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ACTIVITY OF THE PHOTOSYNTHETIC APPARATUS AND PRODUCTIVITY OF TRANSGENIC WINTER WHEAT PLANTS WITH PARTIAL SUPPRESSION OF THE PROLINE DEHYDROGENASE GENE

Galyna Priadkina, Oksana Dubrovna, †Serhiy Sytnyk, Maksym Tarasiuk

Institute of Plant Physiology and Genetics, NAS of Ukraine
31/17 Vasylkivska St., Kyiv 03022, Ukraine

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Background. Partial suppression of the proline dehydrogenase (*ProDH*) gene in transgenic winter wheat plants leads to an increase in the level of free proline accumulation. However, the effect of increasing the content of this amino acid on the physiological and biochemical characteristics of this crop is still not fully understood. In this regard, the aim of the work was a comparative analysis of the influence of the free proline accumulation on the activity of the photosynthetic apparatus parameters of transgenic wheat plants at reproductive period under variable weather conditions, as well as on their productivity.

Materials and Methods. The study involved non-transformed winter bread wheat plants of genotype UK 997/19 and transgenic lines of seed generation T_2 obtained on their basis. The content of free proline, photosynthetic pigments and parameters of the photosynthetic apparatus activity were determined. The analysis of the elements of the crop structure was carried out at full ripeness.

Results. Under conditions of increased air temperature or lack of moisture in the soil, it was established that the total chlorophyll content in the leaves of plants of the transgenic lines at milk-wax maturity exceeded its level in the wild-type plants by 15.9–32.5 %. At this phase, they had a higher effective quantum yield (ϕ_{PSII}) by 16–28 %, the coefficient of photochemical quenching (qP) by 23–26 % and the fraction of open reaction centers (qL) by 28–61 % of photosystem II (PSII). No specific regularities were found in the changes in the non-photochemical quenching parameter (NPQ) in the antenna complexes of PS II leaves of the transgenic plants relative to the wild-type

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ones. The grain yield of plants of the modified lines was higher than that of the wild type. A significant positive correlation was found between the grain productivity of the transgenic plants with the fraction of open reaction centers of PSII, the effective quantum yield and photochemical quenching of fluorescence parameter (the coefficient of determination of the relationship varied from 0.762 to 0.966).

Conclusions. The study results indicate that the elongation of the functioning of the flag leaf during the reproductive period and the higher activity of the photosynthetic apparatus in the transgenic wheat lines with an increased proline content under the conditions of increased air temperature or lack of moisture in the soil contributed to an increase of their grain productivity.

Keywords: wheat, transgenic plants, proline, chlorophyll *a* fluorescence, grain yield

INTRODUCTION

The frequency of periods with increased air temperature and drought during the growing season of an important food crop – winter wheat – necessitates the creation of varieties tolerant to their effects. The creation of such genotypes by both classical selection and biotechnological methods requires the identification of features that distinguish them from less resistant ones. The study of physiological and biochemical characteristics of resistant genotypes contributes to the identification of selection criteria that can be used to assess the tolerance of plants to stresses (Monirul *et al*., 2015; Ahmed *et al*., 2019; Yasir *et al*., 2019; Uhr *et al.*, 2022). This will allow breeders and biotechnologists to direct their programs to identify specific genes and edit them to achieve increased plant adaptability (Adel & Carels, 2023).

Since the growth, development and generative processes of plants largely depend on their ability to absorb, transform and use light energy to ensure metabolic processes, important physiological characteristics can be parameters of the photosynthetic apparatus itself. In particular, the photosynthetic pigment content and chlorophyll *a* fluorescence indices are used to detect stress in plants (Noor *et al*., 2018; Yasir *et al*., 2019). Notably, a smaller decrease in the maximum quantum efficiency of PSII (F_v/F_m) was found in the group of spring wheat varieties that had high F_v/F_m values under the effects of heat stress (1 week at 36/30°C day/night) than in the group of varieties with low values (Sharma *et al*., 2015). At the same time, the total chlorophyll content of the varieties of the former group exceeded the value of the latter group (Sharma *et al*., 2015).

An improved adaptability of plants to abiotic stresses is associated with an increase in the proline content, which acts as an osmoprotectant (Anjum *et al*., 2017; Renu *et al*., 2019). Accumulation of this amino acid actively or passively helps plants retain water in cells and protects cell organelles from dehydration-induced damage or maintains turgor pressure during water stress. In particular, it was shown that exogenous foliar treatment of wheat plants with proline increased the chlorophyll content, antioxidant enzymes activity, and water-holding capacity, ultimately alleviating the impact of stress on wheat yield, which in treated plants increased by 3–11 % under mild drought and 34–53 % under severe drought, compared to the control variant (Li *et al*., 2024).

Free proline is one of the most multifunctional stress metabolites in plants. In addition to its well-known function as an inert compatible osmolyte, proline under the influence of stressors performs a number of other interconnected functions, namely membrane protective, chaperone, and antioxidant. It also participates in the regulation of the expression of some genes (Meena *et al*., 2019; Ghosh *et al*., 2022), and is a source of energy, nitrogen and carbon depot (Sarker & Oba, 2020). Therefore, proline accumulation is a widespread response not only to water stress but also to other abiotic stresses (Jogawat, 2019). An increase in plant tolerance may be due to osmotic regulation and chaperone-like activity in the stabilization of membranes and proteins and detoxification by absorption of reactive oxygen species.

Currently, genetic engineering methods allow the transfer of various genes, but their influence on physiological and biochemical processes in plant cells is still not fully understood. Metabolic differences between transgenic and wild-type plants are widely discussed in the current scientific literature (Gao *et al.,* 2018; Noor *et al*., 2018; Anwar *et al*., 2020; Dubrovna *et al*., 2022). At the same time, there is often no information about specific changes that occur in transgenic plants and the exact effects of transferred genes and their products on cells.

It was shown that transgenic wheat plants with overexpressing proline synthesis genes had relatively higher proline content, a higher number of cells with an intact membrane (De Lima *et al*., 2019), and increased tolerance to water deficit and salinity (Anwar *et al*., 2020, 2021). Partial suppression of the proline dehydrogenase (*ProDH*) gene in transgenic plants of winter and spring wheat led to an increase in the level of accumulation of this amino acid, and the plants were characterized by a higher activity of antioxidant enzymes (Dubrovna *et al*., 2020), as well as increased tolerance to soil drought (Dubrovna *et al*., 2022).

Considering the fact that intensive intercellular transport of proline occurs between the cytosol, chloroplasts and mitochondria (Kaur & Asthir, 2015), an increase in the content of free proline can be expected to have a positive effect on the photosynthetic apparatus of plants. This hypothesis can be confirmed by data on an increase in the chlorophyll content after their exogenous treatment with this amino acid (Li *et al*., 2024), a positive correlation of the content of proline with photosynthesis rate (Bekka *et al*., 2018).

The aim of this work was a comparative analysis of the influence of the accumulation of free proline on the parameters of the photosynthetic apparatus activity at reproductive period under variable weather conditions, as well as the productivity of original and transgenic plants of bread wheat.

MATERIALS AND METHODS

The research material included non-transformed winter bread wheat plants of genotype UK 997/19 and transgenic lines of seed generation T_2 obtained on the basis of wild type (WT) by the method of *Agrobacterium*-mediated transformation *in planta* (Dubrovna & Slivka, 2021). The transformation was carried out using the AGL0 strain, which contains the binary vector construct pBi2E, which includes a double-stranded RNA suppressor of the Arabidopsis proline dehydrogenase gene and a selective neomycin phosphotransferase II gene of *Escherichia coli*. From the obtained T_1 transgenic plants, T_2 seed generation plants were obtained by self-pollination. The integration of the vector construct elements was established by the PCR based on the presence of fragments of the exon and intron of the Arabidopsis *ProDH1* gene and the selective neomycin phosphotransferase gene – *npt*II.

The seeds of wild type and transgenic lines were all sown in autumn in open ground in a fenced area. Measurements of the photosynthetic apparatus activity parameters, as well as photosynthetic pigments content, of WT and seed generation T_2 were carried out for the following year at anthesis (GS 60-63) and milk-wax maturity (GS 83-85).

The average samples for biochemical and spectrophotometric research were formed from flag leaves of 5 individuals main shoots. Three replicates for each lines were used to measure the pigments and free proline content. The free proline content was determined at booting (GS 45-47) by the method based on the formation of a colored product of the interaction between L-proline and ninhydrin (Bates *et al*., 1973). Determination of the photosynthetic pigments content (chlorophylls *a* and *b* and total carotenoids) was carried out by the maceration-free method by extracting pigments from green flag leaves with dimethylsulfoxide according to the A. P. Wellburn method (Wellburn, 1994). The optical density of the solutions was determined on a Specord 200 spectrophotometer (Analytic Jena, Germany) at wavelengths of 480, 649, and 665 nm. Recalculation of pigment content per g of dry weight was carried out taking into account all dilutions and leaf weight.

The parameters of the pulse amplitude-modulated induction of chlorophyll *a* fluorescence were determined using a Junior-PAM Fluorometer (WALZ, Germany) on the flag leaves of the main shoot. Parameters were calculated according to standard formulas (Murchie & Lawson, 2013). The maximum quantum efficiency of photochemistry of PS II (F_v/F_m) was measured after 30 minutes of leaf adaptation in the dark, and effective quantum yield of PSII (ϕ_{PSII}) was measured in light-adapted leaves. Four replicates for each line were used to measure the chlorophyll fluorescence parameters.

The analysis of the elements of the crop structure was carried out at full ripeness (GS 89-90).

Weather conditions of the spring-summer wheat vegetation period of 2023–2024 according to the data of the weather station closest to the research area (http://cgo-sreznevskyi.kyiv.ua/en/activity/klimatolohichna/climate-data-for-kyiv).

The obtained data were processed by conventional methods of variation statistics using Microsoft Excel software. According to the experimental design, data analysis was performed using two-way ANOVA with post-hoc analysis using the Turkey test. Results in the text and tables are presented as mean values and standard error (m ± SE). The significance of the difference between indicators was assessed at the $p < 0.05$ and $p < 0.01$.

RESULTS AND DISSCUTION

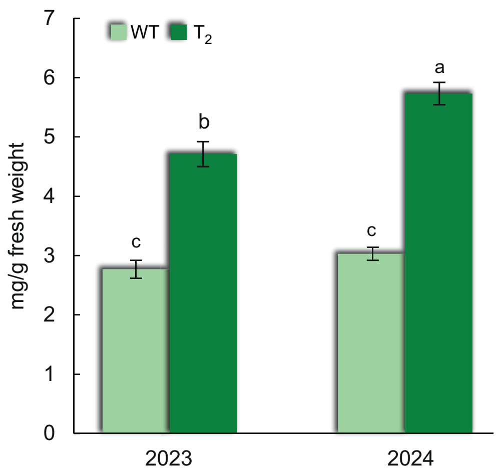
The period of wheat generative organs formation and the beginning of the reproductive period in both years was characterized by very dry conditions: in 2023, only 1 mm fell, and in 2024 – 15 mm, which is significantly below the long-term climatic norm (**Table 1**). The amount of precipitation in June was less than the norm in 2023, and in July in 2024. Temperature conditions during June–July 2023, on average, were close to the climatic norm; in 2024 they exceeded it by 2–3 °C. A significant and long-term increase in air temperature in 2024, which caused the increase in its average monthly values, was observed after the phase of waxy grain ripeness.

The higher air temperature in 2024 accelerated the development of plants and led to a shortening of the period from anthesis – milk-wax maturity to 16 days, compared to 21 days in 2023. Therefore, in both years the plants were affected by adverse conditions.

Table 1. **Weather conditions of the spring-summer wheat vegetation period of 2023–2024**

Month	Average monthly air temperature, °C			Precipitation, mm		
	Climatic norm	2023	2024	Climatic norm	2023	2024
April	10.0	9.6	12.8	42	102	78
May	15.8	16.0	16.3	65	1	15
June	19.5	19.6	21.5	74	87	135
July	21.3	21.5	24.3	68	136	52

Analysis of the free L-proline content in the leaves at booting (in May) showed an increase in the amino acid content in the transgenic plants by 1.7–1.9 times compared to WT. In the wild type its concentration was 2.77±0.15 mg/kg fresh weight in 2023 and 3.03±0.11 mg/kg fresh weight in 2024, while in the modified ones, respectively, 4.71±0.21 and 5.73±0.19 (see **Figure**).



The free L-proline content in flag leaves of winter bread wheat UK 997/19 (WT) and its transgenic lines (T_2) at booting in 2023 and 2024

Note: data are means ± SE of three biological replicates, different letters indicate means that differ significantly ($p < 0.05$)

A comparative analysis of the content of photosynthetic pigments and parameters of photosynthetic processes activity in flag leaves of the plants of wild type winter wheat with the transgenic plants of the T_2 generation was carried out at anthesis and at milk-wax maturity. At anthesis in 2023, total chlorophyll content (*a*+*b*) in the flag leaf of the transgenic plants was higher than in WT (by 12.8 %), while in 2024 the difference between them was insignificant (**Table 2**).

At milk-wax maturity in both years, the content of this pigment in modified plants exceeded the corresponding values of WT by 15.9–32.5 %. The patterns of changes in the content of total carotenoids in the transgenic lines compared to WT were similar to the changes in the chlorophyll content (**Table 2**).

No unequivocal regularities were found in the chlorophyll forms ratio in the flag leaves of the transgenic plants in both phases comparatively to WT: the ratio of chlorophyll *a*/*b* in the lines was both higher and lower than in the line UK 997/19 (**Table 2**). The difference between them in terms of the ratio of carotenoid content to chlorophyll was significant in both phases and in both years (**Table 2**). Thus, the photosynthetic pigments content in the flag leaf of the transgenic winter wheat plants exceeded its value in WT during the grain-filling period.

Table 2. **The content of total chlorophyll and carotenoids, mg/g of dry matter, in the flag leaf of winter wheat plants of the line UK 997/19 (WT) and the transgenic lines of generation T_2 at anthesis and milk-wax maturity (n = 3, x±SE)**

Phase	Year	Genotype	Chlorophyll (*a*+*b*)	Carotenoids	Ratio *a*/*b*	Car/ Chl
Anthesis	2023	WT	7.43±0.43[b]	1.47±0.10[a]	3.69±0.06[b]	0.20±0.01[b]
		T_2	8.38±0.31[a]	1.73±0.06[a]	3.90±0.06[a]	0.21±0.01[a]
	2024	WT	9.27±0.28[a]	1.55±0.05[a]	3.35±0.01[a]	0.17±0.01[b]
		T_2	9.21±0.13[a]	1.57±0.02[a]	3.20±0.01[b]	0.17±0.01[a]
Milk-wax maturity	2023	WT	4.92±0.25[b]	1.15±0.05[b]	3.88±0.03[a]	0.23±0.01[a]
		T_2	5.70±0.13[a]	1.28±0.04[a]	3.65±0.07[b]	0.22±0.01[b]
	2024	WT	6.67±0.12[b]	1.21±0.04[b]	2.87±0.06[b]	0.18±0.01[a]
		T_2	8.84±0.35[a]	1.50±0.06[a]	3.00±0.03[a]	0.17±0.01[b]
Analysis of variance						
Anthesis		G	ns	ns	ns	*
		Y	**	ns	**	**
		GxY	ns	ns	ns	ns
Milk-wax maturity		G	**	**	ns	**
		Year	**	*	**	**
		GxY	*	ns	**	ns

Note: different letters indicate significant differences (p <0.05) within each growth stage, as well as each year. Here and in the Tables 3 and 4 in twovariante variance analysis, G and Y represent the lines and year, respectively, * – indicates significant differences at p <0.05, ** – p <0.01, ns – non-significance

The fluorescence parameter of chlorophyll *a* F_v/F_m, which characterizes the maximum quantum efficiency of PS II, in the flag leaf of the modified plants at anthesis was significantly (by 3 %) higher than in WT in 2023, while in 2024 the difference was insignificant (**Table 3**). At milk-wax maturity in both years, F_v/F_m in the transgenic plants and the original line were close. A number of researchers use this parameter to assess the impact of stress on plants. In particular, it was established that there is a close correlation between F_v/F_m and wheat yield under conditions of drought of varying degrees of severity during the grain filling period (Paknejad *et al*., 2007), with the percentage of yield loss due to severe drought during flowering (Sommer *et al*., 2023), as well as with a mass of 1000 grains under at high-temperature stress (Jain *et al*., 2018). However, in our experiments, no significant difference was found between the WT and the modified plants. This, could probably be due to insufficiently severe stress conditions.

Quantum efficiency of PSII photochemistry characterizes the real activity of photochemical processes in PSII reaction centers in chloroplasts of light-adapted flag leaves (Baker & Rosenqvist, 2004). At anthesis, the transgenic plants exhibited significantly higher ϕ_{PSII} values (by 12 %) than the WT only in 2023, while at milk-wax maturity these values were higher in both years (by 16–28 %).

Similar patterns of changes in transgenic lines compared to WT were noted for other parameters of the activity of photochemical processes: coefficient of photochemical quenching of fluorescence (by 23–26 %) and the fraction of open PSII reaction centers (by 28–61 %) (**Table 3**).

Table 3. **Parameters of photochemical activity of FS II in chloroplasts of flag leaves of the original wheat genotype UK 997/19 (WT) and the transgenic lines of generation T_2 at anthesis and milk-wax maturity (n = 4, x±SE)**

Year	Genotype	Maximum photochemical quantum yield of PSII, F_v/F_m	Effective quantum yield of PSII, ϕ_{PSII}	Coefficient of photochemical quenching, qP	Fraction of open reaction centres, qL	Non-photochemical quenching parameter, NPQ
Anthesis						
2023	WT	0.799±0.002^{b}	0.251±0.012^{b}	0.397±0.028^{a}	0.196±0.026^{a}	1.306±0.181^{a}
	T_2	0.824±0.008^{a}	0.281±0.002^{a}	0.402±0.010^{a}	0.169±0.017^{a}	0.964±0.177^{a}
2024	WT	0.771±0.028^{a}	0.493±0.067^{a}	0.818±0.072^{a}	0.647±0.103^{a}	1.242±0.118^{a}
	T_2	0.790±0.028^{a}	0.543±0.042^{a}	0.775±0.022^{a}	0.596±0.082^{a}	0.617±0.162^{b}
Milk-wax maturity						
2023	WT	0.767±0.015^{a}	0.279±0.004^{b}	0.474±0.031^{b}	0.271±0.039^{a}	1.293±0.112^{a}
	T_2	0.770±0.022^{a}	0.358±0.023^{a}	0.582±0.043^{a}	0.348±0.052^{a}	1.085±0.029^{b}
2024	WT	0.796±0.043^{a}	0.377±0.032^{b}	0.548±0.024^{b}	0.274±0.025^{a}	0.478±0.232^{b}
	T_2	0.777±0.026^{a}	0.436±0.056^{a}	0.688±0.047^{a}	0.440±0.071^{b}	1.139±0.252^{a}
Analysis of variance						
Anthesis	G	*	ns	ns	*	**
	Y	**	**	**	**	*
	GxY	ns	ns	ns	ns	ns
Milk-wax maturity	G	ns	**	**	**	*
	Y	ns	**	**	ns	**
	GxY	ns	ns	ns	ns	**

The parameter of non-photochemical quenching of chlorophyll fluorescence, i.e., a loss of absorbed light energy in the form of thermal dissipation, in the antenna complexes of PSII of leaves of the transgenic plants and the WT at anthesis did not differ significantly in 2023, while in 2024, in the modified lines, NPQ was twice as low as in the wild-type (WT) plants (**Table 3**). At milk-wax maturity in 2023, NPQ was 16 % lower in transformants than in line UK 977/19, and in 2024, on the contrary, it was more than 2 times higher. Therefore, at the late stages of ontogenesis, the loss of absorbed light energy due to thermal dissipation in the antenna complexes of PSII in the transgenic plants depended on the conditions of the year. The greater non-photochemical quenching of chlorophyll fluorescence in modified plants, which had almost a third higher chlorophyll content in 2024, was probably due to a greater need to protect the photosynthetic apparatus from excess absorbed solar radiation.

The grain productivity of both the main shoot and the whole plant of the transgenic lines exceeded the corresponding values of line UK 997/19 in both years (**Table 4**). A greater number and weight of grains were also characteristic of the transgenic lines, with the exception of 2023, when the difference between them was insignificant.

Effective quantum yield of PSII in light-adapted leaves determines the share of light absorbed by chlorophyll, associated with the second photosystem, and used for photochemical processes (Baker & Rosenqvist, 2004). It is known that this parameter of chlorophyll *a* fluorescence changes under stress. Thus, heat stress significantly (by 14–63 %) reduced the quantum yield of PSII in two heat-resistant and two heat-sensitive wheat cultivars subjected to heat stress (40 °C for two to three days at different stages) (Haque *et al*., 2014).

It was found that high temperatures (up to 38 °C at midday and above 20 °C at night) reduced by 40–50 % in comparison to the control the quantum efficiency of PSII in 8 wheat genotypes both during and after stress (Chovancek *et al*., 2019). A decrease in ϕ_{PSII} – the effective quantum yield of PS II – in light-adapted leaves of common wheat and six cultivars of spelt from different European countries (by 19–45 %) was also shown under the effects of drought caused by withholding water in the soil for 10 days during the flowering phase (Radzikowska *et al*., 2022). The influence of source-sink strength on the quantum efficiency of PSII photochemistry under conditions of an increased CO_2 content was also revealed. In the variety with a large ear-type, ϕ_{PSII} was higher by 16.3 % than in the control, while in the variety with a small multiple ear-type, on the contrary, it decreased by 9.9 % (Li *et al*., 2021).

In our experiments, the effective quantum yield of PSII in the chloroplasts of light-adapted flag leaves of the transgenic plants with an increased proline content differed significantly from WT at milk-wax maturity in both years: by 28 % in 2023 and by 16 % in 2024. Photochemical quenching of fluorescence and the fraction of open PSII reaction centers in transformants leaves were also higher, compared to WT.

Literature data show that genetically modified wheat plants with a higher free proline content than the wild type, due to the presence of other heterologous genes, differ in certain physiological and biochemical indicators (Yu *et al*., 2017; Noor *et al*., 2018; Gao *et al*., 2018; Bai *et al*., 2022). In particular, T_2 transgenic (At-DREB1A) and non-transgenic line of cv lasani-08 exposed to a 15-day drought, which differed in proline content by almost 1.5 times, had significant differences in the content of chlorophyll in the flag leaf: respectively, 5.75 and 12.47 mg/g of fresh weight (Noor *et al*., 2018). It was also established that higher a proline content (by 17–22 % compared to the non-transformed wheat plants) in the transgenic lines of wheat T_5 and T_7 with overexpression of exogenous *SeCspA* contributed to an increase of chlorophyll content by almost 40 % under the conditions of a 7-day drought (Yu *et al*., 2017). Under drought stress at the seedling stage, in 2 modified *GmDREB3-OE* wheat lines with a higher proline content (445 and 464 mg/g) compared to the wild type (359 mg/g), the chlorophyll content on average for 2 years was smaller compared to the control plants, respectively by 49–52 % and by 61 % (Bai *et al*., 2022). However, no significant differences of the maximum quantum efficiency of FS II were shown (Bai *et al*., 2022).

Table 4. **Grain productivity of the main shoot and whole plant of winter wheat of the original line UK 997/19 (WT) and its transgenic lines of the T_2 generation (n = 8, x±SE)**

Year	Genotype	Number of grains, pcs.	Grain weight, g	Weight of 1000 grains, g	Number of stems, pcs.
Main shoot					
2023	WT	53.4±10.4[b]	2.05±0.36[b]	38.68±3.33[b]	
	T_2	59.0±4.7[a]	2.75±0,34[a]	46.58±4.63[a]	
2024	WT	47.5±9.9[b]	2.37±0,48[b]	50.02±3.05[b]	
	T_2	59.3±7.2[a]	3.58±0,58[a]	60.31±4.41[a]	
Whole plant					
2023	WT	131.4±23.3[a]	4.66±0.65[b]	35.73±3.20[a]	3.3±0.5[a]
	T_2	154.4±11.7[a]	6.55±0.31[a]	42.61±3.78[a]	3.4±0.5[a]
2024	WT	126.8±20.2[b]	5.47±0.86[b]	43.28±3.21[b]	3.8±0.5[a]
	T_2	180.8±14.8[a]	9.44±1.09[a]	52.09±2.26[a]	3.8±0.5[a]
Analysis of variance					
Main shoot	G	**	**	**	
	Y	ns	**	**	
	GxY	ns	ns	ns	
Plant	G	ns	**	**	ns
	Y	**	**	**	ns
	GxY	*	**	ns	ns

An increase in the grain yield of the transgenic wheat lines with reduced activity of the *ProDH* gene, observed in our experiment, may be associated with the formation of a greater amount of photoassimilates due to the prolongation of leaves photosynthetically activity, which subsequently improved the grain-filling process. Preservation of functional capabilities during the reproductive period is an important feature of transgenic lines, since the stay-green trait is considered the basis of genetic improvement of major grain crops, including wheat (Kamal *et al*., 2019). This is also confirmed by a comparative analysis of the photosynthetic traits of flag leaves of winter wheat varieties bred in the 1950s, 1970s, and 1990s. The varieties bred in 1990s, compared with those bred in 1950s and 1970s, had a higher chlorophyll content, net photosynthetic rate, maximum and actual photochemical efficiency of FS II, and photochemical fluorescence quenching coefficient at the grain filling stage. In addition, their flag leaf had a longer duration of functioning and senesced slower, and the grain yield exceeded values of varieties bred in 1950s by 26 % and in 1970s by 11 % (Wang *et al*., 2008).

An increased content of this multifunctional metabolite may be associated with a number of mechanisms of plant adaptation to stress. The accumulation of this amino acid affects both physiological and biochemical processes in plant cells (Jogawat, 2019; Meena *et al*., 2019; Ghosh *et al*., 2022), as well as genetic ones: it triggers the expression of stress-induced genes (Kaur & Asthir, 2015). Therefore, the accumulation of proline in the leaves as a result of stress relief has a positive effect on the functional and structural changes of the photosynthetic apparatus.

CONCLUSIONS

It was established that under natural growing conditions, the main photosynthetic activity parameters in the chloroplasts of light-adapted flag leaves of the transgenic wheat plants (**Table 3**) and the grain productivity of the main shoot and the whole plant (**Table 4**) significantly exceeded the corresponding parameters of the wild type UK 997/19. The coefficient of determination of the relationship of ϕ_{PSII}, qP and qL with the grain productivity of the whole plant ranged from 0.762 to 0.966. No dependence of grain yield with the maximum quantum yield of PSII and non-photochemical quenching of chlorophyll *a* fluorescence was found.

The higher capacity for photoassimilation in the transgenic wheat lines with reduced activity of *ProDH* gene, revealed in our research under conditions of increased air temperature or lack of moisture in the soil, may contribute to a rise in the formation of photoassimilates, which are responsible for the accumulation of dry matter in the grain. The received lines of winter wheat can serve as valuable breeding material for the creation of new stress-resistant plants.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: the authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Human Rights: this article does not contain any studies with human subjects performed by any of the authors.

Animal Studies: this article does not include animal studies.

AUTHOR CONTRIBUTIONS

Conceptualization, [G.P.]; methodology, [G.P.; O.D.; S.S.; M.T]; formal analysis, [G.P.; O.D.]; investigation, [G.P.; O.D.; S.S.; M.T.]; resources, [O.D.]; data curation, [G.P.; O.D.; M.T.]; writing – original draft preparation, [G.P.; O.D.; M.T.]; writing review and editing, [G.P.; O.D.]; translating, [G.P.]; visualization, [G.P.; O.D.]; supervision, [O.D.]; project administration, [G.P.; O.D.].

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АКТИВНІСТЬ ФОТОСИНТЕТИЧНОГО АПАРАТУ І ПРОДУКТИВНІСТЬ ТРАНСГЕННИХ РОСЛИН ПШЕНИЦІ ОЗИМОЇ З ЧАСТКОВОЮ СУПРЕСІЄЮ ГЕНА ПРОЛІНДЕГІДРОГЕНАЗИ

Галина Прядкіна, Оксана Дубровна, †Сергій Ситник, Максим Тарасюк

Інститут фізіології рослин і генетики НАН України
вул. Васильківська, 31/17, Київ 03022, Україна

Обґрунтування. Часткова супресія гена проліндегідрогенази (*ProDH*) у трансгенних рослин озимої пшениці приводить до збільшення рівня накопичення вільного проліну. Однак вплив підвищення вмісту цієї амінокислоти на фізіолого-біохімічні характеристики рослин цієї культури досі залишається не до кінця з’ясованим. У зв’язку з цим метою роботи був порівняльний аналіз впливу накопичення вільного проліну на показники активності фотосинтетичного апарату трансгенних рослин пшениці в репродуктивний період вегетації за змінних погодних умов, а також на їхню продуктивність.

Матеріали та методи. Матеріалом досліджень були нетрансформовані рослини пшениці м’якої озимої генотипу УК 997/19 і трансгенні лінії насіннєвого покоління T_2, отримані на їхній основі. Визначали вміст вільного проліну, фотосинтетичних пігментів і показники активності фотосинтетичного апарату. Аналіз елементів структури урожаю проводили у фазу повної стиглості зерна.

Результати. За умов підвищеної температури повітря або нестачі вологи у ґрунті встановлено, що вміст сумарного хлорофілу в листках рослин трансгенних ліній у фазу молочно-воскової стиглості перевищував його рівень у вихідної лінії на 15,9–32,5 %. У цю фазу в них також були вищими показники ефективного квантового виходу фотосистеми II (на 16–28 %), фотохімічного гасіння флуоресценції (на 23–26 %) та частки відкритих реакційних центрів ФСII (на 28–61 %). Не виявлено певних закономірностей у змінах показника нефотохімічного гасіння флуоресценції хлорофілу в антенних комплексах ФС II листків трансгенних і вихідних рослин. Зернова продуктивність рослин модифікованих ліній була вищою, ніж у вихідної лінії. Виявлено істотну позитивну кореляцію між зерновою продуктивністю трансгенних рослин і показниками частки відкритих реакційних центрів ФСII, ефективного квантового виходу у них та фотохімічного гасіння флуоресценції (коефіцієнт детермінації зв’язку – від 0,762 до 0,966).

Висновки. Результати дослідження свідчать про те, що подовження функціонування прапорцевого листка протягом репродуктивного періоду та вища активність фотосинтетичного апарату в трансгенних ліній пшениці зі збільшеним вмістом проліну за умов підвищеної температури повітря або нестачі вологи в ґрунті сприяли збільшенню їхньої зернової продуктивності.

Ключові слова: пшениця, трансгенні рослини, пролін, флуоресценція хлорофілу *а*, зернова продуктивність

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