

STUDY ON CHANGES AND RELATIONSHIPS OF PHYSIOLOGICAL
AND MORPHOLOGICAL PARAMETERS OF RYE SUBJECTED
TO SOIL DROUGHT STRESS*

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Abstract. The study was aimed at the evaluation of the impact of drought stress on the efficiency of the photosynthetic apparatus of rye inbred line GULbw, evaluated based on measurements of chlorophyll fluorescence and gas exchange parameters, water balance, assimilation pigments and morphological characters, and by the analysis of the relationship between these parameters. The experiment was performed on the rye inbred line GULbw (original name: Gülzow 661-67, accession numbers: GueR 412; R 1599), obtained from the gene bank of The Federal ex situ Gene Bank for Agricultural and Horticultural Crop Species of The Leibniz Institute of Plant Genetics and Crop Plant Research Gatersleben. Because of drought, the PSII (photosystem PS II) performance index was reduced, and the decrease tendency of the PI (overall performance index of PSII) value intensified with the length of the stress period. The tested rye line did not exhibit any considerable variability of the maximum quantum efficiency of the PS II (Fv/Fm). Significant differences in the intensity of transpiration, stomatal conductance, and substomatal concentration of CO₂ was determined on day 18 of drought. A significant positive value of the correlation coefficient *r* was found between PLSN, LSW, LSGN, LSGW, and E, gs, ci.

Key words: morphology, photosynthesis, *Secale cereale* L.

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LIST OF SYMBOLS USED

C – control, well-watered variant of the experiment; c_i – intercellular CO₂ concentration; D – drought, water deficit variant of the experiment; E – transpiration rate; F_m – maximal fluorescence; F_v – maximal variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; LSDW – lateral stalk spikes dry weight; LSGN – productive lateral spikes grain number; LSGW – productive lateral spikes grain weight; LSN – lateral stalk number; LSTGW – productive lateral spikes thousand grain weight; LSW – productive lateral spikes weight; MSGN – main stem grain number; MSGW – main stem grain weight; MSSL – main stem spike length; MSSW – main stem spike weight; MSTGW – main stem thousand grain weight; MSW – main stem dry weight; PC1 – principal component 1, PC2 – principal component 2; PH – plant height; PI – overall performance index of PSII; PL – peduncle length; PLSN – productive lateral spike number; P_n – net photosynthetic rate; PW – plant dry weight; RWC – relative water content; SN – stalk number; T_{FM} – time required to reach maximal fluorescence; WSD – water saturation deficit; WUE – photosynthetic index of water use efficiency; WUEI – instantaneous photosynthetic index of water use efficiency.

INTRODUCTION

Drought is one of the most important environmental factors limiting the growth and the productivity of crops. Plant response to water stress is a complex process, leading to significant physiological and biochemical changes and eventually to morphological changes (Mishra *et al.* 2012). Water deficiency disables the efficient use of the obtained light energy, through increased dispersion caused by heat and enhanced fluorescence (Cetner *et al.* 2014). To evaluate plant reaction to water stress, physiological, biochemical, and morphological plant parameters are used, chlorophyll fluorescence tests that allow recording the changes taking place in the photosynthetic apparatus are performed, and the plant physiological status is determined (Yordanov *et al.* 2000, Mahajan and Tuteja 2005, Richards 2006, Anjum *et al.* 2011, Desotgiu *et al.* 2012, Kalaji *et al.* 2012).

Rye is considered to be the most drought-resistant cereal. A parameter which indicates this feature can be the water-use-per-dry-weight unit – rye requires as much as 20-30% less water than wheat (Starzycki 1976). Thus, rye could constitute a valuable source of information for studying resistance mechanisms, and yet it is weakly studied in this field, particularly in the aspect of the course of photosynthesis.

In the climate of our country, lack of water is one of the most important factors limiting crop yields. These conditions force us to ask what phenotypes of cereals will ensure stable and high yields in areas threatened with drought.

The study was aimed at the evaluation of the impact of drought stress on the efficiency of the photosynthetic apparatus of rye inbred line GULbw, evaluated based on measurements of chlorophyll fluorescence and gas exchange parameters, water balance, assimilation pigments and morphological characters, and by the analysis of the relationships between these parameters. Verification of the inbred line of GULbw rye, understanding the physiological basis of its resistance to drought stress, will make it possible to initially determine the suitability of this variety in areas threatened by drought.

MATERIALS AND METHODS

Plant material and growth conditions

The experiment was performed on the rye inbred line GULbw (original name: Gülzow 661-67, accession numbers: GueR 412; R 1599), obtained from the gene bank of The Federal ex situ Gene Bank for Agricultural and Horticultural Crop Species of The Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) Gatersleben, Germany. This line is characteristic due to its green colour, which is unusual for typical, glaucous plants of rye. GULbw was grown in a vegetation hall of the West Pomeranian University of Technology in Szczecin, Poland (53.45°N, 14.53°E).

Seeds were sown in January, singly, in pots (15 cm diameter, 20 cm high) filled with a mixture of soil and sand in equal proportions by volume. The pots were filled with the same soil mass (3.8 kg) and same water content. Initially, plants were grown in a greenhouse at the temperature of 15°C for first three weeks, followed by a gradually decreasing temperature until it was close to atmospheric conditions. Further vegetation proceeded under natural conditions of the winter-spring period (February-September), with natural daylight duration, under a foil tunnel.

Two irrigation regimes were applied: well-watered control and a water-limited variant, referred to as drought. The plants were watered with an appropriate volume of water, on the basis of plant viability, soil appearance, and soil moisture that is measured as volumetric water content (VWC) (TDR 100 Soil Moisture Meter, Spectrum Technologies, Inc.). In our study, 60-70% VWC was adopted as well-watered control and 20-30% VWC as drought. For the drought treatment, the watering was limited to 20-30% VWC for 18 days. The period of drought coincided with the phases of tillering, shooting, heading, and the beginning of flowering. Each variant of the experiment was represented by five plants.

Physiological determinations

Determinations of physiological parameters were conducted on two dates: on day 12 and 18 of drought. Measurements of the gas exchange parameters (CO_2 assimilation, transpiration, stomatal conductance, and substomatal concentration of CO_2) were conducted (in five replicates) on leaves with the use of a mobile gas analyser TPS-2, operating in an open system with PLC-4 chamber. The following conditions were adopted in the analyser cuvette: constant carbon dioxide supply, humidity equal to the ambient humidity, and illumination equal to 2053 PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$), supplied through the light attached to the cuvette.

Determination of the induction of chlorophyll fluorescence was performed using a Handy PEA fluorimeter (Hansatech, UK). The measurements were performed in the mid-portion of the leaf, with its prior shading with a clip for about 20 minutes. The measurement was performed on eight leaves of each analysed plant in control ($n = 40$) and dried ($n = 40$). Based on the measurements of chlorophyll fluorescence, the energy flow theory in PSII and using the OJIP test proposed by Strasser, the following parameters of chlorophyll fluorescence kinetics were calculated and analysed: F_V/F_M – maximal photochemical efficiency of PSII, PI – overall performance index of PSII, T_{FM} – time needed to reach the maximal chlorophyll fluorescence, and F_V – variable fluorescence.

Based on the obtained results of the assimilation intensity, transpiration and stomatal conductance, the photosynthetic index of water use efficiency (WUE) and instantaneous photosynthetic index of water use efficiency (WUEI) were calculated.

The determination of the content of assimilation pigments (chlorophyll "a" and "b" and carotenoids) was conducted on the same leaves for which the gas exchange parameters were defined. The analyses were conducted in five replicates of each analysed plant in the control ($n = 25$) and dried ($n = 25$). The chlorophyll content was determined using the method of Arnon *et al.* (1956) with Lichtenthaler modification (1987), whereas for the carotenoid content, the Hager and Meyer-Bethenrath method was used (1966).

The relative water content index (RWC) and water saturation deficit (WSD) were determined in accordance with Bandurska (1991).

Agronomic traits

At final maturity, the plants were cut at the soil surface, weighed, and separated from the main shoot and remaining parts. For each plant, the following parameters were measured or counted: stalk number (SN), plant dry weight (PW), plant height (PH), peduncle length (PL), main stem dry weight (MSW), main stem spike length (MSSL), main stem spike weight (MSSW), main stem grain number (MSGN), main stem grain weight (MSGW), main stem thousand grain weight (MSTGW), lateral

stalk spikes dry weight (LSDW), number of lateral stalks with spikes (LSN), number of productive lateral spikes (PLSN, which means spikes with at least one grain), productive lateral spikes weight (LSW), productive lateral spikes grain number (LSGN), productive lateral spikes grain weight (LSGW), productive lateral spikes thousand grain weight (LSTGW).

Statistical analyses

Presented results are based on 5 biological and 5-8 technical replicates. Data were analysed using the STATISTICA 12.0 software package (StatSoft, Inc., USA). Significant differences were calculated using Duncan's multiple range test at $p = 0.01$. Pearson linear correlation (r) was computed ($p = 0.01$) to test the significance between the parameter correlations. Principal Component Analysis (PCA) was performed.

RESULTS AND DISCUSSION

The reaction of plants to water deficiency is complex and it is related to the coordination of numerous biochemical chains leading to the expression of genes responsible for the adaptation to stress conditions (Bray 1997, Neill and Burnett 1999). Photosynthesis is one of the physiological processes that is strongly modified by water stress, thus the research of its course is used to evaluate plants in reaction to the stress (Rekika *et al.* 1998, Desotgiu *et al.* 2012, Kalaji *et al.* 2012). Restriction of CO_2 assimilation and transpiration resulting from water stress may be due to the decreased aperture or closing of the stomata, caused by the difference between external and internal humidity of a leaf, as well as increased synthesis of the abscisic acid, causing a decrease of stomatal cell turgor pressure (Popova *et al.* 2000). Apart from the inhibition of these processes, caused by the closing of the stomata, water stress contributes to a reduction of photosynthesis intensity through reduced activity of enzymes participating in the carboxylation process, restriction of electron transport by PS II, destruction of the photosystem structures, and by a reduction of chlorophyll and carotenoid content (Yordanov *et al.* 2000, Jaleel *et al.* 2009, Zlatev 2009). Reduction of the amount of assimilation pigments may impact the reduction of photosynthesis intensity (Anjum *et al.* 2011).

In the conducted study, significant differences between chlorophyll a and total chlorophyll content were observed between the tested rye lines in the control and those subjected to stress conditions. The tendencies for the changes of the content of assimilation pigments in leaves of the tested rye line in the control and those subjected to stress conditions were similar. The content of assimilation pigments in the GULbw line was reduced in the course of drought. The mean values of total chlorophyll and carotenoids on day 18 of drought were $1855 \mu\text{g g}^{-1}$ d.w. and $808 \mu\text{g g}^{-1}$ d.w. and were lower by 21.2 and 35.3%, respectively, relative to their concentration on

day 12 of drought (Fig. 1). The content of chlorophyll a, chlorophyll b, and carotenoids in GULbw leaves on day 18 of drought constituted 57.3, 55.9, and 46.6% of the amount of these pigments in the leaves of the control plant, respectively (Fig. 1). Czyczyło-Mysza and Myśków (2017), after four weeks of drought, did not determine significant differences in the content of total chlorophyll in two rye inbred lines. A reduced concentration of chlorophyll in tissues of plants growing in drought conditions was demonstrated by Ranjbarfordoei *et al.* (2000). Anjum *et al.* (2003) showed that water stress changed the ratio of chlorophyll a and b. A reduction in chlorophyll content was reported in drought stressed cotton (Massacci *et al.* 2008). Kiani *et al.* (2008) revealed that the chlorophyll content decreased to a significant level at higher water deficits in sunflower plants. Arji and Arzani (2008) showed that the amount of chlorophyll a and b significantly decreased under drought stress. Water stress also has the ability to reduce concentrations of chlorophylls and carotenoids, primarily by the production of ROS (reactive oxygen species) in the thylakoids. Both chlorophyll a and b are prone to soil drying. Low concentrations of photosynthetic pigments can directly limit photosynthetic potential (Anjum *et al.* 2011). Carotenoids play additional roles and partially help the plants to withstand drought stress. Carotenes are very susceptible to oxidative damage (Jaleel *et al.* 2009).

The share of stomatal regulation in controlling the photosynthesis and transpiration processes depends on the stress intensity (Yordanov *et al.* 2003). Exposure of the tested rye line to drought stress caused considerable reduction of CO₂ assimilation and transpiration processes. Differences in parameters of gas exchange on the dates of the drought period were observed. On day 12 and 18 of drought, significant differences in the intensity of CO₂ assimilation were determined in the WUE and WUEI between the tested rye lines in the control and those subjected to stress conditions. Significant differences in the intensity of transpiration, stomatal conductance and substomatal concentration of CO₂ were determined on day 18 of drought. The reduction of transpiration intensity had a more subdued character (Fig. 1). Net photosynthesis and transpiration intensity in the GULbw line in drought conditions was reduced by 24.5% and 22.3%, respectively, relative to the intensity of these processes in the control plant (Fig. 1). Net photosynthesis and transpiration intensity depended on stomatal conductance, to a large degree. Stomatal conductance in the tested rye lines in drought conditions was reduced by 17% compared to the control (Fig. 1). Significant positive relationship among net photosynthesis, transpiration, and stomatal conductance was determined (Tab. 1). In stress conditions, the concentration of substomatal CO₂ was 77.5% as compared to the control (Fig. 1). The intensity of net assimilation was significantly dependent on the concentration of substomatal CO₂ (Table). A reduction of stomatal conductance in raspberries in drought conditions was observed by Stoll *et al.* (2002) and Klamkowski *et al.* (2015). Mishra *et al.* (2012) determined that a prolonged stress leads to the closing of stomata and to

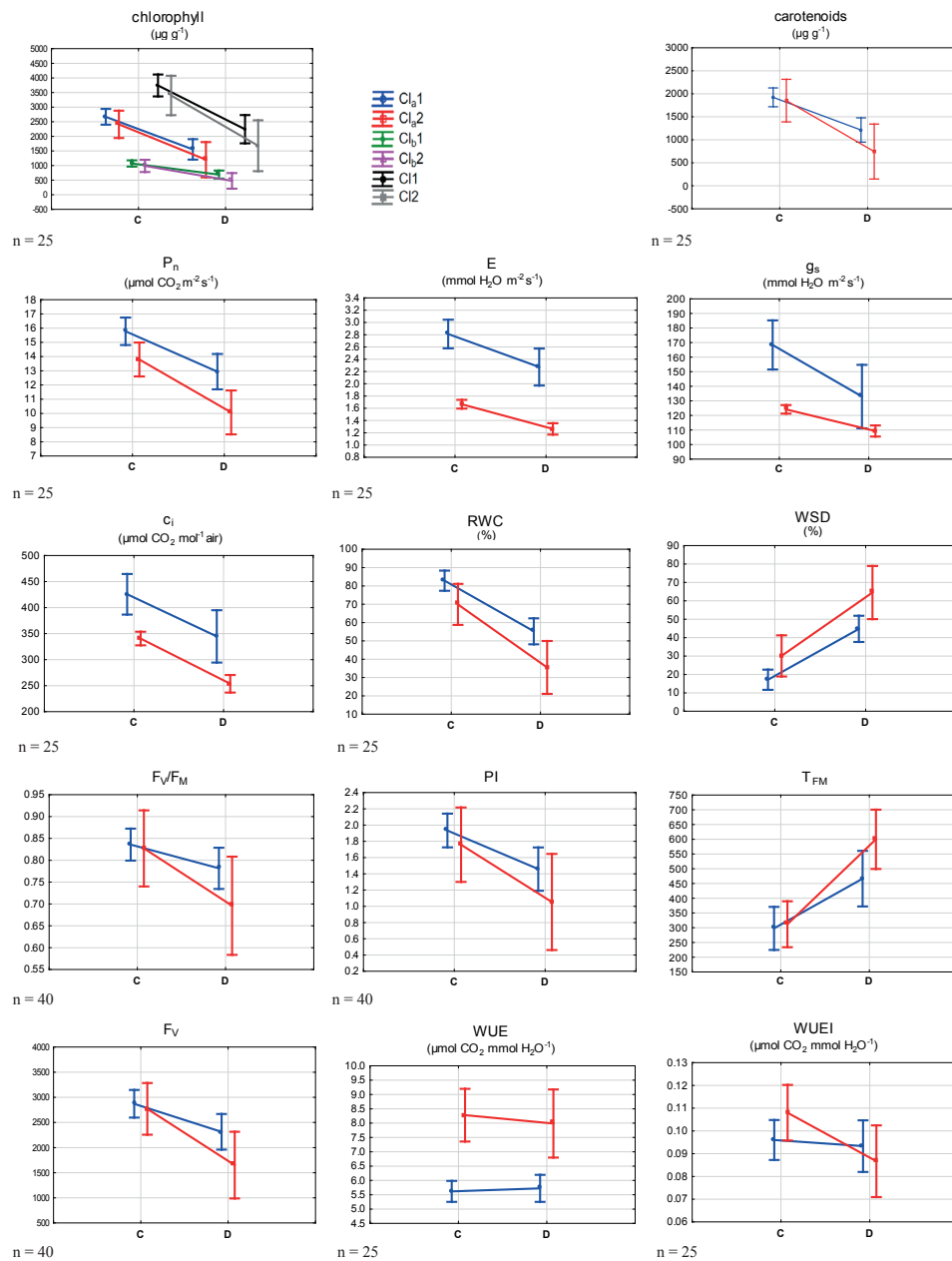


Fig. 1. Differences of selected physiological parameters between rye inbred lines of GULbw plants grown in well-watered conditions (C) and under drought stress (D). Blue line – measurements made after 12 days of drought; red line – measurements made after 18 days of drought; vertical lines – 0.95 confidence levels

a reduction of the intensity of CO₂ assimilation. Research conducted by Olszewska (2004) on the activity of assimilation of two white clover cultivars in water stress conditions exhibited a reduction in the activity of the process. Olszewski *et al.* (2007) demonstrated that the gas exchange indices, which include the intensity of photosynthesis, transpiration, and intercellular concentration of CO₂ and the stomatal conductance, in two winter wheat cultivars were reduced in water deficit conditions. Kocoń (2006) obtained an average of 30% lower values of photosynthesis, transpiration and stomatal conductance intensity in three cultivars of spring wheat in drought conditions. Restriction of CO₂ assimilation in conditions of water stress in raspberry was obtained by Morales *et al.* (2013) and Klamkowski *et al.* (2015). In the present study, for the tested rye line on day 12 of drought, higher values of WUE were obtained, in comparison to the control conditions (Fig.1). Similar relationships were determined by Jaroszewska *et al.* (2011) for cherry, and by Olszewska and Gregorczyk (2013) for different grass species subjected to water stress. The increase of water use by plants is of particular importance to maintain their yielding level in drought conditions (Blum 2009).

Table 1. Physiological and morphological parameters of rye inbred line GULbw whose values measured at control and drought conditions showed statistically significant differences, according to Duncan test at $p = 0.01$

assimilation pigments	Cl a1	P_{n1}	WUE1	F _v /F _{M1}	SN	MSGW
	Cl a2	P_{n2}	WUE2	F _v /F _{M2}	PW	MSTGW
	Cl b1	E1	WUEI1	PI1	PH	LSDW
	Cl b2	E2	WUEI2	PI2	PL	LSN
	Cl1	g_{s1}	RWC1	T_{FM1}	MSW	PLSN
	Cl2	g_{s2}	RWC2	T_{FM2}	MSSL	LSW
	Ct1	c_{i1}	WSD1	F_{v1}	MSSW	LSGN
	Ct2	c_{i2}	WSD2	F_{v2}	MSGN	LSGW
						LSTGW

Significant differences in the level of relative water content and water saturation deficit were obtained between the tested rye lines in control and those subjected to stress conditions. On day 18 of drought, the water content in tissues was reduced by 31.7% relative to the control (Fig. 1). The duration of the stress conditions resulted in an increase of the water saturation deficit by 17.3% in the tested rye line (Fig. 1).

The tested rye line did not exhibit any considerable variability of the maximum quantum efficiency of PS II (F_v/F_m). In stress conditions, the value of the maximum photochemical efficiency of PSII was 95.5% as compared to the control (Fig. 1). On day 18 of drought, the reduction of the maximum photochemical efficiency of PSII was 8.8%, relative to day 12 of drought. Kalaji *et al.* (2014) emphasise that the F_v/F_m parameter is not sensitive to drought stress. Similar results were obtained for other plant species in variable conditions of water stress intensity (Havaux 1992, Cechin 1998, Klamkowski *et al.* 2015, Czyczyło-Mysza and Myśków 2017).

Under the influence of water deficiency, the possibility of damaging the PS II photosystem increases. The decrease of the maximum photochemical efficiency of PS II indicates a reduced demand of the plant for the products constituting the so-called assimilation force and disturbances in the photosynthesis process (Faraloni *et al.* 2011). According to certain authors, the overall performance index of PS II appears to be one of the sensitive indices of the effect of stress factors on plants (Rapacz 2007, Rapacz and Woźniczka 2009, Czyczyło-Mysza 2013). In the conducted study, an unfavourable influence of drought on the efficiency of PSII performance in the tested rye line was found. Because of the drought, the PSII performance index was reduced, and the decrease tendency of the PI value was intensified with the duration of the stress period. In stress conditions, the PI value was 68.5% as compared to the control (Fig. 1). On day 18 of drought, the reduction in the PSII functioning index was 33.7%, compared to day 12 of drought. Similar results in two inbred rye lines after 28 days of drought were obtained by Czyczyło-Mysza and Myśków (2017). Changes in the time of attaining maximal chlorophyll fluorescence were observed. In stress conditions, in the tested rye line, an increase in the T_{FM} value, relative to control, was observed. Moreover, an increase tendency was observed for the T_{FM} along with the time of the stress conditions. On day 18 of drought, the T_{FM} value was 23.4% higher than on day 12 of the stress (Fig. 1). The value of this parameter was higher when the period of the stress to which the plant was exposed was longer (Cetner *et al.* 2016). The Fv value was not subject to larger changes for rye in the control. In the drought conditions, variable fluorescence exhibited a decreasing tendency in comparison to the control (Fig. 1). The Fv value in GULbw line in drought conditions was reduced by 26.5%, compared to the control. Lower values of this parameter indicate a reduced efficiency of the PSII photosystem (Cetner *et al.* 2016).

Statistically significant differences between well-watered and stressed plants were noted for the following morphological characteristics: SN, PH, LSDW, PLSN, LSW, LSGN, and LSGW. All morphological traits values, excluding SN, decreased due to drought (Fig. 2). Many researchers confirmed that water stress leads to growth reduction, which is reflected in the plant height, dry weight, and other growth functions. Greater tillering is rarely observed; however, it was shown to be an adaptation to low-stress conditions of winter wheat (Duggan *et al.* 2000). The ability of winter wheat to produce large numbers of tillers was evident in the spring, but this early season potential was not maintained due to extensive tiller die-back (Duggan *et al.* 2000). We observed a similar situation; many tillers of stressed plants bore no heads and the number of productive stalks was lower compared to control plants.

The stalk number of all tillers (with and without heads) was strongly negatively correlated to the plant height (-0.97). SN and PH were significantly associated with RWC (-0.89 and 0.91 , respectively) and with WSD, inversely. Positive and significant correlation between RWC and plant height was observed previously for

wheat (Jatoi *et al.* 2011). The stalk number of all tillers (with and without heads) was strongly negatively correlated to the plant height (-0.97). SN and PH were significantly associated with RWC (-0.89 and 0.91 , respectively) and with WSD, inversely. Positive and significant correlation between RWC and plant height was observed previously for wheat (Jatoi *et al.* 2011).

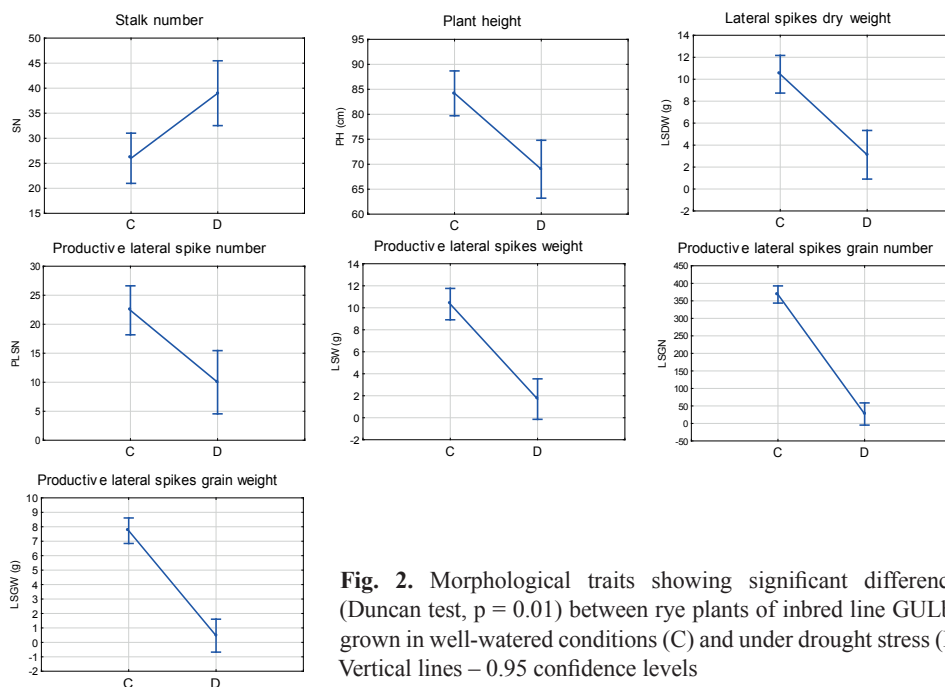


Fig. 2. Morphological traits showing significant differences (Duncan test, $p = 0.01$) between rye plants of inbred line GULbw grown in well-watered conditions (C) and under drought stress (D). Vertical lines – 0.95 confidence levels

Correlation of morphological and physiological characteristics was also found, mainly for spikes/grains number and weight, and gas exchange parameters. A significant positive value of coefficient r was found between PLSN, LSW, LSGN, LSGW, and E , g_s , c_i (0.90 - 0.98). The same morphological characteristics revealed a negative correlation with T_{FM} , ranged from -0.91 to -0.86 .

PCA analysis was performed for the physiological and morphological traits of plants of two experiment variants (C and D). Because of numerous characteristics analysed, the data were divided into four groups (Fig. 3): assimilation pigments, gas exchange, water balance, and fluorescence parameters. In all the cases, the data demonstrated high variability, for PC1 it ranged from 60 to 67% and 14-16% for PC2. Physiological parameters analysed separately showed 70% for PC1 and 16% for PC2, and morphological traits were 63% and 15%, respectively (data not shown).

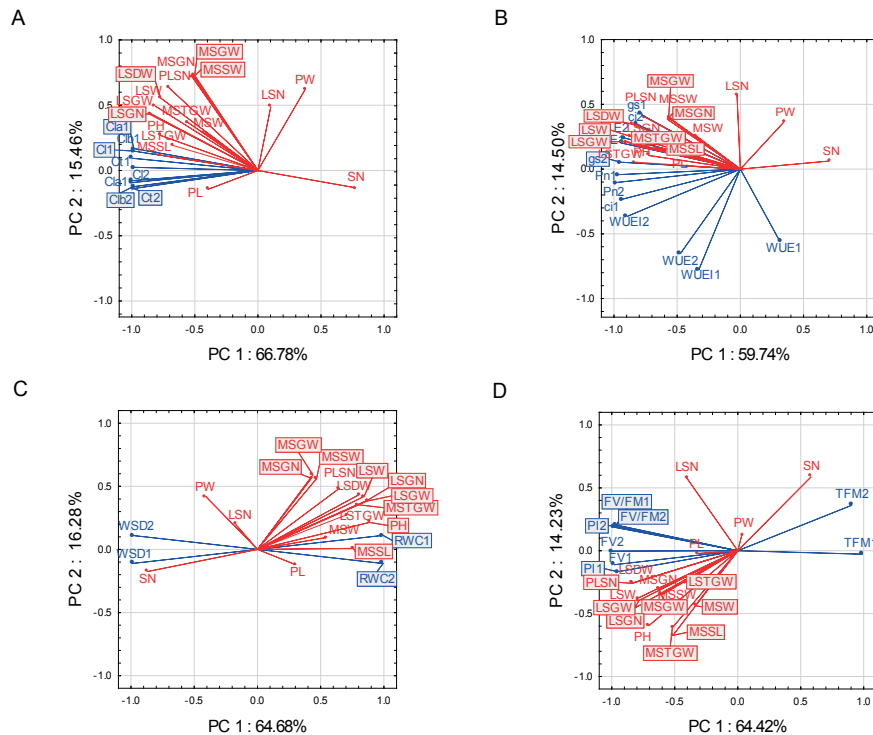


Fig. 3. Vector view of biplot showing interrelationships among studied traits. Morphological traits are marked in red colour. Blue colour is for photosynthesis characteristics: A – assimilation pigments, B – gas exchange parameters, C – water balance parameters, D – fluorescence parameters. An acute angle between the measured parameters means positive correlation, obtuse angle – negative correlation, right angle – no correlation; PC1 – principal component 1, PC2 – principal component 2. Each variable is represented by a vector. The direction and length of vectors determine to what extent individual variables affect the main components. The longer they are, and the closer the variables are to the circle, the greater part of the information contained in an input variable is carried by the main components

CONCLUSIONS

1. Significant differences in the level of relative water content and water saturation deficit were obtained between the tested rye lines in control and those subjected to stress conditions.

2. Net photosynthesis and transpiration intensity in the GULbw line in drought conditions was reduced by 24.5 and 22.3%, respectively, relative to the intensity of these processes in the control plant.

3. Because of the drought, the PSII performance index was reduced, and the decrease tendency of the PI value was intensified with the duration of the stress period. In stress conditions, the PI value was 68.5% as compared to the control.

4. The inbred line of GULbw rye reacted with quite a significant reduction of photosynthetic activity. This demonstrates the high sensitivity of the photosynthetic apparatus of this variety of plants to the stress caused by the lack of water in the substrate.

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ZMIANY I ZALEŻNOŚCI PARAMETRÓW FIZJOLOGICZNYCH I MORFOLOGICZNYCH ŻYTA PODDANEGO STRESOWI SUSZY GLEBOWEJ

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Streszczenie. Celem badań była ocena wpływu stresu suszy na sprawność aparatu fotosyntetycznego żyta odmiany Gulz, którą oceniono na podstawie pomiarów parametrów fluorescencji chlorofilu oraz wymiany gazowej, bilansu wodnego, barwników asymilacyjnych i parametrów morfologicznych. Eksperyment przeprowadzono na linii wsobnej żyta GULbw (oryginalna nazwa: Gülzow 661-67, numery akcesyjne: GueR 412, R 1599), uzyskanej z banku genów Federalnego Banku Genów dla Rolniczych i Ogrodniczych Gatunków Roślin z Leibniz, Instytut Genetyki Roślin i Badań Roślin Uprawnych (IPK) Gatersleben, Niemcy. W wyniku suszy zmniejszył się wskaźnik funkcjonowania PS II (fotosystem PS II), przy czym tendencja spadkowa wartości PI (ogólny wskaźnik funkcjonowania PS II) nasilała się wraz z długością trwania warunków stresu. Testowana linia żyta w kontroli nie wykazała znaczącej zmienności maksymalnej wydajności kwantowej PS II (Fv/Fm). Istotne różnice w natężeniu transpiracji, przewodności szparkowej i podszparkowego stężenia CO₂ stwierdzono w 18 dniu suszy. Zauważono istotną dodatnią zależność współczynników korelacji pomiędzy PLSN, LSW, LSGN, LSGW i E, gs, ci (PLSN – liczba kłosów produkcyjnych z pędów bocznych, LSW – masa kłosów produkcyjnych z pędów bocznych, LSGN – liczba ziaren z pędów bocznych, LSGW – masa ziaren z pędów bocznych, E – intensywność transpiracji, ci – podszparkowe stężenie CO₂, gs – przewodnictwo szparkowe).

Słowa kluczowe: morfologia, fotosynteza, *Secale cereale* L.