GENOTYPIC PECULIARITIES OF WHEAT PHOTOSYNTHESIS LIGHT INDUCTION AND PRODUCTIVITY UNDER THE DROUGHT EFFECT

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Background. In agrocenoses, leaf light conditions are known to be unstable due to intermittent cloud cover and shading by other leaves or spikes. However, with a change in irradiance, photosynthesis does not reach its final value instantly, but with a certain delay. Due to this photosynthetic efficiency of leaves and crops is generally lower compared to stationary conditions. At the same time, the vast majority of works devoted to the problems of photosynthetic apparatus functioning under unstable light conditions do not take into account an adverse impact on photosynthesis of such a common stressor as drought. The aim of the present work was to study the peculiarities of flag leaves CO_2 and H_2O gas exchange parameters with changes in illumination under conditions of optimal and insufficient water supply in order to explore the pattern of drought effect on the photosynthetic induction processes in connection with productivity of wheat plants of different genotypes.

Materials and Methods. The research was carried out on bread winter wheat varieties Yednist, Bohdana, Perlyna Podillia under conditions of pot experiment. Control plants were grown under an optimal soil moisture of 70 % field capacity (FC). In the experimental pots, soil drought was created at the level of 30 % FC for 7 days during the earing–flowering period, after that the soil moisture was restored to the optimal level. The parameters of flag leaf gas exchange were measured on the seventh day of drought. Components of plants grain productivity were determined after reaching full grain maturity.

Results. It was found that according to the parameters of light induction curves of CO_2 assimilation and transpiration, wheat plants of different genotypes under drought conditions are differentiated more clearly than under normal water supply. An increase in the limiting role of stomata in the induction of photosynthesis under drought conditions and changes in illumination was shown. Drought disrupts the coherence of stomatal

conductance regulation in interaction with CO_2 assimilation processes. This affects the light induction curves of photosynthesis and transpiration, and ultimately leads to a decrease in grain productivity.

Conclusions. It was shown that in order to assess the efficiency of the photosynthetic apparatus in providing wheat plants with assimilates and maintaining their grain productivity under unfavorable conditions, the parameters of the response to the changes in illumination must be taken into account.

Keywords: Triticum aestivum L., drought, photosynthesis, transpiration, light induction, productivity

INTRODUCTION

In recent years, in connection with the slowdown of the increase in yield of one of the world's leading food crops – wheat, and the approach of harvest index (HI) to the biological limit (about 60 % of the aboveground part weight), the problem of finding new ways to increase the genetic potential of productivity arises (Long *et al.*, 2015). The photosynthetic efficiency of wheat is believed to be below its theoretical potential, although it has been slightly improved by breeding (Carmo-Silva *et al.*, 2017). In particular, it has been shown that with the increase of HI, the share of photoassimilates obtained by the ear from the flag leaf has increased during the last decades. Therefore, photosynthesis is currently considered an important direction for further improvement of the yield genetic potential (Murchie *et al.*, 2023).

In agrocenoses, leaf light conditions are known to be unstable due to intermittent cloud cover and shading by other leaves or spikes because of the wind (Tanaka *et al.*, 2019; Taylor & Long, 2017; Wang *et al.*, 2020). However, with a change in irradiance, photosynthesis does not reach its final value instantly, but with a certain delay (Deans *et al.*, 2019a). Due to the slowing of photosynthetic apparatus adaptation to light changes caused by both biochemical and diffusion effects, the photosynthetic efficiency of leaves and crops is generally lower compared to stationary conditions, for example, a phytotron. According to some assessments, losses of the assimilated carbon due to the instability of lighting conditions can be about 20 % compared to those measured under stable bright lighting (Taylor & Long, 2017).

At the biochemical level, limitations in the rate of photosynthesis induction during the transition from darkness to light are due to the activation of Rubisco with the participation of Rubisco-activase enzyme, the activation of redox-dependent enzymes involved in the regeneration of ribulose bisphosphate, and the accumulation of intermediate products of carbon metabolism (Acevedo-Siaca *et al.*, 2021; Salter *et al.*, 2019; Taylor *et al.*, 2022). At the leaf level, under normal water availability conditions, photosynthesis is inhibited by the influx of CO_2 into intercellular spaces due to slow stomatal opening, potentially creating a significant limitation of assimilation (Deans *et al.*, 2019b; Zhang *et al.*, 2019). According to some data, mesophyll conductance has a lesser effect on CO_2 assimilation under light changes compared to stomatal conductance (Sakoda *et al.*, 2021).

It was also found that under a dynamic lighting environment, the correlation between stomatal conductance and the CO_2 assimilation rate can be disturbed, which leads to an imbalance of these physiological processes, limitation of assimilation, and a decrease in the efficiency of water use (Faralli *et al.*, 2019a). Significant genotypic variations revealed for the time of stomatal opening and the achievement of a steady state of CO_2 assimi-

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lation (Salter *et al.*, 2019; Taylor *et al.*, 2020) open up prospects for improving the processes of photosynthesis induction under changes in lighting conditions to increase the photosynthetic apparatus performance, water use efficiency and, consequently yields (Tanaka *et al.*, 2019; Kaiser *et al.*, 2018; Lawson & Vialet-Chabrand, 2018; Taylor & Long, 2017). The use of biotechnological methods to genetically improve the speed of adaptation to changes in lighting showed positive results (Faralli *et al.*, 2019b; Long *et al.*, 2022). Intraspecific variability of stomatal response speed is also considered as a potential target for selection to optimize the physiological responses of wheat to dynamic field conditions (Deans *et al.*, 2019ab; Eyland *et al.*, 2021; Wang *et al.*, 2020; Yamori *et al.*, 2020).

However, the vast majority of works devoted to these problems do not take into account the stressful impact of drought on photosynthesis, the risk of which is increasing due to the global climate change. It is known that wheat genotypes differ significantly in response of stomatal conductance and CO_2 assimilation to water shortage (Morgun *et al.*, 2019ab). But there is little information on how changes in lighting will affect these processes under drought conditions, and in the post-drought recovery period. To the best of our knowledge, only one work addresses this issue inter alia, and notes that a reduced water availability caused asymmetric stomatal opening and closing responses under dynamic illumination (Faralli *et al.*, 2019a).

The aim of our work was to study the peculiarities of flag leaves CO_2 and H_2O gas exchange parameters with changes in illumination under conditions of optimal and insufficient water supply in order to explore the pattern of drought effect on the photosynthetic induction processes in connection with productivity of wheat plants of different genotypes.

MATERIALS AND METHODS

The research was carried out on winter bread wheat plants (*Triticum aestivum* L.) of the Yednist variety from the Plant Breeding and Genetics Institute of the National Center of Seed and Cultivar Investigation, National Academy of Agrarian Sciences of Ukraine (https://sgi.in.ua), and the Bohdana and Perlyna Podillia varieties from the Institute of Plant Physiology and Genetics, National Academy of Sciences of Ukraine (https://www.ifrg.kiev.ua). In accordance with the declared characteristics, the Yednyst variety is drought-resistant, selected in the arid southern Steppe zone of Ukraine, the Bohdana variety is also drought-resistant, but selected in a more temperate Forest-Steppe zone, the Perlyna Podillia variety is moisture-loving.

The plants were grown under pot experiment conditions in the vegetation period of 2021/2022. After overwintering under natural conditions (Kyiv, 50°39′N, 30°49′E), the plants at the spring tillering stage were transplanted into pots in early April (10 kg of 3:1 mixture of gray podzolic soil – pH salt (KCl) 5.8, organic matter content 1.8 %, nitrogen 30 mg/kg, phosphorus 25 mg/kg, potassium 30 mg/kg, and sand). Nitrogen, phosphorus, and potassium were additionally added to the pots at the rate of 160 mg per kg of soil for each element. The pots were placed on a shelving with a transparent polyethylene film roof on the territory of the Institute. The temperature and light were natural. The plants were grown until the grain reached full ripeness (early August).

Control plants were grown under the optimal soil moisture (70 % of soil field capacity (FC)) throughout the growing season. At the beginning of the flowering stage, watering of the experimental plants was stopped, which caused a reduction of the soil moisture to the level of 30 % FC within 3 days. This level was maintained for the following 7 days. After that, watering of the experimental plants was restored to the control level

(70 % FC), which was maintained until the harvest. The soil moisture in pots was controlled gravimetrically twice a day. For each treatment, 5 pots with 20 plants per each pot were set up (in total 100 plants for each treatment). Thus, the number of biological repetitions of each treatment was 5-fold.

Determination of flag leaf gas exchange indices of the control and experimental plants was conducted on the seventh day of drought. The components of plant grain productivity were determined after reaching full grain maturity by weighing air-dry material.

Net assimilation (A_n) and transpiration (T) rates were recorded on intact flag leaves of main shoots under controlled conditions (temperature 25 °C, photosynthetically active radiation 1500 µmol/(m²·s) using the gas analyzer EGM-5 (PP Systems, Amesbury, USA). Conditioned air (humidity 10 mbar, CO_2 concentration 410–415 ppm) was blown through the chamber at a rate of 1 L/min. Gas exchange parameters – A_n, T, stomatal conductance (g_s) and CO_2 concentration in leaf intercellular spaces (C_i) were calculated according to F. A. Busch *et al.*, (2024).

Induction curves of A_n and T in flag leaves were recorded according to the following method. After placing the leaves in the chamber, they were illuminated for 1 hour (at full power), and at the end of this period the A_n was recorded, whose level was considered maximum for a given measurement cycle. Then the light was turned off and the leaves were left in the dark for 30 minutes. At the end of this period, the dark respiration rate was recorded, and the light was turned on (immediately at full power). Air from the chamber was supplied to the gas analyzer with an interval of 10 min, and CO_2 and H_2O gas exchange indices were recorded. In this case, the total lighting time was 50 min.

Biometric indices – plant dry weight and grain productivity were determined in 20-fold repetitions, the A_n and T rates – in 4-fold. The data obtained were processed by methods of variation statistics using Microsoft Excel. The significance of differences between samples was evaluated by one-way analysis of variance (ANOVA), where differences were considered significant at $P < 0.05$ using Tukey's test. The validation analysis of data approximation by the linear function (illustrated in Fig. 4) was performed using Fisher's F-test; determination coefficients (R^2) were at least 0.92 for the linearized charts. The Figures and the Table show the arithmetic mean and the standard error of the mean (x±SE).

RESULTS AND DISCUSSION

After turning on the light, the gradual increase in the A_n and T during a certain time was observed, reaching a saturation plateau at the end of the measurement period. Such dynamics is caused by the gradual opening of stomata and the launch of biochemical processes of CO_2 fixation in the light. In the literature, they are usually called light induction curves of photosynthesis (Acevedo-Siaca *et al.*, 2021; Deans *et al.*, 2019ab; Sakoda *et al.*, 2021; Taylor *et al.*, 2020).

Measurement of the A_n induction curves after transition from darkness to light revealed noticeable varietal differences in the dynamics of this process in both control and drought-treated plants (**Fig. 1*A***). It should be noted that the index of CO_2 gas exchange, which corresponded to the zero time point, reflected the loss of assimilated carbon in the dark due to respiration and therefore lay below the abscissa axis. In 30 min after the start of lighting, a fairly clear differentiation in A_n of the studied varieties plants was observed. It was the highest in the Bohdana variety plants, followed by the Yednist and Perlyna Podillia varieties in a descending order. In 40 min after turning on the light,

the plants of the first two varieties already showed a clear tendency for the induction curve to reach the saturation plateau, while the Perlyna Podillia variety still showed a gradual rise, although it was much slower than in the first 30 min. As a result, in 50 min after the start of illumination, the A_n in flag leaves of the plants of the Yednist and Perlyna Podillia varieties was practically the same, while the Bohdana variety exceeded them by 24 % (P <0.05 in both cases).
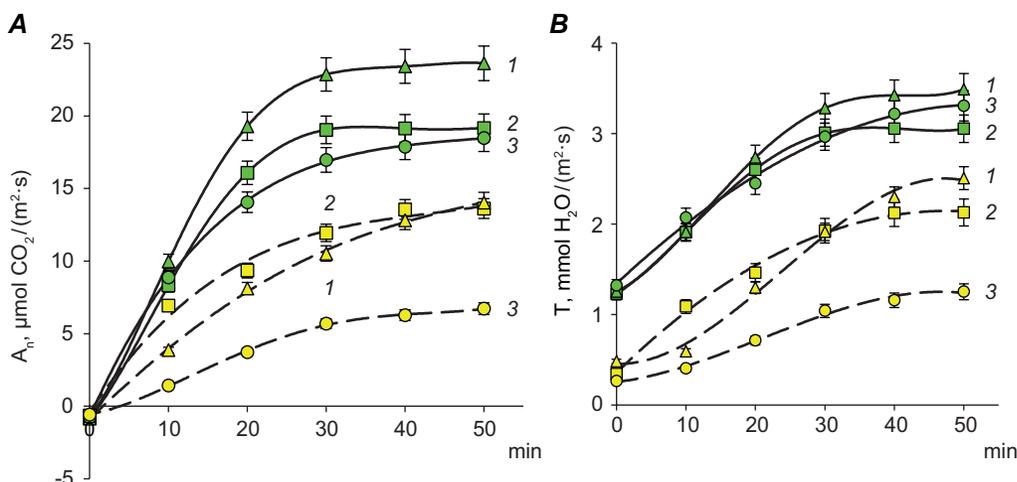

Fig. 1. Average induction curves of the net assimilation rate (A_n) (**A**) and transpiration (T) (**B**) in flag leaves of winter wheat plants of different varieties after turning on the light (here and in Fig. 2, 3): *1* – Bohdana variety; *2* – Yednist variety; *3* – Perlyna Podillia variety; green markers – optimal soil moisture (70 % FC); yellow markers – drought (30 % FC)

At the same time, the plants subjected to a seven-day drought showed differences from the control ones both in terms of the induction curve dynamics, and the actual level of A_n. Firstly, the increase of this index after turning on the light was noticeably slower than in control plants. A plateau (or a tendency to it) was noted only at the end of the studied time period, and the final A_n values were significantly lower than in the control plants. Thus, in plants of the Yednist variety, this index was only 69 % of the control (P <0.01), the Bohdana variety – 59 % (P <0.01), and the Perlyna Podillia variety – 36 % (P <0.001).

Under drought conditions, the relative arrangement of genotypes by the A_n level was also different. This index was the highest, and nearly consimilar in most of the induction curves, in plants of the Yednist and Bohdana varieties, and the lowest in the Perlyna Podillia variety. It should be noted that during the first 10 min after turning on the light, the A_n in leaves of the Yednist variety increased much faster than in other genotypes, followed by a gradual slowdown, and in the Bohdana variety, this increase occurred more slowly, but for a longer period, which at the end of measurements equaled to the first variety.

Another important index of leaf gas exchange is the water evaporation rate or transpiration (T). The induction curves of T after turning on the light were somewhat similar to those for the A_n, with the exception that they started with values above zero (**Fig. 1B**). The similarity consisted in a gradual increase of this index, and reaching a saturation plateau at the end of the measurement period. Among the control plants, the highest T was observed in the leaves of the Bohdana variety, followed by Perlyna Podillia and Yednist.

A seven-day soil drought led to a significant decrease in T of leaves of all varieties, albeit to a varying degree. According to the final value (50 min after the start of illumi-

nation), this index for the plants of Yednist variety was 69.8 % of the control, Bohdana – 71.9 % (P <0.01 in both cases), Perlyna Podillia – 37.8 % (P <0.001). It should be noted that a faster increase in T during the first 10 minutes was observed in plants of the Yednist variety compared to other varieties (a similar trend was also observed for the A_n (see **Fig. 1*A***)). In general, 50 min after the start of illumination, the T in drought-exposed plants was the highest in the Bohdana variety, slightly lower in the Yednist variety, and the lowest in the Perlyna Podillia variety.

It is known that the main factors inhibiting the A_n under drought conditions are a decrease in stomatal conductance (g_s), a slowdown in the diffusion of CO_2 from the intercellular spaces in leaf to the centers of carboxylation (mesophyll conductance), as well as a violation of electron transport and ATP synthesis in chloroplasts, a decrease in activity of Rubisco and other enzymes of the Calvin–Benson cycle, and an increasing photorespiration rate (Zahra *et al.*, 2023).

The main stomata function is to optimize the balance between the entry of CO_2 into the leaf and the loss of water during transpiration, thereby maintaining a certain CO_2 concentration in the leaf intercellular spaces (C_i), sufficient to ensure its assimilation in the chloroplasts of the mesophyll cells in accordance with the speed of their light and dark reactions (Nunes *et al.*, 2020; Zhang *et al.*, 2024). Accordingly, C_i and the leaf water regime are the main factors in the regulation of g_s (Ehonen *et al.*, 2019). At the normal state of the stomatal apparatus in the light, the concentration of CO_2 inside the leaf is lower than that in the air around the leaf, since the supply of CO_2 is limited by its diffusion through the stomata. In the dark, it is higher than atmospheric due to the CO_2 release by the mesophyll cells as a result of dark respiration, while the state of the stomata is characterized by a minimal aperture, and consequently the minimal conductance. These provisions are confirmed by our calculations of CO_2 g_s and C_i dynamics in wheat leaves after turning on the light (**Fig. 2**).

In the control plants of all varieties, g_s increased almost linearly within the first 30 min after turning on the light (**Fig. 2*A***). Then the rate of increase slowed down and after 50 min this index reached a plateau with the highest value in plants of the Bohdana variety. At the same time, it should be noted that A_n showed a tendency to slow down already 20 min after the start of illumination, i.e. earlier than g_s.

Usually, the slowing of the A_n increase at high values of g_s is explained by an increase in the share of non-stomatal factors in limiting of CO_2 assimilation (Deans *et al.*, 2019a). The latter include, in particular, the rate of ribulose bisphosphate regeneration in the Calvin-Benson cycle, the Rubisco activation rate by the Rubisco-activase enzyme, and the efficiency of ETC functioning (Amaral *et al.*, 2024).

In drought-treated plants, g_s was significantly lower than in the control (**Fig. 2*A***). In 30 min after turning on the light, this index also began to reach the saturation level in leaves of all varieties, but the Bohdana variety was significantly ahead of the other two. In drought-exposed plants at the end of the studied period after turning on the light, the difference between the Bohdana and Yednist varieties in g_s was negligible, and in Perlyna Podillia plants this index was more than twice as low. As noted, the main limiting factor for the A_n under drought conditions is stomata closure, which leads to a strong decrease in their conductance (Urban *et al.*, 2017). This effect of drought is well illustrated in **Fig. 2**. It should be noted that the strength of this effect varied markedly between genotypes. Thus, in plants of the Bohdana variety, g_s under drought conditions decreased by 1.93 times compared to the control (P <0.001), in the Yednist variety – by 1.74 times (P <0.001), and in the Perlyna Podillia variety – by 4.51 times (P <0.0001).
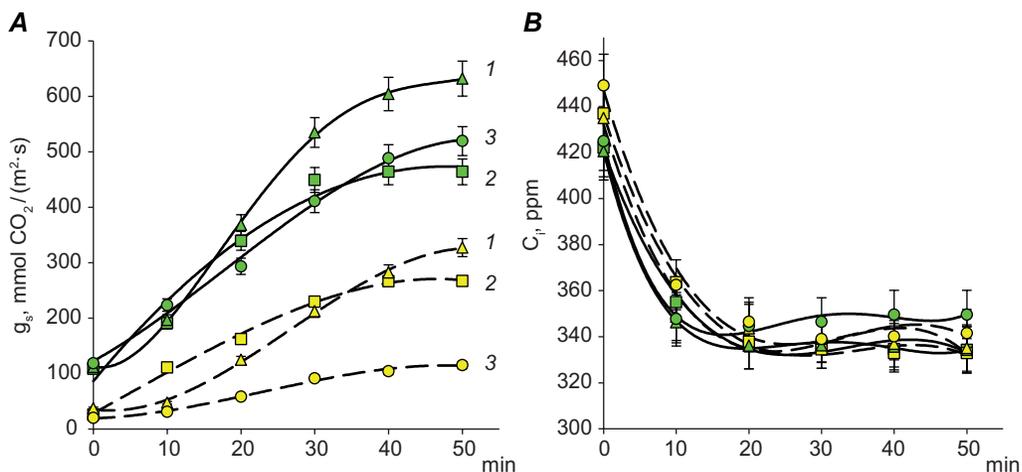
Fig. 2. Average induction curves of stomatal conductance (g_s) (**A**) and CO_2 concentration in intercellular spaces (C_i) (**B**) in flag leaves of winter wheat plants of different varieties after turning on the light under optimal soil moisture and drought

Calculations of C_i showed that in the dark (point 0 on the abscissa axis) it was higher than atmospheric. With the beginning of illumination, it fell rapidly, and after 20 min it stabilized at the level of approximately 340 ppm without significant differences between the treatments (**Fig. 2B**).

These results show that in wheat plants, short-term drought at the level of 30 % FC suppresses the mesophyll cells photosynthetic apparatus activity more strongly than the stomata functional state. The latter only adjust to the real CO_2 flow rate from the intercellular spaces to the chloroplasts, which is determined by the speed of its fixation in the Calvin–Benson cycle. This is confirmed by the lack of difference in C_i between the control and drought-treated plants after 20 min of illumination, although A_n in the latter under drought conditions was significantly lower than in the control plants.

During the first 10–20 min after turning on the light, the functioning of stomatal and actual photosynthetic apparatus is coordinated, which was accompanied by a certain decrease in C_i due to a slower increase in g_s relative to CO_2 assimilation. Greater stomatal inertia compared to CO_2 assimilation is a typical feature of photosynthesis induction in cultivated plants (Long *et al.*, 2022). Thus, in experiments with wheat, it was found that in the first minutes of photosynthesis induction, the share of stomatal limitation of photosynthesis was about 50 % and decreased to 30 % when the gas exchange rate reached the plateau (Taylor & Long, 2017).

For a more detailed analysis of the A_n induction dynamics in wheat leaves after turning on the light, we normalized the intermediate points of the curves to the maximum values obtained after 1 hour of preceding illumination, and expressed them as a percentage of the maximum (**Fig. 3**). The obtained curves were analyzed according to two parameters: (1) – the time during which the A_n rate in leaf reached 50 % of the maximum, and (2) – the percentage of maximum A_n, which was reached 30 min after the light was turned on. Control plants reached 50 % of maximum A_n after 10.5–11.5 min (P <0.01) (**Fig. 3A**), and 30 min after the start of illumination, the A_n in their leaves was 92–95 % of the maximum (P >0.05). At the same time, there were no significant differences between the varieties regarding both parameters.
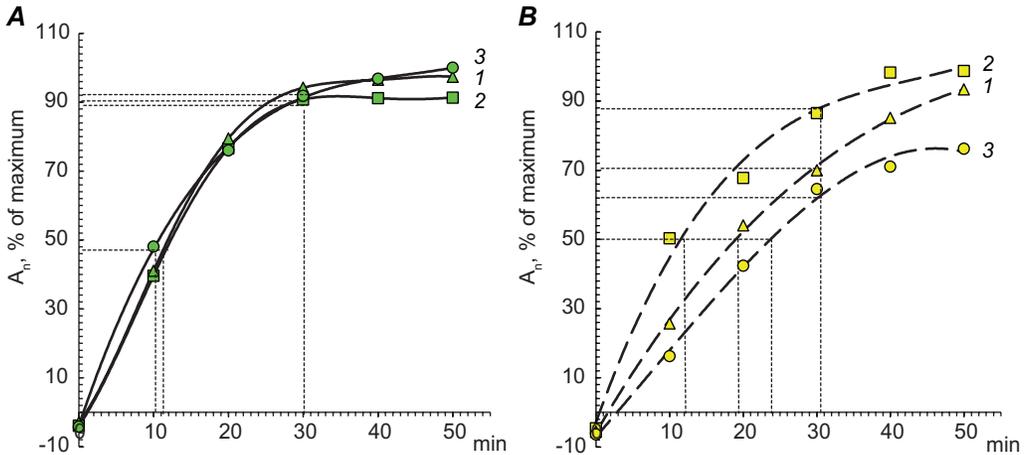
Fig. 3. Average induction curves of the net photosynthetic rate (A_n) in flag leaves of wheat plants of different varieties after turning on the light, normalized to maximum values, under optimal soil moisture (**A**) and drought (**B**)

Drought led to a significant differentiation of the plants of the studied genotypes in terms of both parameters (**Fig. 3B**). Thus, A_n reached 50% of the maximum (under the stressor effect) the fastest in plants of the Yednist variety (11.8 min). Next, in order of increasing time (i.e. increasing inhibition of induction), were the varieties Bohdana (19 min) and Perlyna Podillia (23.5 min). In 30 min after turning on the light, the maximum increase in the A_n was again observed in the plants of the Yednist variety (88 % of the maximum under drought). The Bohdana (70 %) and Perlyna Podillia (62 %) varieties followed in decreasing order of this parameter. So, if we take into account both investigated parameters of the A_n induction curve dynamics in wheat leaves under drought conditions, the Yednist variety showed itself the best. Then there were the Bohdana and Perlyna Podillia varieties.

Additionally, we have investigated the relationships between the T and A_n, which included all points obtained for induction curves after turning on the light in the control and drought-treated plants. It was revealed that these relationships are well approximated by linear equations (**Fig. 4**).

Their information content is in the fact that the coefficient of function argument quantitatively characterizes such an important physiological parameter as the instantaneous water use efficiency (WUEi) during photosynthesis, i.e., how many micromoles of CO_2 are fixed in a leaf when 1 mmol of H_2O evaporates (Endres *et al.*, 2010). Under field conditions, this index depends on lighting, temperature, air and soil moisture, growth stage and genotypic peculiarities of plants, and can vary widely during the growing season (Lopez *et al.*, 2019). Since in our experiments the A_n and T measurements were taken under controlled light and temperature conditions, while the humidity of the air supplied to the chamber and the soil moisture in pots were also stabilized, the parameter obtained as a result of the analysis of the discussed relationships can be considered quite representative for wheat.

It can be seen from the equations in **Fig. 4** that WUEi was significantly lower in drought-treated plants than in the control ones. In the control plants of the Bohdana variety this index was 8.63 µmol CO_2/mmol H_2O, while in the treated – 5.16 µmol CO_2/mmol H_2O, in the Yednist variety – 9.41 and 6.32, respectively, in the Perlyna Podillia

variety – 7.27 and 6.23 µmol CO_2/mmol H_2O respectively. In other words, the treated plants assimilated less CO_2 for the same amount of evaporated water. This indicates a certain suppression of leaf mesophyll cell photosynthetic apparatus under the influence of drought, caused not only by a decrease in g_s, but also at the biochemical level.
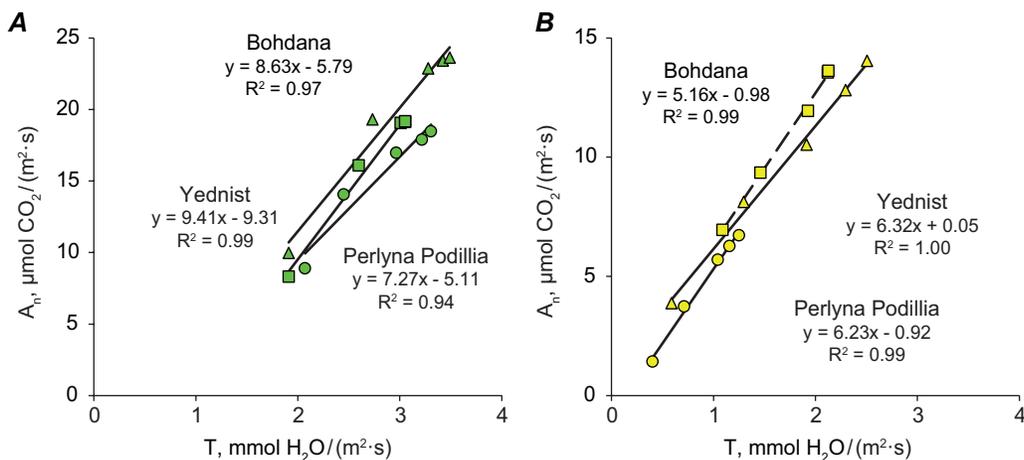
A

Bohdana
$y = 8.63x - 5.79$
$R^2 = 0.97$

Yednist
$y = 9.41x - 9.31$
$R^2 = 0.99$

Perlyna Podillia
$y = 7.27x - 5.11$
$R^2 = 0.94$

A_n, µmol CO_2/(m²·s)

T, mmol H_2O/(m²·s)

B

Bohdana
$y = 5.16x - 0.98$
$R^2 = 0.99$

Yednist
$y = 6.32x + 0.05$
$R^2 = 1.00$

Perlyna Podillia
$y = 6.23x - 0.92$
$R^2 = 0.99$

A_n, µmol CO_2/(m²·s)

T, mmol H_2O/(m²·s)

Fig. 4. The relationships between transpiration (T) and photosynthetic (A_n) rates in control (**A**) and drought-treated (**B**) winter wheat plants

Our results clearly demonstrate that for wheat plant drought tolerance, not only the ability to maintain the A_n at the maximum possible level under these conditions is important, but also the speed of photosynthetic apparatus response to changes in illumination. The study revealed that under drought, wheat plants of different varieties differ more clearly and differently in terms of the parameters A_n induction curves during the transition from darkness to light, than under normal conditions. This suggests that drought affects the state of the photosynthetic apparatus not only through inhibition of its maximum functioning rate, but also the ability to respond to changes in lighting, which is also related to its efficiency.

The analysis of wheat grain productivity components after reaching full grain maturity revealed that a one-week soil drought during the flowering period significantly reduced grain productivity of all varieties, albeit to varying degrees (**Table**). In the control plants, the highest grain productivity of both the main shoot and the whole plant was obtained for the Perlyna Podillia variety. In the plants of the Yednist and Bohdana varieties, productivity was lower and differed insignificantly, both for the main shoot and the whole plant.

At the same time, among drought-treated plants, the lowest degree of decrease in grain productivity of the main shoot and the whole plant was observed in the Bohdana variety (by 18.6 and 20.8 % compared to the control, respectively) (see **Table**). In the Yednist variety, these indices were slightly higher (a decrease by 25.5 and 29.5 %, respectively), whereas the drought had the strongest effect on the grain productivity of plants of the Perlyna Podillia variety (a decrease by 37.2 and 35.9 %, respectively). The harvest index (HI) of the control plants was quite high – in the range of 0.52–0.57. Under the influence of drought, this index decreased by 11–13 % in the Bohdana and Yednist varieties, and by 23 % – in the Perlyna Podillia variety. In general, the Yednist and Bohdana varieties showed higher grain productivity resistance under the influence of drought than the Perlyna Podillia variety.

Drought influence on the grain productivity components of winter wheat plants of different varieties (x±SE; n = 20)

Variety	Treatment	Grain weight, g	Grain number, pcs.	1000 grains weight, g	HI
Main shoot					
Yednist	Control	1.77±0.09	41.2±1.7	42.9±0.9	–
	Drought	1.32±0.05*	30.1±1.1*	44.3±0.9	–
Bohdana	Control	1.89±0.10	39.9±1.9	47.2±0.9	–
	Drought	1.54±0.10*	33.3±1.3*	45.8±1.6	–
Perlyna Podillia	Control	2.05±0.08	44.5±1.2	46.1±0.8	–
	Drought	1.29±0.08*	31.1±1.1*	41.2±1.7*	–
Whole plant					
Yednist	Control	3.44±0.17	83.5±3.7	41.2±1.0	0.52±0.01
	Drought	2.43±0.13*	58.6±4.4*	41.7±0.8	0.46±0.01*
Bohdana	Control	3.40±0.26	73.5±5.7	46.5±0.8	0.53±0.01
	Drought	2.69±0.20*	59.8±3.6*	44.8±1.2	0.48±0.01*
Perlyna Podillia	Control	3.71±0.21	86.5±5.1	43.2±0.9	0.53±0.01
	Drought	2.38±0.22*	62.6±4.7*	37.6±1.6*	0.41±0.01*

Note: * significant difference compared to the control (P <0.05)

As mentioned above, a decrease in the speed and completeness of the photosynthetic apparatus response to changes in lighting conditions leads to a decrease in the amount of assimilated carbon, and eventually plant productivity (Taylor *et al.*, 2017). Under drought conditions, plants of the Bohdana and Yednist varieties maintained a higher A_n and had better induction curve parameters than the Perlyna Podillia variety. This can explain a smaller decrease in their grain productivity compared to the conditions of optimal water supply. Plants of the Perlyna Podillia variety had a worse CO_2 assimilation induction time under changes in lighting, and the maximum A_n under drought was the lowest in this variety.

CONCLUSIONS

It was revealed that according to the parameters of CO_2 assimilation light induction curves, wheat plants of different genotypes differentiate more clearly and differently under drought conditions than under normal conditions. That is, drought affects the state of photosynthetic apparatus not only in terms of its maximum functioning rate, but also the ability to respond to changes in lighting, which also affects its efficiency. Drought disrupts the coherence of g_s regulation and CO_2 assimilation processes, which affects the induction curves of photosynthesis and transpiration under dynamic conditions of the light regime.

Under drought conditions, the WUEi in wheat leaves was lower than under optimal soil moisture, i.e. plants fixed less CO_2 for the same amount of evaporated water. This indicates the inhibition of the photosynthetic apparatus of the leaf mesophyll cells under the influence of drought, caused not only by a decrease in g_s, but also at the biochemical level.

It was shown that in order to assess the efficiency of the photosynthetic apparatus in providing wheat plants with assimilates and maintaining their grain productivity under

unfavorable conditions, the parameters of the response to the changes in illumination, which are inherent to the natural environment, must be taken into account.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of Interest: the authors declare that 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

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ГЕНОТИПНІ ОСОБЛИВОСТІ СВІТЛОВОЇ ІНДУКЦІЇ ФОТОСИНТЕЗУ ПШЕНИЦІ ТА ПРОДУКТИВНОСТІ ЗА ДІЇ ПОСУХИ

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Вступ. В агроценозах освітленість листків, як відомо, є нестабільною через періодичну хмарність і затінення іншими листками або колосами. Проте за зміни освітленості фотосинтез досягає кінцевого значення не миттєво, а з певною затримкою. Внаслідок цього ефективність фотосинтезу листків і посівів зазвичай нижча, порівняно зі стаціонарними умовами. Водночас переважна більшість робіт, присвячених проблемам функціонування фотосинтетичного апарату в умовах нестабільної освітленості, не враховує негативний вплив на фотосинтез такого поширеного стресора, як посуха. Метою роботи було вивчити особливості параметрів газообміну CO_2 та H_2O прапорцевих листків за зміни освітленості в умовах оптимального та недостатнього водозабезпечення, щоб з'ясувати характер впливу посухи на процеси фотосинтетичної індукції у зв'язку з продуктивністю рослин пшениці різних генотипів.

Матеріали та методи. Дослідження проводили на м'якій озимій пшениці сортів Єдність, Богдана, Перлина Поділля в умовах вегетаційного досліду. Контрольні рослини вирощували за оптимальної вологості ґрунту 70 % повної вологоємності (ПВ). У дослідних посудинах у період колосіння–цвітіння створювали ґрунтову посуху протягом 7 діб на рівні 30 % ПВ, після чого відновлювали оптимальну вологість ґрунту. Параметри газообміну прапорцевих листків вимірювали на сьому добу посухи. Компоненти зернової продуктивності рослин визначали після досягнення повної стиглості зерна.

Результати. Встановлено, що за параметрами світлових індукційних кривих асиміляції CO_2 і транспірації рослини пшениці різних генотипів за умов посухи диференціюються більш чітко, ніж за нормального водопостачання. Показано підвищення лімітувальної ролі продихів у індукції фотосинтезу за умов посухи та змін освітленості. Посуха порушує узгодженість регуляції продихової провідності у взаємодії з процесами асиміляції CO_2. Це впливає на світлові індукційні криві фотосинтезу і транспірації, що зрештою призводить до зниження зернової продуктивності рослин.

Висновки. З'ясовано, що для оцінки ефективності фотосинтетичного апарату у забезпеченні рослин пшениці асимілятами та збереженні їхньої зернової продуктивності за несприятливих умов необхідно враховувати параметри реакції на зміни освітленості.

Ключові слова: *Triticum aestivum* L., посуха, фотосинтез, транспірація, світлова індукція, продуктивність