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Photosynthetic apparatus activity in relation to high and low contents of cell wall-bound phenolics in triticale under drought stress

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Abstract

Cell wall-bound phenolics (CWP) play an important role in the mechanisms of plant acclimation to soil drought. The study involved CWP analyses in 50 strains and 50 doubled haploid (DH) lines of winter triticale exposed to drought at their vegetative and generative stages. CWP in the plants experiencing drought at the generative stage positively correlated with their leaf water contents. The strains and DH lines characterized by high content of CWP showed higher leaf water content and higher activity of photosynthetic apparatus when exposed to drought at the generative stage compared to the strains and DH lines with the low CWP content. Furthermore, when drought subsided at the generative stage, the strains and DH lines richer in CWP demonstrated higher regeneration potential and their grain yield loss was smaller.

Additional key words: chlorophyll fluorescence; doubled haploids; leaf water content; strains; × *Triticosecale* Witt.; yield.

Introduction

The role of soluble phenolics in the mechanisms of crop plant acclimation to soil drought has been demonstrated in numerous studies (Estiarte *et al.* 1994, Bouchereau *et al.* 1996, Grzesiak *et al.* 1999, Alexieva *et al.* 2001, Sánchez-Rodríguez *et al.* 2010, Hura *et al.* 2007, 2011, 2012, 2013, Rosales *et al.* 2012). The function of cell wall-bound phenolics (CWP) seems to be equally interesting in this aspect, as an increased content of phenolics in the cell wall may indirectly affect plant water management, activity of photosynthetic apparatus, plant biomass or grain yield (Hura *et al.* 2012, 2013). Moreover, the process of phenolics incorporation into the cell walls is mediated by hydrogen peroxide (Wakabayashi *et al.* 1997). Therefore, an increase in CWP may be a possible mechanism of H_2O_2 neutralization under drought stress.

An enhanced content of phenolics in the cell walls inhibits carbohydrate consumption for structural purposes (Fry 1979, Wakabayashi *et al.* 1997, Hura *et al.* 2009a). Such a limitation in carbohydrate use for leaf cell wall biomass growth may mean the carbohydrates are rather used in the synthesis of organic compounds that would ensure plant cell adaptation to stress conditions.

The presence of phenolics in the cell walls affects also its mechanical properties (Fry 1982, Kamisaka *et al.* 1990). As their content increases, the cell wall becomes less elastic and more dense and tight. It may be therefore presumed that an increased content of phenolics, *i.e.* hydrophobic benzene rings and corresponding hydrocarbon chains, may enhance hydrophobic nature of the cell wall under leaf dehydration (Bernards *et al.* 2000, Graça

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Abbreviations: ABS/CS$_m$ – light energy absorption; Chl – chlorophyll; CWP – cell wall-bound phenolics; CS$_m$ – leaf cross-section; DH – doubled haploid; DI$_o$/CS$_m$ – energy amount dissipated from PSII; ET$_o$/CS$_m$ – amount of energy used for the electron transport; F$_v$/F$_m$ – quantum yield of PSII; HCWP – high content of cell wall-bound phenolics; LCWP – low content of cell wall-bound phenolics; L$_{DM}$ – leaf dry mass; LWC – leaf water content; L$_{FM}$ – leaf fresh mass; MCWP – medium content of cell wall-bound phenolics; PI – overall performance index of PSII photochemistry; Q_A^- – plastochinone A; RC/CS$_m$ – number of active reaction centers; SPh – soluble phenolics; TR$_o$/CS$_m$ – amount of excitation energy trapped in PSII reaction centers; δR_o – efficiency with which an electron can move from the reduced intersystem electron acceptors to PSI end electron acceptors; φR_o – quantum yield of electron transport from Q_A^- to PSI end electron acceptors; Ψ_o – leaf osmotic potential; ψR_o – probability, at time 0, that a trapped exciton moves an electron into the electron transport chain beyond Q_A^-.

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and Santos 2007). In such conditions, poorly water-permeable and hydrophobic environment of an apoplast may significantly inhibit water movement from a symplast to the apoplast, limit capillary transport of water in the apoplast, and consequently reduce cuticular transpiration. This is essential for effective water management under drought by retaining water in the symplast, *i.e.* in a metabolically active structure of the protoplast (Hura *et al.* 2013). CWP may also limit penetration of cells by UV radiation. This way, they act as photoprotectants of the photosynthetic apparatus by absorbing UV radiation and transforming it into blue fluorescence with lower disruptive potential towards leaf structures (Burchard *et al.* 2000, García-Plazaola and Becerril 2000, Close *et al.* 2007, Hura *et al.* 2007, Zhou *et al.* 2016).

The above mentioned properties of CWP indicate their multidirectional roles in the mechanisms of plant acclimation to drought. Therefore, the main aim of this study was to analyze CWP in 50 strains and 50 DH lines of winter triticale exposed to drought with reference to leaf water content, activity of photosynthetic apparatus, and plant regeneration after drought measured by the grain yield. The second objective was to evaluate the usefulness of CWP content as a biochemical indicator for (*1*) the selection of cultivars resistant to soil drought, and for (*2*) the selection of cultivars with improved water management mechanisms that may be better adapted to global climatic changes.

Materials and methods

Plant material and plant growth conditions: The study involved 50 strains and 50 DH lines of winter triticale (Table 1). Seeds were obtained from *DANKO Plant Breeders Ltd.*, Choryń (strains) and Laski (DH lines), Poland. Before sowing the seeds (nine per pot), the pots (3.7 dm^3) were tared to equal mass and filled with a homogeneous mixture of soil and sand (1:3; v/v).

The pots with seedlings at the stage of two leaves were subjected to 8-week vernalization in a cool chamber at +4°C (±1°C), PPFD of 150 $\mu mol\ m^{-2}\ s^{-1}$, and light/dark photoperiod of 10/14 h. After vernalization, the plants were transferred into air-conditioned greenhouse chambers. Air temperature in the greenhouse was 25–30/18–20°C (± 2°C) day/night, and relative air humidity was about 40%. The plants were additionally illuminated to ensure that PPFD was about 200 $\mu mol\ m^{-2}\ s^{-1}$ (high pressure sodium lamps, 400 W; *Philips SON-T AGRO*, Brussels, Belgium). The seedlings were irrigated with full-strength Hoagland's nutrient solution once a week (Hoagland 1948).

Drought conditions: Soil drought at the vegetative stage was applied when the plants formed the main shoot with three leaves and one or two lateral shoots (lateral shoot comprised two or three leaves). At the generative stage, water supply was limited after an emergence of the flag leaf. The water content in the pots was gradually reduced to 35% for seven days. Then, it was maintained at that level for the next two weeks. The water content in the control pots was maintained at 75%. Soil moisture in the pots was inspected daily using a gravimetric method, between 8:00 and 10:00 h and plant mass was taken into account.

Measurements and analyses were performed after 21 d of limited irrigation for both growth stages. First top fully developed leaves from the plants exposed to drought at the vegetative stage and the flag leaves from the plants exposed to drought at the generative stage were sampled for analysis. Biochemical analyzes were performed in freeze-dried plant material (*Freeze Dry System/Freezone® 4.5 LABCONCO*, Kansas City, Missouri, USA).

Chlorophyll (Chl) fluorescence measurements were done using a fluorometer (*Handy PEA, Hansatech Ltd.*, Kings Lynn, UK). Data were scored after 20 min of leaf adaptation to darkness. F_v/F_m (quantum yield of PSII) was calculated according to van Kooten and Snel (1990). Light intensity reaching the leaf was 3,000 $\mu mol(quantum)\ m^{-2}\ s^{-1}$ (peak at 650 nm). The following parameters were calculated per excited leaf cross-section (CS_m): ABS/CS_m (light energy absorption), PI (overall performance index of PSII photochemistry), DI_o/CS_m (energy amount dissipated from PSII), RC/CS_m (number of active reaction centers), ET_o/CS_m (amount of energy used for the electron transport), and TR_o/CS_m (amount of excitation energy trapped in PSII reaction centers), ψ_o (probability, at time 0, that a trapped exciton moves an electron into the electron transport chain beyond Q_A^-), δR_o (efficiency with which an electron can move from the reduced intersystem electron acceptors to PSI end electron acceptors), φR_o (quantum yield of electron transport from Q_A^- to PSI end electron acceptors). Calculation of the parameters was based on the theory of energy flow in PSII and involved the JIP test (Strasser and Tsimilli-Michael 2001, Strasser *et al.* 2010). The measurements for each DH line/strain were done in ten replicates.

Phenolics analysis: Total content of soluble phenolics (SPh) and cell wall-bound phenolics (CWP) were measured according to Singleton and Rossi (1965) with Folin-Ciocalteu reagent. SPh were extracted with 80% ethanol. CWP were removed from insoluble material by alkaline hydrolysis (1N NaOH) according to Hura *et al.* (2012). Absorbance was measured spectrophotometrically (*Ultrospec 2100 Pro, Amersham Biosciences,* Cambridge, UK) at 760 nm. Chlorogenic acid was used to prepare the calibration curve. The measurements for each DH line/strain were done in ten replicates. Results were expressed as milligrams of chlorogenic acid equivalent per gram of dry mass.

Leaf water content, leaf osmotic potential and grain yield analysis: Leaf water content (LWC) was estimated by quantitative sampling of the leaf fresh mass (L_{FM}), followed by lyophilization (*Freeze Dry System/Freezone® 4.5 LABCONCO*, Kansas City, Missouri, USA) for 72 h. Leaf dry mass (L_{DM}) was assessed and water content was calculated according to the following equation:

$LWC = [(L_{FM} – L_{DM})/L_{FM}] \times 100\%$. The measurements for each DH line/strain were done in ten replicates.

Leaf osmotic potential was analyzed with a dew point microvoltmeter (*HR-33T Dew Point Microvoltmeter, Wescor, Inc.,* Logan, Utah, USA) according to Hura *et al.* (2012). The measurements were performed on paper discs of 5 mm in diameter, soaked with cell juice squeezed with a syringe from the collected leaves. The measurements for each DH line/strain were done in seven replicates.

After the drought period was completed, soil water content was brought back to 75% and maintained at this level until the grain yield was estimated. Grain yield analysis for each DH line/strain within treatments was done in 15 replicates.

Statistical analysis and data calculation: Statistical analysis was carried out using *Statistica v. 12.0* (*Statsoft Inc.*). *Student*'s *t*-test and *Duncan*'s multiple range test at 0.05 probability level were selected to determine the significance of differences between means. Correlations between the investigated parameters were analyzed at a probability of $p<0.05$.

The data concerning soluble phenolics, leaf water content, leaf osmotic potential, and grain yield are mean values that were calculated for 13 HCWP (high content of cell wall-bound phenolics) strains, 11 LCWP (low content of cell wall-bound phenolics) strains, 18 HCWP DH lines, and 13 LCWP DH lines.

Results

Leaf water status and content of phenolics: The content of cell wall-bound phenolics (CWP) positively correlated with leaf water content (LWC) only in the plants experiencing drought at their generative stage (Fig. 1). The highest CWP content was observed in the flag leaves of the strains [40–55 mg g^{-1}(DM)] (Fig. 1*B*) and DH lines [35–45 mg g^{-1}(DM)] (Fig. 1*D*) that were also characterized by the highest LWC (68–80%) under soil drought conditions. Correlation coefficient for triticale strains was $r = 0.91$, and for DH lines it was $r = 0.78$. The strains with the highest phenolics content in the cell wall were CT06013/03/2 [CWP = 53.3 mg g^{-1}(DM); LWC = 75.2%] and cL169/06/05/5 [CWP = 50.5 mg g^{-1}(DM); LWC = 78.3%]. For DH lines, the highest CWP content was detected in GZDH56 [CWP = 45.0 mg g^{-1}(DM); LWC = 70.9%] and GZDH41 strain [CWP = 44.9 mg g^{-1}(DM); LWC = 74.6%]. The lowest CWP was detected in DT 278/10 strain [CWP = 21.6 mg g^{-1}(DM); LWC = 58.7%], and in GZDH202 DH line [CWP = 19.4 mg g^{-1}(DM); LWC = 60.0%].

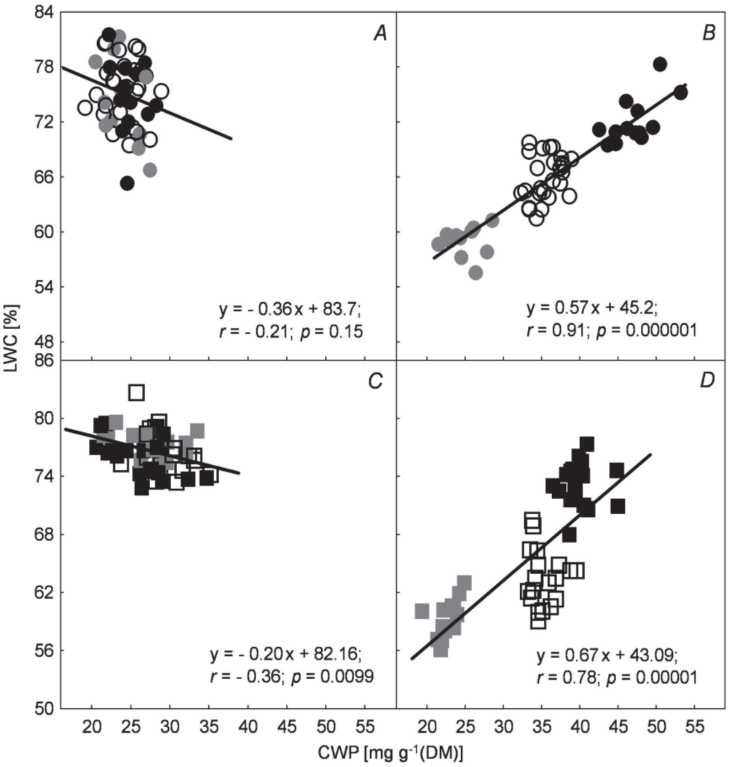

Fig. 1. Correlations between leaf water content (LWC) and the content of cell wall-bound phenolics (CWP) in the strains (*A*, *B*, *circles*) and DH lines (*C*,*D*, *squares*) exposed to drought at the vegetative (*A*,*C*) and generative (*B*,*D*) stage. *Black circles/squares*: strains and DH lines with high cell wall-bound phenolics content (HCWP); *white circles/squares*: strains and DH lines with medium cell wall-bound phenolics content (MCWP); *gray circles/squares*: strains and DH lines with low cell wall-bound phenolics content (LCWP). Data are means from nine replicates for each strain and DH line. Lines represent linear adjustment. Correlations between parameters were analyzed at a probability of $p<0.05$.

Table 1. Strains and DH lines were classified into three groups depending on the content of cell wall-bound phenolics. HCWP: strains and DH lines with high cell wall-bound phenolics content; MCWP: strains and DH lines with medium cell wall-bound phenolics content; LCWP: strains and DH lines with low cell wall-bound phenolics content.

Strain		Number
HCWP	cL 169/06/05/5; CT 06013/03/2; DT 58/10; 2837/12; 2988/12; DC 338/05; DC 04369/01; DL 1171/11; CT 08159-3; DL 1047/11; CT 07003-10; CT 07171/03/01; DL 402/11	13
MCWP	CT 07004-4; CT 08088-39; CT 07017/02/01; cD 593/07/01/05; DL 1028/11; DT 266/11; DC 125/03/1 kr-Salto; CT 07028/01/01; DL 1023/11; CT 06041/03/1; DL 1070/10; DL 1069/10; DL 562/11; DT 93/10; DL 29/12; CT 07127/03/01; DL 1179/11; DT 233/11; DL 1014/11; DL 535/10; 2629/12; DL 359/11; CT 07066/05/01; CT 08203-13; DT 248/11; DL 1142/11	26
LCWP	DL 639/09; DL 1109/11; 3550/12; DC 228/05/1; 2633/12, CT 06055/03/2; DL 1146/10; 2616/12; DS. 4101/11; 3407/12; DT 278/10.	11
DH line		**Number**
HCWP	GZ DH1; GZ DH18; GZ DH19; GZ DH28; GZ DH41; GZ DH56; GZ DH88; GZ DH94; GZ DH111; GZ DH118; GZ DH142; GZ DH144; GZ DH147; GZ DH156; GZ DH177; GZ DH189; GZ DH199; GZ DH207	18
MCWP	GZ DH35; GZ DH67; GZ DH80; GZ DH84; GZ DH102; GZ DH110; GZ DH113; GZ DH119; GZ DH125; GZ DH163; GZ DH167; GZ DH173; GZ DH176; GZ DH197; GZ DH210; GZ DH211; GZ DH212; GZ DH214; GZ DH221	19
LCWP	GZDH 24; GZDH 33; GZ DH43; GZ DH62; GZ DH70; GZ DH74; GZ DH81; GZ DH93; GZ DH181; GZDH 192; GZ DH202; GZ DH218; GZ DH227	13

Table 2. Soluble phenolics (SPh, [mg g^{-1}(DM)]) and leaf osmotic potential (Ψ_o, [MPa]) in the strains and DH lines with high cell wall-bound phenolics content (HCWP) and low cell wall-bound phenolics content (LCWP). Data are means for 13 strains and 18 DH lines with HCWP and 11 strains and 13 DH lines with LCWP. *Student*'s *t*-test at 0.05 probability level was performed in order to determine the significance of differences between means. Means indicated with the same letters for SPh and Ψ_o within the strains and DH lines were not significantly different.

	SPh	Ψ_o
Strains		
LCWP	65.3^{a}	-2.53^{a}
HCWP	68.0^{a}	-2.73^{a}
DH lines		
LCWP	95.4^{a}	-2.92^{a}
HCWP	83.8^{b}	-3.03^{a}

The strains and DH lines exposed to drought during the generative stage showed a greater variation in CWP and water contents in the flag leaves than the plants exposed to drought at the vegetative stage. Distinct differences in CWP allowed identification of three groups of the strains and DH lines characterized by the high content of CWP (HCWP), medium content of CWP (MCWP), and low content of CWP (LCWP). HCWP was comprised of 13 strains and 18 DH lines, MCWP included 26 strains and 19 DH lines, and LWCP consisted of 11 strains and 13 DH lines (Table 1).

No significant differences between HCWP and LCWP strains were found for soluble phenolics (SPh) (Table 2). The SPh content in DH lines was significantly higher in LCWP than that in HCWP. In general, triticale DH lines exposed to drought at the generative stage had the higher content of SPh than that of the strains.

No significant differences in leaf osmotic potential (Ψ_o) were observed between HCWP and LCWP for either the strains or DH lines (Table 2).

When drought was applied at the vegetative stage (Fig. 1*A*,*C*), CWP ranged from 19 to 29 mg g^{-1}(DM) in the strains and from 20 to 35 mg g^{-1}(DM) in DH lines. A significant correlation was discovered only for DH lines (Fig. 1*C*). It demonstrated that enhanced content of phenolics in the cell wall was accompanied by a lower leaf water content. The range of LWC changes was markedly smaller when drought was applied at the vegetative stage as compared to the generative stage. LWC for the strains ranged from 65 to 82% and for DH lines from 72 to 83%.

Table 3. Activity of photosynthetic apparatus based on chlorophyll fluorescence parameters for the strains and DH lines with high cell wall-bound phenolics content (HCWP) and low cell wall-bound phenolics content (LCWP). Data are means for 13 strains and 18 DH lines with HCWP and 11 strains and 13 DH lines with LCWP. *Student*'s *t*-test at 0.05 probability level was performed in order to determine the significance of differences between means. Means indicated with the same letters for each parameter within the strains and DH lines were not significantly different.

	F_v/F_m	ABS/CS_m	TR_o/CS_m	ET_o/CS_m	DI_o/CS_m	RC/CS_m	PI	δR_o	φR_o	ψR_o
Strains										
LCWP	0.766^a	2510^a	1926^a	844^a	584^a	636^a	0.66^a	0.209^a	0.070^a	0.091^a
HCWP	0.816^b	2971^b	2424^b	1237^b	547^b	915^b	1.47^b	0.256^b	0.107^b	0.131^b
DH lines										
LCWP	0.764^a	2525^a	1933^a	845^a	592^a	638^a	0.65^a	0.211^a	0.070^a	0.092^a
HCWP	0.806^b	2832^b	2285^b	1042^b	547^b	989^b	1.23^b	0.311^b	0.117^b	0.145^b

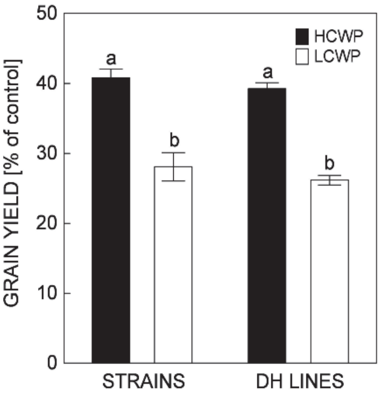

Fig. 2. Grain yield for the strains and DH lines as a percentage of control. Data are means for 13 strains and 18 DH lines with high cell wall-bound phenolics content (HCWP) and 11 strains and 13 DH lines with low cell wall-bound phenolics content (LCWP). *Duncan*'s test at 0.05 probability level was performed in order to determine the significance of differences between means. Means indicated with *the same letters* were not significantly different.

Chl fluorescence parameters: The strains and DH lines with significantly different content of CWP (LCWP and HCWP) were analyzed for the activity of their photosynthetic apparatus (Table 3).

As compared with HCWP, LCWP strains and DH lines showed lower activity of photosynthetic apparatus as demonstrated by significantly lower F_v/F_m, ABS/CS_m, TR_o/CS_m, ET_o/CS_m, PI, RC/CS_m, δR_o, φR_o, and ψR_o or significantly higher DI_o/CS_m values. HCWP plants showed mainly a clear increase in the amount of energy used for electron transport (ET_o/CS_m), and a greater amount of excitation energy trapped in PSII reaction centers (TR_o/CS_m) that translated into higher value of PSII performance index (PI). Photosynthetic apparatus of HCWP strains and DH lines was also characterized by higher probability that a trapped exciton moves an electron into the electron transport chain beyond Q_A^- (ψR_o), higher efficiency with which an electron can move from the reduced intersystem electron acceptors to PSI end electron acceptors (δR_o), and higher quantum yield of electron transport from Q_A^- to PSI end electron acceptors (φR_o) (Table 3).

Grain yield: The strains and DH lines with the higher content of CWP more effectively regenerated during the rehydration period as indicated by the results of the grain yield analysis (Fig. 2). However, the rehydration period following drought at the heading stage was too short for the plants to achieve complete regeneration. Neither the strains nor DH lines exposed to soil drought produced such a yield as the plants grown under optimal conditions. The grain yield for the drought-exposed strains and DH lines was similar to HCWP control (41% of control for strains; 39% of control for DH lines), as compared to LCWP (28% of control for strains; 26% of control for DH lines).

Discussion

Soil drought is an unfavorable and unpredictable environmental factor seriously limiting the yield of crops (Barnabás *et al.* 2008, Ji *et al.* 2010). It also affects winter triticale, a relatively 'young' crop, cultivation of which began only at the turn of 1960s and 1970s (Ammar *et al.* 2004). This is one of the reasons why our knowledge on the mechanisms of triticale acclimation to soil drought is relatively modest, as compared to other cereals. Traditional plant breeding, now supported by modern methods of molecular biology, is focused on the selection of cultivars resistant to drought occurring at key developmental stages, *e.g.* tillering, heading or flowering (Quarrie *et al.* 1999, Mergoum *et al.* 2004). An important step in obtaining cultivars resistant to soil drought is identification of biochemical and physiological basis of triticale tolerance to leaf tissue dehydration (Hura *et al.* 2009b).

This study showed that soil drought applied at the generative stage of triticale development differentiated the investigated strains and DH lines in terms of their CWP content, as compared to drought applied at the vegetative stage (Fig. 1). The strains and DH lines with the high CWP content showed also the high leaf water content and high activity of photosynthetic apparatus (Fig. 1, Table 3). These outcomes are consistent with the results of our earlier experiments involving selected cultivars of winter triticale (Hura *et al.* 2012, 2013). The activity of the photosynthetic apparatus in HCWP strains and DH lines was a consequence of better leaf cell hydration (Ashraf and Harris 2013). Higher water content was probably due to a more hydrophobic nature of the cell walls resulting from the presence of benzene rings (Bernards *et al.* 2000, Graça and Santos 2007). In this way, transport of water from the protoplast to cell wall structures and then to the external environment was limited. Moreover, a higher content of CWP means also greater density and tightness of the cell walls that further protects plant cells against water loss (Hura *et al.* 2012, 2013). Phenolic compounds, which bind by ester and/or ether bonds to cell-wall carbohydrates, form cross-bridges responsible for improved density of tightness of the cell walls (Fry 1979, 1982).

Disturbed performance of the photosynthetic apparatus during drought is known to be due to dehydration accompanied by light-induced photoinhibition damage (Lu and Zhang 1998, Ma *et al.* 2006). Shen *et al.* (2015) reported that UV radiation may damage to a greater degree the photosynthetic apparatus in soybean than soil drought alone. The strains and DH lines showing high CWP were also characterized by high PI and low values of heat emission index (DI_o/CS_m) that indicated smaller damage inflicted to the photosynthetic apparatus (Table 3). In our previous study, we have found that higher activity of the photosynthetic apparatus positively correlated with increase of CWP content in triticale under drought stress (Hura *et al.* 2012). The CWP through absorption, may limit the Chl excitation under excessive light conditions for the photosynthetic apparatus. Photoprotective role of phenolic compounds against UV radiation was also reported in other works (Kolb *et al.* 2001, Semerdjieva *et al.* 2003, Kolb and Pfündel 2005, Barthod *et al.* 2007). It has been proved that drought predisposes plants to injury of the photosynthetic apparatus through its reaction with UV light (García-Plazaola and Becerril 2000).

The outcomes of our experiment indicated that cell wall-bound phenolics may be used as biochemical markers for the selection of cultivars resistant to drought and with improved water management mechanisms only when drought is applied at the generative stage. We suggest that the higher content of cell wall-bound phenolics may be accompanied by increased effectiveness of the mechanisms for winter triticale acclimation to soil drought, considering multidirectional activity of CWP serving as photoprotectants towards the photosynthetic apparatus and the agents tightening the cell wall. However, further studies are needed to understand more precisely the role of the cell-wall bound phenolics in plant resistance to drought stress. The results obtained in the present study may be the basis for further research on genetic foundations of phenolics incorporation into the cell walls under drought stress. The first step in this direction has already been taken, as we conducted the first experiments in two mapping populations of triticale and identified the areas of its genome associated with the content of cell wall-bound phenolics during soil drought.

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