study of physical processes in agrophytocenoses of the Siberia Physical and Engineering Institute of Agrarian Issues, SFSCA RAS.

To identify informative parameters of ChlF, greenhouse experiments (water cultures) under laboratory conditions were carried out under separate and combined effects of sodium chloride, the causative agent of common root rot of cereals and elevated temperature (seed heating) on the seedlings of released varieties of spring wheat: Sibirskaya 12 (relatively unstable) selected by Siberian Research Institute of Plant Industry and Breeding - branch of the Institute of Cytology and Genetics, SB RAS, and Omskaya 18 (relatively stable) selected by Omsk Agrarian Scientific Center.

Experiment options:

- Control (seeds without heating) and elevated temperature (seed heating at 43 °C);
- seeds without heating + infection with *B. sorokiniana* (5000 conidia per grain);
- seeds without heating + chloride salinity 1,3%;
- seeds without heating + infection with *B. sorokiniana* (5000 conidia per grain) + chloride salination 1.3%;
- seed heating at 43°C + infection with *B. sorokiniana* (5000 conidia per grain);
- seed heating at 43°C + chloride salination 1.3%;
- seed heating at 43 °C + infection with *B. sorokiniana* (5000 conidia per grain + chloride salination 1.3%.

The levels of stress loads - conidial suspension of *B. sorokiniana* 5000 conidia per grain and concentration of sodium chloride (NaCl) 1.3% - were determined by us in specially conducted greenhouse experiments as allowing to differentiate wheat varieties of Siberian breeding in evaluation of their resistance to these stress factors by biometric indices and cell membrane permeability [3, 4] [29].

Wheat seeds were presterilized with 96% ethyl alcohol for 2 min followed by three-fold rinsing with distilled water. The seeds were heated for 20 min in hot water in a water bath according to VIR method[5]. After cooling, the seeds were placed in Petri dishes with moistened filter paper and germinated in the thermostat at 22 ºC for three days. Simultaneously, soaked seed samples were germinated without heating. On the third day of cultivation, the seeds were infected with a conidial suspension of a mixture of medium pathogenic *B. sorokiniana* isolates prepared on 0.1% aqueous agar (one drop per grain).

[2]Goltyapin V.Y., Mishurov N.P., Fedorenko V.F., Golubev I.G., Balabanov V.I., Petukhov D.A. Digital technologies for surveying agricultural land by drones: analytical review. Moscow: Rosinformagrotech, 2020. 88 p.

[3]Patent RU 2446671 IPC A01G7/00, A01H1/04. Method of determination of relative resistance of varieties of soft spring wheat to chloride salinity. T.A. Gurova, V.Y. Berezina, N.S. Kutserubova. Published on 10.04.2012.

[4]Patent RU 2625027 IPC A01C12N 1/14, A01H 5/12. Method for determining the relative resistance of varieties of soft spring wheat to the pathogen of common root rot of cereals. T.A. Gurova, V.V. Alt, O.S. Lugovskaya. Published on 11.07.2017.

[5]Diagnostics of plant resistance to stresses: method recommendations, edited by G.V. Udovenko. Л., 1988. 228 p.

Then the seedlings were grown in the climatic chamber Biotron-7 in a roll culture with tap water (variants - control and infection with *B. sorokiniana*) and sodium chloride at the photoperiod "day-night" 16 and 8 h, respectively, illumination 20 000 and 0 lux (day-night), temperature 22 and 18 ºC (day-night), humidity 60%.

The kinetics and parameters of ChlF PS II were recorded using a Dual- PAM-100/F fluorimeter (Heinz Walz GmbH, Germany) using amplitude-pulse modulation in the mode of recording the slow kinetics of dark induction curves with saturation pulse analysis (Slow Kinetics). The delay time for recording the induction curves after determining the minimum and maximum ChlF α is 40 s, which is sufficient for complete re-oxidation of acceptors ("opening" of reaction centers). The interval between saturation pulses during recording of induction curves is 20 s, the data recording time is 4 min. Excitation of chlorophyll α molecules was performed by a "blue" light-emitting diode with a wavelength of 460 nm, detection of the ChlF was performed by a "red" photodiode with a wavelength of 680 nm. The fluorimeter was controlled by specialized software. Before measuring the ChlF, 10-day-old wheat seedlings were adapted to darkness in a sample chamber for 30 min to reach completely oxidized state of PS II acceptors (all PS II reaction centers were "open"). To record the ChlF parameters, a seedling sheet was fixed on a rack with an optical holder and a program for recording ChlF induction curves was run.

The following fluorescence parameters were obtained: *Fo, Fm* - minimum and maximum levels of ChlF induced by the light pulse after leaf adaptation to darkness; *Fo', Fm'* - minimum and maximum levels of ChlF induced by the light pulse after leaf adaptation to light; *Fv / Fm* - maximum photochemical quantum yield of PS II; *Y*(II) - effective photochemical quantum yield of PS II after leaf adaptation to light; *Y*(*NPQ*) - quantum yield of regulated non-photochemical quenching of ChlF; *Y*(*NO*) - quantum yield of unregulated non-photochemical quenching of ChlF; *qP* - photochemical quenching factor of ChlF; *qN* - non-photochemical quenching factor of ChlF; *ETR* - electron transport rate. The variable (variable) ChlF was calculated: $Fv = Fm - Fo$.

Variety response was determined by the relative change in the measured parameters of seedlings after exposure of plants to stressors. The smaller changes in parameters, the higher the resistance in the studied group of varieties. Repetition of the experiments were analytical and biological - 6-fold and 3-fold. Statistical processing of data was performed in Microsoft Excel 2000 program using a standard data analysis package. The parameters of ChlF recorded for 4 min were analyzed. Error of mean did not exceed 3-5%. Three series of experiments were performed. Student's t-test was used to determine the significance of differences in mean values.

RESULTS AND DISCUSSION

ChlF parameters, the changes of which reflect structural and functional characteristics of the photosynthetic apparatus of plants, were evaluated in seedlings of two wheat varieties under infection with common rot pathogen, chloride salinity and seed pre-heating with the possibility of diagnosing stress tolerance of varieties. PAM measurements of the ChlF generate different parameters, which are mainly derived from five mutually independent levels of ChlF: minimum (background) *Fo* and maximum fluorescence yields *Fm* in the dark-adapted state; steady-state *Fs*; minimum (background) *Fo*' and maximum fluorescence yields *Fm*' in the light adapted state of samples, respectively.

The variable ChlF after dark leaf adaptation is Fv. The parameter depends on the maximum quantum yield of PS II. The decrease in the value of this parameter indicates the weakening of photosynthetic activity and energy dissipation in the form of heat. The value of *Fv* decreases under stresses which cause damage to thylakoids [13]. Stress factors in the conditions of our experiment slowed down the activity of photosynthetic apparatus of the seedlings of both varieties, which was expressed in reliable ($p \leq 0.05$) decrease of *Fv* parameter values in all variants of the experiment (from 14.0 to

42.4%), the highest in the variant of combined stressors compared with the control (see the table).

We found that seed pre-heating increased seedling resistance (by cross-adaptation) to the subsequent action of the pathogen and salinity [30]. Cross-adaptation is the process of increasing the resistance of an organism to a particular stress factor as a result of adaptation to a factor of another nature. It can be assumed that in our experiment, pre-warming of seeds activates the protective mechanisms of plants and keeps them active for a long time. Subsequent action of pathogen and salinity increases the level of signaling molecules and the already activated defense systems try to prevent stress development.

The protective effect of hyperthermia was noted in the variant of infection in the variety Sibirskaya 12: reliable ($p \leq 0{,}05$) decrease of *Fv* inhibition by 13,3%, and also in the variants of combined action of the stressors in the variety Sibirskaya 12 by 34,6% and in the variety Omskaya 18 by 41,7%. In the variant of salinity after seed heating, the increase of inhibitory effect of the stressor - 2-fold reduction of *Fv* parameter, most pronounced in the variety Sibirskaya 12 - was observed.

The parameter of ChlF variable can be considered as informative in the study of the influence of stress factors (infection with common rot pathogen, chloride salinity and pre-heating of seeds) on photosynthetic activity of wheat seedlings. However, reliable inter-variety differences in this parameter were not revealed in the conditions of our experiment.

Maximum photochemical quantum yield of PS II – Fv / Fm. This parameter is one of the basic characteristics of photosystems work. It evaluates the maximum photochemical activity of PS II and is defined as the ratio of the number of light quanta used in the charge separation of PS II to the total number of quanta absorbed by the antenna complex of this photosystem [16]. The parameter is registered immediately after dark adaptation of plant tissues. Significant influence of stress factors and associated with them slowing down the activity of photosynthetic apparatus of seedlings of both varieties in the conditions of our experiment expressed by changes in the parameter *Fv / Fm* in all the experimental variants was not found (see the table). At the same time, the values of the background *Fo* and maximum *Fm* ChlF under the conditions of our experiment significantly decreased in both varieties almost in all the variants. Stress factors influenced the antennal complex, i.e. there were losses of energy during its migration, and fluorescence was excited. At the same time, unreliable changes of *Fo* were established in the variety Sibirskaya 12 in the variant of infection with seed heating and in the variety Omskaya 18 in the variants of combined stress and salinization with and without seed heating. *Fm* indicator did not change significantly in both varieties in the variants of infection without heating and with heating of seeds. The maximum photochemical quantum yield is a frequently used parameter in assessing the effect of environmental stressors on the photosynthetic apparatus of plants, but in the studies on the assessment of phytotoxic states of duckweed, insufficient sensitivity and uninformativeness of this parameter are also noted [31].

Effective photochemical quantum yield of PS II in the light – Y(II). $Y(\text{II}) = (Fm' - Fs)/Fm'$. The parameter reflects the part of light energy that can potentially be used in photochemical reactions. It is measured after adaptation of plant tissues to the light at "closed" RC PS II, when the primary acceptors plastoquinones are in reduced state. We found that infection of wheat seedlings with *B. sorokiniana*, chloride salinity and their combined effect have a negative effect on the efficiency of photochemical quenching of ChlF, which leads to a decrease in the intensity of photosynthesis. The effect of stressors is associated with the disturbance of electron acceptance by RC PS II [14]. Under the conditions of our experiments, *Y*(II) decreased significantly ($p \leq 0.05$) from 18.6 to 56.6% in the seedlings of both varieties in all experimental variants compared to the control, most significantly in the variant of combined action of stressors (see the table).

Pre-heating of seeds with subsequent overlapping of infection and chloride salinity influ-

Изменение значений параметров флуоресценции хлорофилла проростков пшеницы при раздельном и совместном действии стрессоров (отн. ед.)
Changing values of chlorophyll fluorescence parameters of wheat seedlings under separate and combined stressors (relative units)

Variety	Option	Indicator									
		Y(II)	*Y*(*NPQ*)	*Y*(*NO*)	*qP*	*qN*	*ETR*	*F*o	*Fm*	*Fv*	*Fv*/ *Fm*
Without seed heating											
Sibirskaya 12	Control	4,1 ± 0,2	2,9 ± 0,1	3,0 ± 0,1	6,3 ± 0,3	5,3 ± 0,2	204,7 ± 9,1	7,6 ± 0,4	22,9 ± 1,4	15,3 ± 0,2	0,67 ± 0,02
	B. sorokiniana	3,3 ± 0,1*	3,6 ± 0,2*	3,1 ± 0,1	5,1 ± 0,2*	5,9 ± 0,2	159,9 ± 7,3*	6,8 ± 0,3	20,0 ± 1,3*	13,2 ± 0,2*	0,66 ± 0,02
	NaCl	2,8 ± 0,1*	3,8 ± 0,1*	3,4 ± 0,2	4,3 ± 0,1*	5,8 ± 0,1	133,5 ± 4,0*	6,2 ± 0,2*	19,4 ± 0,3*	13,2 ± 0,2*	0,68 ± 0,02
	B. sorokiniana+ NaCl	1,8 ± 0,1*	4,8 ± 0,2*	3,4 ± 0,1	3,0 ± 0,1*	6,7 ± 0,3*	77,5 ± 1,7*	6,1 ± 0,2*	16,2 ± 0,2*	10,1 ± 0,1*	0,63 ± 0,03
Omskaya 18	Control	3,3 ± 0,1	3,2 ± 0,1	3,5 ± 0,2	4,9 ± 0,2	5,4 ± 0,1	161,0 ± 7,8	6,3 ± 0,2	20,7 ± 0,5	14,4 ± 0,3	0,70 ± 0,03
	B. sorokiniana	3,0 ± 0,1	4,1 ± 0,2	2,9 ± 0,1	4,7 ± 0,1	6,5 ± 0,3*	155,4 ± 5,1	7,5 ± 0,3*	22,6 ± 0,6	15,1 ± 0,3	0,67 ± 0,02
	NaCl	2,0 ± 0,1*	4,7 ± 0,2	3,3 ± 0,1	3,2 ± 0,1*	6,5 ± 0,3*	87,6 ± 1,9*	6,2 ± 0,2	18,1 ± 0,3	11,9 ± 0,2*	0,66 ± 0,02
	B. sorokiniana + NaCl	1,8 ± 0,1*	5,1 ± 0,3	3,1 ± 0,1	3,1 ± 0,1*	7,0 ± 0,3*	80,9 ± 1,6*	4,9 ± 0,1*	13,2 ± 0,2*	8,3 ± 0,1*	0,63 ± 0,01
Seed heating 43°C											
Sibirskaya 12	Control	4,3 ± 0,2	2,2 ± 0,1	3,5 ± 0,2	6,2 ± 0,3	4,3 ± 0,2	214,5 ± 10,5	7,9 ± 0,4	26,4 ± 0,9	18,5 ± 0,5	0,70 ± 0,06
	B.sorokiniana	3,5 ± 0,1*	2,9 ± 0,1*	3,3 ± 0,1	5,2 ± 0,2*	5,0 ± 0,2*	171,3 ± 8,1*	7,6 ± 0,4	23,9 ± 0,5	16,3 ± 0,3	0,68 ± 0,05
	NaCl	2,7 ± 0,1*	3,8 ± 0,2*	3,5 ± 0,2	4,2 ± 0,2*	5,8 ± 0,2*	127,9 ± 3,2*	6,6 ± 0,3*	19,9 ± 0,4*	13,3 ± 0,2*	0,67 ± 0,04
	B. sorokiniana+ NaCl	2,3 ± 0,1*	3,6 ± 0,2*	4,1 ± 0,2*	3,7 ± 0,1*	5,4 ± 0,2*	107,9 ± 2,1*	6,7 ± 0,2*	21,1 ± 0,6*	14,4 ± 0,2 *	0,68 ± 0,02
Omskaya 18	Control	3,5 ± 0,2	2,9 ± 0,1	3,6 ± 0,1	4,4 ± 0,2	4,7 ± 0,1	173,3 ± 5,4	7,3 ± 0,4	23,9 ± 0,7	16,6 ± 0,3	0,69 ± 0,03
	B. sorokiniana	2,8 ± 0,1*	4,1 ± 0,2*	3,1 ± 0,1*	4,6 ± 0,2	6,4 ± 0,3*	147,2 ± 2,9*	6,5 ± 0,3	19,4 ± 0,5*	12,9 ± 0,2*	0,67 ± 0,03
	NaCl	2,3 ± 0,1*	3,8 ± 0,1*	3,9 ± 0,2	3,6 ± 0,1*	6,0 ± 0,3*	106,6 ± 1,9*	5,9 ± 0,2*	18,4 ± 0,5*	12,5 ± 0,1*	0,68 ± 0,04
	B. sorokiniana+ NaCl	1,9 ± 0,1*	4,0 ± 0,2*	4,1 ± 0,2*	3,0 ± 0,1*	5,7 ± 0,2*	85,2 ± 1,4*	6,9 ± 0,3	19,4 ± 0,6*	12,5 ± 0,2*	0,65 ± 0,02

* Differences with the control are significant at the significance level $p \leq 0.05$.

enced the parameter *Y*(II) in different degree. Significant ($p \leq 0{,}05$) increase of the parameter was observed in the variety Omskaya 18 under salinization by 28,0%, and in the variety Sibirskaya 12 under combined action of stressors and infection by 18,0 and 59,6%, respectively, which means that the positive effect of seed pre-heating on the functional activity of PS II was revealed. Similar results on the protective role of the temperature factor in maintaining the stability of photosynthetic membranes were obtained in hyperthermia and infection with *B. sorokiniana* of barley seedlings [32]. The parameter *Y*(II) changed to the least extent relative to the control in the seedlings of the variety Omskaya 18. Inter-variety differences in all the variants of experiments were 1.2-2.0 times with reliability of differences at the level of $p \leq 0.05$. The greatest differences in the variant of infection with and without seed heating were 1.7-2.0 times. Fig. 1 shows the changes of *Y*(II) parameter under the action of *B. sorokiniana* and chloride salinity without seed pre-heating.

Quantum yield of regulated non-photochemical quenching of ChlF – Y(NPQ). $Y(NPQ) = 1 - Y(\mathrm{II}) - 1 / (NPQ + 1 + qL\ (Fm/ Fo - 1))$. The parameter reflects the energy-dependent thermal dissipation of excited chlorophyll PS II energy [13]. Regulated non-photochemical quenching of ChlF acts as a protective mechanism against excess excitation energy, i.e., it dissipates it into safe heat. This avoids damage to the RC of PS II by light, the intensity of which exceeds the electron transport capabilities [33]. Regulated heat dissipation is stimulated by the xanthophyll cycle [14, 34]. We found that under the action of *B. sorokiniana*, chloride salinity and hyperthermia of seeds there is an activation of the dissipation of part of the excitation energy of chlorophyll PS II into heat. Parameter *Y(NPQ)* was reliably ($p \leq 0{,}05$) increased in both cultivars in all the experimental variants from 24,1 to 72,7%, and more in the variety Sibirskaya 12, especially in the variants of salinity and combined action of stressors with seed pre-heating - 72,7 and 63,6%, respectively (see the table).

Protective effect of hyperthermia was observed only in the variety Omskaya 18 under the combined effect of stressors and chloride salinity - reliable ($p \leq 0.05$) reduction of the parameter by 35.1 and 18.8%. In the variety Sibirskaya 12 we observed a 24.1% decrease in the parameter in the control variant compared to the control without seed heating.

Inter-variety differences in all the variants of experiments ranged 1.2-1.7 times with reliability of differences at the level of $p \leq 0.05$. The greatest differences in the variant of salinity without heating and with seed heating were 1,5-1,7 times.

Fig. 2 shows changes in the Y(NPQ) parameter under the action of B. sorokiniana and chloride salinity without seed pre-heating.

Quantum yield of unregulated non-photochemical quenching of ChlF – Y(*NO*). $Y(NO) = 1 / (NPQ + 1 + qL\ (Fm/Fo–1))$. The parameter is related to the thermal losses resulting from the "closure" of the RC of PS II as a result of blocking the electron transfer along the electron-transport chain [14]. Side reactions in this case are associated with the formation of active oxygen radicals. An increase in the index means that photochemical energy conversion and protective regulatory mechanisms are ineffective. Very high value of the index indicates not only blocking of RC PS II, but also violation of proton gradient of thylakoid membranes [35]. Under the conditions of our experiments, unreliable changes of the index in the variety Sibirskaya 12 in all the experimental variants were established (see the table). In the variant of infection with *B. sorokiniana*, the stimulating effect of seed hyperthermia was observed in the variety Omskaya 18; the index decreased by 13,9% relative to the control with unreliable changes in all the test variants, except for the variant of combined action of stressors with seed heating - *Y(NO)* increase by 13,8%. The results obtained indicate the effectiveness of protective regulatory mechanisms of photosynthetic reactions in the seedlings of these varieties with the advantage of the variety Omskaya 18. Fig. 3 shows changes in the *Y(NQ)* parameter under the action of *B. sorokiniana* and chloride salinity without seed pre-heating.

Photochemical quenching coefficient of ChlF – qP. $qP = (Fm'– Fs) / (Fm' – Fo')$. The

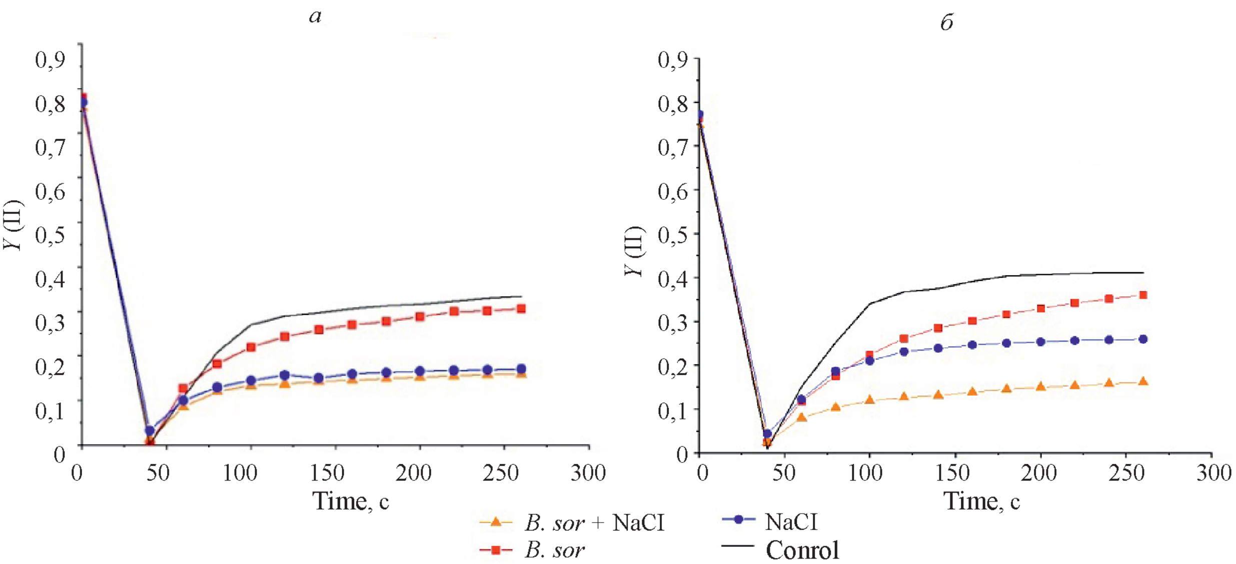

Рис. 1. Усредненные значения эффективного квантового выхода фотохимического превращения световой энергии *Y*(II) проростков яровой пшеницы при действии *B. sorokiniana* и хлоридного засоления:
а – сорт Омская 18; *б* – сорт Сибирская 12

Fig. 1. Average values of effective quantum yield of photochemical conversion of light energy *Y*(II) of spring wheat seedlings under the action of *B. sorokiniana* and chloride salinity:
a - variety Omskaya 18; *б* - variety Sibirskaya 12

parameter estimates the fraction of complexes of PS II with the oxidized primary acceptor QA at the time before the application of saturating light flash. Indicates the fraction of light energy consumed by the "open" RCs of FS II. We found reliable ($p \leq 0{,}05$) decrease of *qP* parameter in all the experimental variants for both cultivars in the range from 16,1 to 52,4%, more so for the variety Sibirskaya 12 (see the table). In the variety Omskaya 18 in the variant of infection reliable changes in the parameter were not found. All stress factors reduced the number of complexes of FS II with oxidized primary acceptor QA, which led to a violation of photochemical quenching of ChlF.

The protective effect of hyperthermia was established in the variant of combined action of stressors in the variety Sibirskaya 12 and in the variants of salinization and combined action of stressors in the variety Omskaya 18 - reliable ($p \leq 0.05$) increase of *qP* parameter by 23.1; 47.6 and 13.6%, respectively. Analysis of the experimental data shows the coincidence of the dynamics of the photochemical quenching coefficient *qP* with the dynamics of the effective photochemical quantum yield of PS II in the light *Y*(II). Inter-variety differences in all the variants of experiments were 1.3-4.7 times with the reliability of differences at the levels of $p \leq 0.05$ and $p \leq 0.01$. The greatest differences in the variants of infection with and without heating of seeds were 3.4-4.7 times.

Fig. 4 shows changes in *qP* parameter under the action of *B. sorokiniana* and chloride salinity without seed pre-heating.

Non-photochemical quenching coefficient of ChlF – qN. $qN = (Fm - Fm') / (Fm - Fo')$. The parameter is related to the processes of conversion of a part of the energy absorbed in the light phase of photosynthesis into heat. It increases in stressed plants [11, 12]. Under our conditions, *qN* increased significantly ($p \leq 0.05$) in all the experimental variants from 16.3 to 36.2% in both varieties, to a lesser extent in the variety Sibirskaya 12 in infection and chloride salinity variants without seed warming (see the table). However, pre-heating of seeds led to an increase in thermal dispersion in both varieties, most pronounced in the variety Sibirskaya 12 (up to 3.5 times in the variant of salinity). At the same time, the protective effect of hyperthermia was also observed. Thus, the variety Omskaya

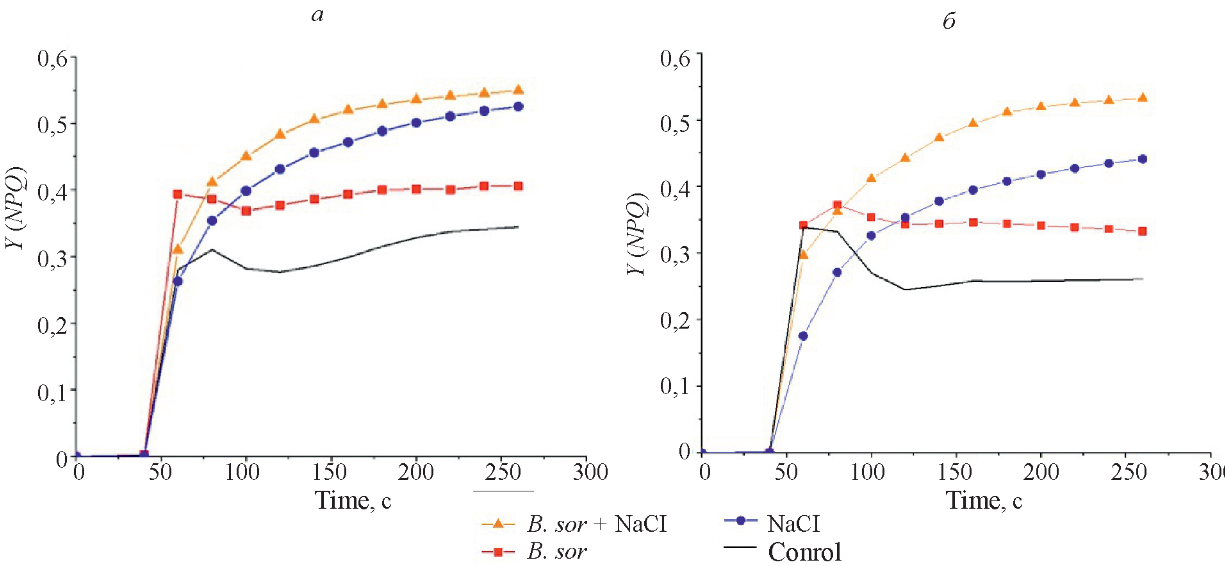

Рис. 2. Усредненные значения квантового выхода регулируемого нефотохимического тушения ФлХ – *Y*(*NPQ*) проростков яровой пшеницы при действии *B. sorokiniana* и хлоридного засоления: *а* – сорт Омская 18; *б* – сорт Сибирская 12

Fig. 2. Average values of quantum yield of regulated non-photochemical quenching ChlF - *Y(NPQ)* of spring wheat seedlings under the action of *B. sorokiniana* and chloride salinity: *а* – variety Omskaya 18; *б* – variety Sibirskaya 12

18 showed a decrease of *qN* parameter values in the variant of combined stressors and control by 28.1 and 27.7%, respectively. In the Sibirskaya 12 variety *qN* parameter decreased only in the control variant by 23.3%. Since photochemical and non-photochemical quenching of chlorophyll fluorescence are competitive, the higher *qP*, the lower *qN*. Analysis of the obtained data confirmed this fact (see Fig. 5, 6). Intersectional differences in all the variants of the experiments were 1,2-2,3 times with the reliability of differences at the level of $p \leq 0,05$ and $p \leq 0,01$. The greatest differences in the variant of salinity without heating and infection with seed heating were 2.2-2.3 times.

The speed of electronic transport through photosystems – ETR. ETR = *Y*(II) × 0,84 × 0,50 × *PPFD*. The parameter shows the rate of charge separation in RC PS II. The electron transport rate decreases under stress [12, 13]. We found that *B. sorokiniana* stress factors, chloride salinity and seed hyperthermia significantly ($p \leq 0.05$) reduced the electron transport rate in wheat seedlings of both varieties in all the test variants in the range from 15.2 to 62.7%, especially in the Sibirskaya 12 variety (see the table). The greatest decrease of *ETR* values in comparison with the control was observed in the variant of joint action of stressors - 62,1% (Sibirskaya 12) and 49,8% (Omskaya 18). The pathogen had less effect on the electron transport rate. The *ETR* parameter decreased by 21.9% in the Sibirskaya 12 variety, while the Omskaya 18 variety showed insignificant changes compared to the control (see Fig. 6).

The protective effect of seed hyperthermia was observed in the variety Sibirskaya 21 - reliable ($p \leq 0.05$) increase of *ETR* by 20.7% in the variant of combined effect of stressors and in the variety Omskaya 18 in the variant of salinity by 36.7%. Inter-variety differences in all the variants of the experiments were 1.2-6.2 times with reliability of differences at the levels of $p \leq 0.05$ and $p \leq 0.01$. The greatest differences in the variant of infection without seed heating were 6,2 times.

Thus, the varietal specificity and informativeness of all the applied parameters of ChlF in the study of the combined effect of the causative agent of common root rot, chloride salinity and seed hyperthermia on the seedlings of spring wheat varieties was established.

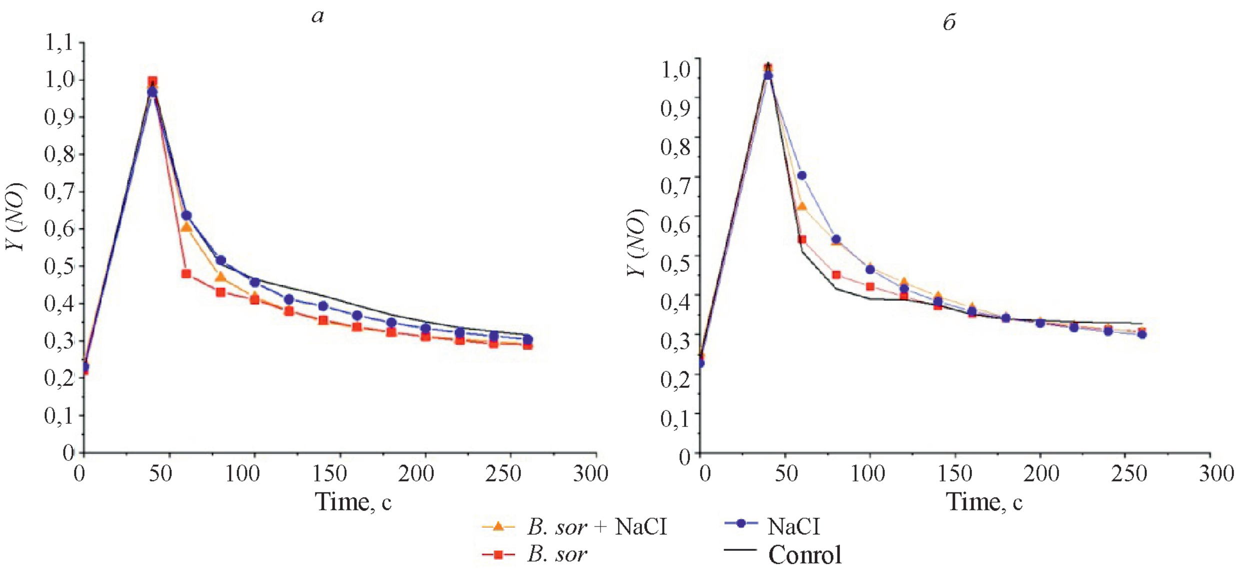

Рис. 3. Усредненные значения квантового выхода нерегулируемого нефотохимического тушения ФлХ – *Y*(*NQ*) проростков яровой пшеницы при действии *B. sorokiniana* и хлоридного засоления:
а – сорт Омская 18; *б* – сорт Сибирская 12

Fig. 3. Average values of quantum yield of unregulated non-photochemical quenching ChlF - *Y(NQ)* of spring wheat seedlings under the action of *B. sorokiniana* and chloride salinity:
а - variety Omskaya 18; *б* - variety Sibirskaya 12

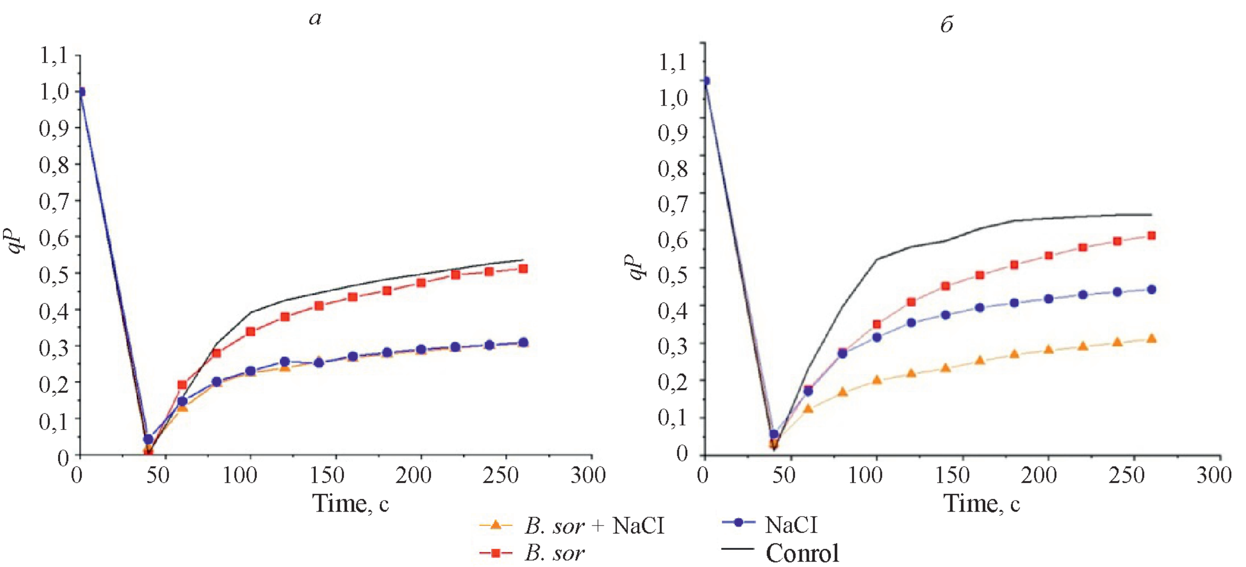

Рис. 4. Усредненные значения коэффициента фотохимического тушения флуоресценции хлорофилла – *qP* проростков яровой пшеницы при действии *B. sorokiniana* и хлоридного засоления:
а – сорт Омская 18; *б* – сорт Сибирская 12

Fig. 4. Average values of photochemical quenching coefficient of chlorophyll fluorescence - *qP* of spring wheat seedlings under the action of *B. sorokiniana* and chloride salinity:
а – variety Omskaya 18; *б* – variety Sibirskaya 12

CONCLUSIONS

1. Separate and combined effects of chloride salinity (1.3%), infection with the cereal root rot pathogen *B. sorokiniana* (5000 conidia per grain) suppressed light and dark reactions of photosynthesis. Reliable ($p \leq 0,05$) decrease of effective quantum yield *Y*(II), photochemical quenching coefficient *qP* and electron transport rate *ETR* was found in both varieties, the greatest - in the variant of combined stressors (up to 62,7%). The maximum photochemical

quantum yield of PS II *Fv / Fm* was less informative, no significant changes in the parameter were found.

2. Inhibition of light-dependent reactions was accompanied by a significant ($p \leq 0.05$) increase in the values of non-photochemical quenching parameters of ChlF - coefficient *qN* and quantum yield of regulated non-photochemical quenching of ChlF Y(NPQ) from 24.1 to 72.1% in both varieties, most pronounced it was in the variety Sibirskaya 12, especially in the variants with salinity and combined stress-

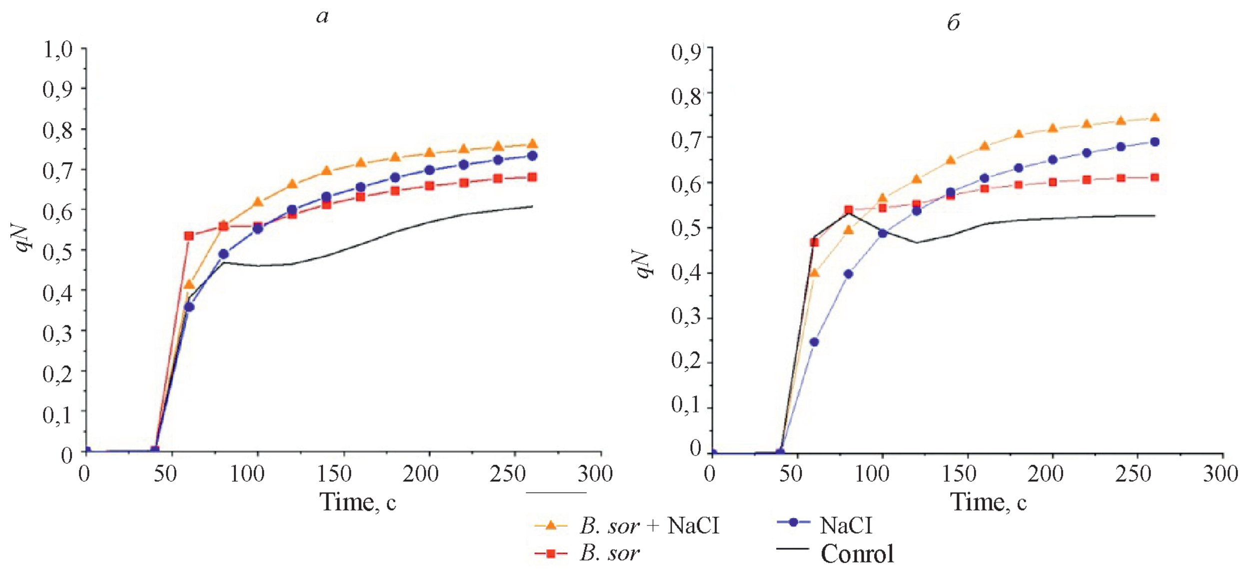

Рис. 5. Усредненные значения коэффициента нефотохимического тушения ФлХ – *qN* проростков яровой пшеницы при действии *B. sorokiniana* и хлоридного засоления:
а – сорт Омская 18; *б* – сорт Сибирская 12

Fig. 5. Averaged values of non-photochemical quenching coefficient ChlF - *qN* of spring wheat seedlings under the action of *B. sorokiniana* and chloride salinity:
а – variety Omskaya 18; *б* – variety Sibirskaya 12

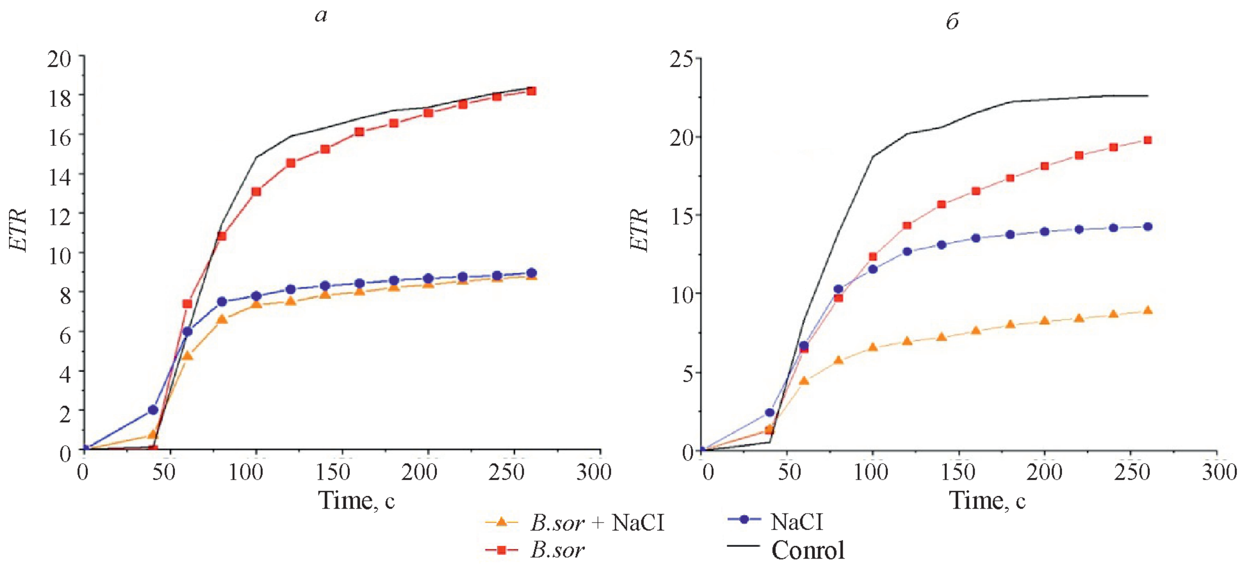

Рис. 6. Усредненные значения скорости электронного транспорта через фотосистемы – *ETR* проростков яровой пшеницы при действии *B. sorokiniana* и хлоридного засоления:
а – сорт Омская 18; *б* – сорт Сибирская 12

Fig. 6. Average values of electron transport rate through photosystems - *ETR* of spring wheat seedlings under the action of *B. sorokiniana* and chloride salinity:
а - variety Omskaya 18; *б* - variety Sibirskaya 12

ors. The parameter *Y(NO)* - quantum yield of unregulated non-photochemical quenching of ChlF changed insignificantly relative to the control in both varieties.

3. The positive effect of preliminary hyperthermia of seeds on the functional activity of photosynthetic apparatus of seedlings was revealed - a significant ($p \leq 0.05$) increase of values of *Y(II), qP, ETR* parameters (by 18.0-59.0%) and decrease of values of *Y(NPQ), Y (NO)* and *qN* parameters (by 18.8-35.1%) under the subsequent action of infection and chloride salinity in both varieties, mainly in the variety Omskaya 18.

4. The informativeness of ChlF parameters for assessment of varieties stress tolerance was established. Significant inter-variety differences (from 1.2-6.2 times) were revealed for almost all parameters (except *Fv / Fm, Y(NO)*, *Fv*) for all the variants of the experiment. Variety specificity was established - the smallest changes of parameters relative to the control were in the stable variety Omskaya 18 in all the variants of the experiment.

5. The studied parameters of photochemical and non-photochemical quenching of ChlF can be used as informative parameters for diagnostics of photosynthetic activity and evaluation of wheat varieties resistance to chloride salinity, infection and seed hyperthermia. The proposed approach will allow to develop a non-invasive method for early diagnosis of stress tolerance (phenotyping) of new genotypes to biotic and abiotic stressors.

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Дата поступления статьи / Received by the editors 14.09.2022
Дата принятия к публикации / Accepted for publication 25.10.2022
Дата публикации / Published 17.12.2022