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Original scientific paper

PHOTOSYNTHETIC EFFICIENCY PARAMETERS AS INDICATORS OF AGRONOMIC TRAITS OF WINTER WHEAT CULTIVARS IN DIFFERENT SOIL WATER CONDITIONS

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In an effort to find breeding methods for improving drought stress tolerance and grain yield, twelve photosynthetic efficiency parameters have been measured on ten cultivars of winter wheat (*Triticum aestivum* L.), along with water use (WU), water use efficiency (WUE) and agronomic traits of grain yield (GYP), biomass weight (BWP), harvest index (HI), yield stability index (YSI) and stress tolerance index (STI) in the vegetative pot trial with control (B1) and drought stress (B2) treatments. Drought stress induced in three different stages of development has caused decrease in water use efficiency based on biomass (WUEb) (B1: 2.94 g L^{-1}; B2: 2.71 g L^{-1}) and grain yield (WUEg) (B1: 1.03 g L^{-1}; B2: 0.89 g L^{-1}), as well as GYP and BWP. Dissipation energy flux per excited cross section (DI_0/CS_0) observed in the drought stress treatment in the tillering stage of growth gave significant negative correlation coefficient ($P \leq 0.05$) with agronomic traits of tested wheat cultivars (GYP:-0.75; WUEg and STI: -0.74; YSI: -0.67). Performance index (PI_{ABS}) measured in the drought stress conditions in the flag leaf stage was in significant positive correlation with GYP and WUEg (r=0.64). Lower values of absorption flux per excited cross section (ABS/CS_0), electron transport per excited CS (ET_0/CS_0) and dissipation energy flux per excited CS (DI_0/CS_0) and higher values of PI_{ABS}, measured on wheat genotypes (cultivars) in the drought stress conditions of pot trial, could indicate higher tolerance to drought stress conditions.

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Results of the studied photosynthetic efficiency parameters of wheat cultivars were also the good predictor for important agronomic traits, especially, when they were detected in the early stage of growth.

Key words: agronomic traits, drought stress tolerance, photosynthetic parameters, *Triticum aestivum* L., wheat cultivars.

Abbreviations: B1 - well-watered or control treatment; B2 - moderate short-term drought stress treatment; BWP - biomass weight per pot; FC - field capacity for water; GYP - grain yield per pot; HI - harvest index; WU - water use; WUEb - water use efficiency for biomass production; WUEg - water use efficiency for grain yield; YSI - grain yield stability index; STI - stress tolerance index; IBM - intermated B73 x Mo17 population;

PSII - photosystem II; Q_A - primary binding site of the plastoquinone; Q_B - secondary binding site of the plastoquinone; ABS/CS_0 - absorption flux per excited cross section (CS); ABS/RC - absorption flux per active reaction centre (RC); DI_0/CS_0 - dissipation energy flux per excited CS; DI_0/RC - dissipation energy flux per active RC; ET_0/ABS - quantum yield for electron transport; ET_0/CS_0 - electron transport per excited CS; ET_0/RC - electron transport flux per active RC; $ET_0/(TR_0\text{-}ET_0)$ - electron transport beyond primary acceptor Q_A; PI_{ABS} - photosynthetic performance index; RC/CS_0 - density of the active reaction centres per CS; TR_0/ABS or F_v/F_m - maximum quantum yield of photosystem II; TR_0/RC - trapping energy flux per active RC.

INTRODUCTION

Considering increasingly more frequent worldwide hot and drought growing conditions, winter wheat (*Triticum aestivum* L.) cultivars need to maintain yield stability and develop a certain degree of drought stress tolerance in order to cope with changing environment. Drought stress affects the photosystems of the plants, and either directly or indirectly, it alters the chlorophyll *a* fluorescence kinetics. Plants first reaction to drought stress is rapid closure of stomata which reduces CO_2 intake into the leaf. This consequently leads to a reduced CO_2 concentration and limits photosynthetic activity by direct inhibition of Rubisco enzyme or ATP synthase (TEZARA *et al*., 1999; HAUP-HERTING and FOCK, 2000; REDILLAS *et al*., 2011). Limitations in the photosynthesis, caused by drought stress, are related to excess energy build-up in photosystem II of plants. If not safely dissipated, this energy causes over reduction of the photosynthetic electron transport chain and leads to formation of reactive oxygen species which may be harmful and irreversibly damage the cells and organism (DEMMIG-ADAMS and ADAMS, 1992; ASADA, 2006). Therefore, chlorophyll *a* fluorescence measurements provide a powerful non-invasive tool for exploring leaf photosynthesis under natural conditions, and in the light of many recent researches became a highly promising method for detection of plants tolerance to various environmental stresses (STRASSER *et al*., 2004).

In the last decade, the most investigated photosynthetic efficiency parameters were F_v/F_m (TR_0/ABS) and PI_{ABS} (sometimes ET_0/ABS), especially their relation to agronomic traits of different cultivated plants and cultivars in different stress conditions and environments (BALOUCHI, 2011; GHOLAMIN and KHAYATNEZHAD, 2011; REDILLAS *et al*., 2011; AKHKHA *et al*., 2013; KOVAČEVIĆ *et al*., 2011; 2013 and 2015). Photosynthetic performance index (PI_{ABS}), among many parameters of photosynthetic efficiency that could be calculated from standard OJIP test, stands out as the best one for assessment of tolerance in stressful environmental conditions, especially when soil water deficiency is in question (STRASSER *et al*., 2004). Many authors investigated a water deficit or drought stress impact on agricultural plants and reported that water deficit leads to the disturbance of some, or all of the physiological and biochemical processes, thus consequently reduces plant growth and yield (DENČIĆ *et al*., 2000; SHAO *et al*., 2005; BOUTRAA, 2010; AKHKHA *et al*., 2011) as well as the rate of photosynthesis in plants (SHARKEY, 1990; CORNIC, 2000; LAWLOR, 2002; AKHKHA *et al*., 2011). Water use efficiency (WUE) in its simplest terms is characterised as crop yield per unit of water considering that rational use of water implies increase in the amount of crop produced from the same volume of water. Yet, at more biological level, WUE refers to carbohydrates formed through photosynthesis from CO_2, sunlight and water per unit of transpiration (HOWELL, 2011) and it is used as a measure of yield variation of different crop varieties, or even among different crops under the same input of water (STEWART and HOWELL, 2003).

Since it is commonly accepted that maintaining photosynthesis in flag leaf as long as possible significantly affects grain yield (GUOTH *et al*., 2009), physiologists and plant breeders worldwide aspire to develop indirect and non-invasive assessment methods, to discover correlations between physiological characteristics and valuable agronomic traits of winter wheat genotypes (LONG *et al*., 2006; ALIYEV 2012).

Due to frequent dry periods recorded globally in the last decade, and the fact that about 60% of world's land area belongs to arid and semiarid zone (SHAO *et al.*, 2005) selection of drought stress tolerant genotypes in order to create new lines that will also carry the same trait becomes very important. Given the very common practice of the exchange of germplasm between the breeders and the demand for the drought stress tolerant cultivars among the producers, we considered it necessary to screen our most cultivated wheat cultivars for this trait. Conventional breeding for yield and yield components along with the study of wheat physiological mechanisms becomes a logical choice for this task since many authors reported that, along with photosynthetic pathways under water deficit, crop photosynthetic efficiency is influenced by many factors including cultivars (genotypes), soil water status, growth stages, redox state and ion homeostasis (CHANDLER and BARTELS, 2003; APEL and HIRT, 2004; DHANDA *et al*., 2004; SHAO *et al*., 2005; ZHU *et al*., 2010).

The objective of this study was to a) determine applicability of the photosynthetic efficiency parameters for successful prediction of winter wheat reaction to drought stress conditions and b) discover correlations between photosynthetic parameters and agronomic traits of wheat cultivars in order to select drought tolerant wheat genotypes.

MATERIALS AND METHODS

Cultivars and plant material

Selection of cultivars (A1-A10) tested in this experiment was based on different levels of diversity and genetic variability (NOVOSELOVIĆ *et al*., 2016). They are also present in wheat production in many countries of Southeast Europe (Croatia, Bosnia and Herzegovina, Slovenia, Kosovo, Serbia, Romania, Macedonia, and Turkey) and tested in conditions of multi-environmental field trials (DREZNER *et al*., 1999; ŠPANIĆ *et al*., 2011). Cultivars genetic background, year of introduction and country of origin are described in Table 1.

Table 1. Winter wheat cultivars (A1-A10) genetic background, year of introduction and country of origin. (Source: Breeding record book of 'Department for breeding and genetics of small cereal crops' at the Agricultural Institute Osijek, Republic of Croatia).

Cultivar	Genealogy	Year of introduction	Country of origin
Super Žitarka (A1)	*GO 3135/Žitarka*	1997	Croatia
Katarina (A2)	*Osk.5.B.4-1-94/Osk.5.140-22-91*	2006	Croatia
Lucija (A3)	*Srpanjka/Kutjevčanka*	2001	Croatia
Žitarka (A4)	*Osk.6.30-20/Slavonka/3/Eph.M68/Osk.154-19//Kavkaz*	1985	Croatia
Alka (A5)	*Osk.5.140-22-91/Sana*	2003	Croatia
Srpanjka (A6)	*Osk.4.50-1-77/Zg 2696*	1989	Croatia
Golubica (A7)	*Slavonija/Gemini*	1998	Croatia
Renata (A8)	*Žitarka//Osk.7.5-4-82/KB.160-86/3/Srpanjka*	2006	Croatia
Renan (A9)	*n/a*	1991	France
Soissons (A10)	*n/a*	1987	France

According to PURDY *et al.* (1968) initial crossing represents one single slash (A/B), two slashes represents next and any further crossings (A/B//C) and between slashes is the ordinal number of crossing (A/B//C/3/D); n/a – not available.

Plants were grown in vegetative pots according to a two-factorial experimental design with three replications. Pots were filled with upper layer (the depth up to 30 cm) of soil from experimental field of the Agricultural Institute Osijek in Republic of Croatia (45˚32″ N, 18˚44″ E). The soil in every pot had good fertility and the same mechanical, physical and chemical composition. Pore volume of the soil was 49%, water capacity 39% and air capacity 10% (ROMIĆ *et al*., 2006). Filled pots were saturated with water to 39% volume of soil (100% FC - field capacity or water holding capacity). Soil volume was 9,800 cm^3 per vegetative pot, and it was measured ten days after filling and saturation of soil with water. Sowing density in pot experiment was calculated to match field sowing density of 450 seeds per m^2 and hence 32 seeds of each wheat cultivar were sown per pot, seven days after soil water saturation on 20th Dec 2008.

Water treatments and growth conditions

Wheat cultivars (A) were studied in two irrigation treatments (B): well-watered as control (B1) and moderate short-term drought stress conditions (B2). Induced drought was performed according to a different growth stage of wheat as follows:

At the end of tillering stage (a) (EC 29 - Eucarpia Code) (REINER *et al*., 1992), from 6th to 13th Mar 2009, soil water content in B2 treatment went down from 30 to 21% of the soil volume (77 - 55% FC). During the same period temperatures varied from 8 °C (minimum night temperature) to 26 °C (maximum daily temperature) and relative air humidity from 80% to 99%. At the moment of the chlorophyll *a* fluorescence measurement, air temperatures varied from 15 to 18 ˚C and relative air humidity from 86 to 92%.

During the flag leaf and the beginning of heading stage (b) (EC 49/51), from 21st to 25th Apr 2009, soil water content in B2 treatment went from 23 to 17% of the soil volume (58 - 44%

FC). In the same period temperatures varied from 3.7˚C to 21.6˚C and relative air humidity from 30% to 99%. At the moment of the chlorophyll *a* fluorescence measurement air temperatures varied from 11 to 15˚C and relative air humidity from 42 to 50%.

At the end of the grain filling period (c) (EC 75/85), from 17th to 21st May 2009, soil water content in B2 treatment went from 33 to 21% of the soil volume (84 - 54% FC). During the same period temperatures varied from 13.1˚C to 32.6˚C and relative air humidity from 28% to 99%.

In B1 treatment in all stages of development soil water content was kept above wilting point and varied from 22 to 38.5% vol. Variations occurred due to significant daily oscillations in air temperature and humidity and consequently intensive growth and high evapotranspiration. Soil air content in the same treatment varied from 11 to 27%, and was calculated by deducting soil water capacity from total value of pore volume (49%). Except in described periods of induced drought conditions in growth stages a, b and c, irrigation of plants in both treatments was equal from sowing to the harvest. The experiment was performed in the greenhouse from sowing to the beginning of stem elongation stage and after that in an open area near the greenhouse.

Water use and fluorescence measurements

Soil water content was measured and calculated every day as the difference between water content at 100% of FC (39% volume of soil) and soil water depletion in each vegetative pot of both irrigation treatments. Monitoring the rate of soil water status was conducted by gravimetric method and with the help of Watermark soil moisture sensor (Watermark 30-KTCD-NL, Irrometer Company, Inc., Riverside, California). Sensors were placed in the pots at the depth of 15 cm. The readings ranged from 0 - 199 kPa (0 stands for wet soil (100% FC), while 199 kPa stands for dry soil). Since there was no capillary rise, downward drainage or surface runoff in vegetative pots, evapotranspiration was calculated using the soil water balance model according to DOORENBOS and KASSAM (1979) from the following equation:

$$WU = \Delta W + I + P$$

Water use (WU) represents evapotranspiration from emergence to the maturation, ΔW is the difference in weight between measurement of soil water content in pots at the time of sowing and soil water content at the time of maturity (kg pot^{-1}), I is irrigation (L pot^{-1}) and P is precipitation (L pot^{-1}).

Measuring of chlorophyll *a* fluorescence was carried out at the end of tillering stage on the 12th Mar in the morning hours from 09:00 h to 10:00 h and at the flag leaf stage on 25th Apr from 08:00 h to 09:00 h. At the moment of measurement average soil water content (% soil volume) in the pots was 38% (B1a) and 21% (B2a) in the tillering stage while in the flag leaf stage was 27% (B1b) and 17% (B2b). In the grain filing period (c) chlorophyll *a* fluorescence was not measured because of very pronounced leaf senescence of wheat cultivars.

Chlorophyll fluorescence was measured on three plants per vegetative pot, on the second fully developed leaf from the top of plant, on 180 plants in total for both treatments, by portable fluorimeter Handy Plant Efficiency Analyser (Handy PEA, Hansatech Instruments Limited, King's Lynn, Norfolk, UK). After the adaptation of leaves to darkness, with the help of three light-emitting diodes (650 nm), a single one second light pulse (3500 μmol m^{-2} s^{-1}) was applied. The fast fluorescence kinetics (F_0 to F_M) were recorded during 10 μs to 1 s. The measured data were analysed by the OJIP test (dark adapted chlorophyll fluorescence technique that is used for plant stress measurement) which is based on the fast rise in polyphasic fluorescence of chlorophyll *a* (STRASSER *et al*., 1995). Rise from minimum to maximum fluorescence has intermediate peaks and dips designated with OJIP or OJIDP nomenclature and the curve's shape provides information about the structure, function and current state of the photosynthetic apparatus (SCHREIBER *et al.*, 1994). Photosynthetic parameters calculated were TR_0/ABS also known as F_v/F_m, ET_0/ABS, ABS/RC, TR_0/RC, ET_0/RC, DI_0/RC, ABS/CS_0, ET_0/CS_0, DI_0/CS_0, RC/CS_0, $ET_0/(TR_0-ET_0)$ and PI_{ABS} according to STRASSER *et al*. (2000).

Absorption of photons by the chlorophyll molecules in the antenna complex refers to the absorbance (ABS). Part of that absorbed energy is trapped (TR_0) by the reaction centre (RC) of PSII while the excess energy is dissipated (DI_0) in the form of heat and fluorescence. Part of the trapped energy is converted to redox energy by electron transport (ET_0) through two specific binding sites plastoquinone A (Q_A) and plastoquinone B (Q_B) (STRASSER *et al*., 2000).

Analysis based on vegetative pot (n = 1 per pot, 60 pots in total for both treatments) included: biomass weight as total weight of air-dry plants without root (BWP); harvest index as ratio between grain weight per pot and biomass weight per pot (HI); water use (WU); water use efficiency for grain yield (WUEg) (VIETS, 1962; SIDDIQUE *et al*., 1990; BOUTRAA, 2010; ZHANG, *et al*., 2010); water use efficiency for biomass production (WUEb) (PASSIOURA, 1977; REYNOLDS *et al*., 2007) and grain yield per pot (GYP).

Water use efficiency for grain yield and biomass production was calculated from the following equations: WUEg = GYP/WU and WUEb = BWP/WU. Original formula: GY (grain yield) = WU × WUEb × HI was obtained from the work of PASSIOURA (1977). Water use efficiency was expressed as gram per liter of evapotranspirated water ($g\ L^{-1}$). Yield stability index (YSI) (BOUSLAMA and SCHAPAUGH, 1984; TALEBI *et al*., 2009) and stress tolerance index (STI) (FERNANDEZ, 1992) for all tested cultivars were calculated as follows:

$$YSIi = YB2i/YB1i \text{ and } STIi = (YB2i * YB1i)/YB1^2$$

Where YB1i represents grain yield of the "i^{th}" winter wheat cultivar in well-watered (B1) treatment, YB2i represents grain yield of the "i^{th}" winter wheat cultivar in water stress (B2) treatment, "i" stands for cultivar A1 to A10, and YB1 represents average grain yield of all cultivars in B1 treatment.

Seven winter wheat cultivars tested in the pot experiment (A2, A3, A4, A5, A6, A8 and A10) were also tested in multi-environmental field trials during 4 year period from 2008 to 2011, applying a randomized complete block design with four repetitions on two locations in the eastern part of the Republic of Croatia.

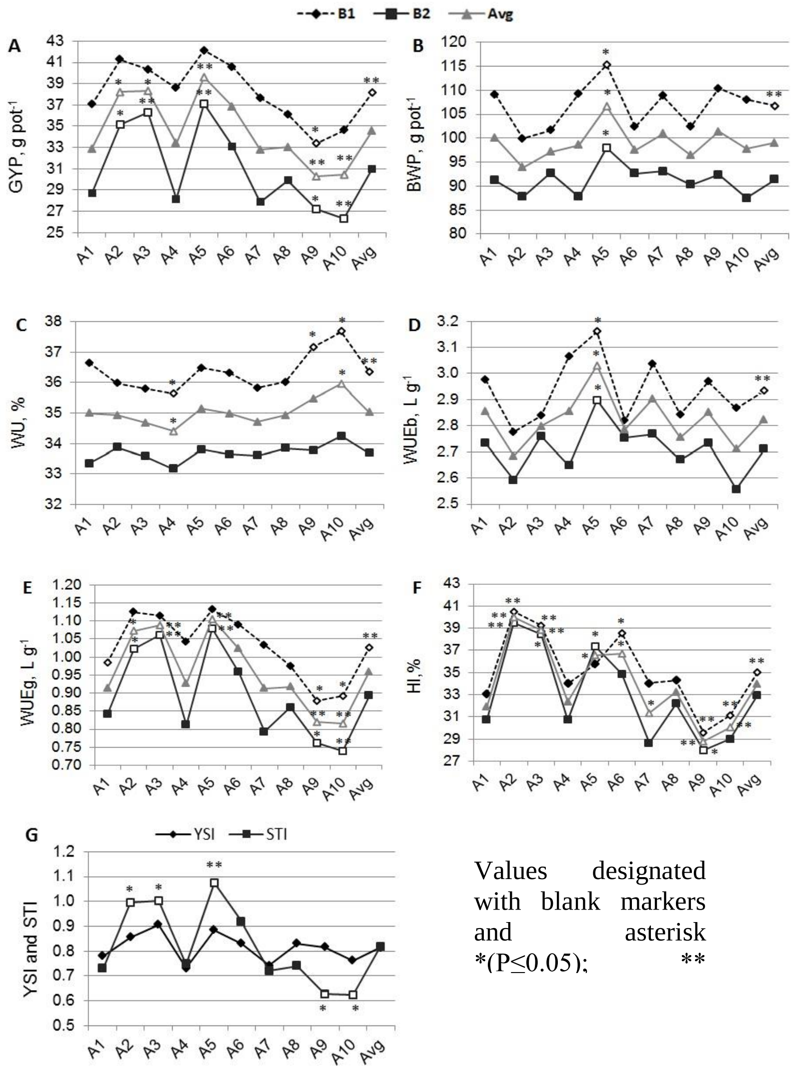
Statistical analysis

The photosynthetic parameters of winter wheat cultivars calculated on the basis of their chlorophyll *a* fluorescence measurement were correlated with the data for grain yield per pot (GYP), water use efficiency for grain yield (WUEg), yield stability index (YSI) and stress tolerance index (STI). Correlation coefficients were calculated using Microsoft Excel 2010. Differences between treatments and cultivars and their interactions were tested by the analysis of variance, F-test and t-test ($p \leq 0.05$; $p \leq 0.01$) using SAS 9.1 statistical software (SAS INSTITUTE, 2003).

RESULTS

Agronomic traits of winter wheat cultivars

Moderate short-term drought stress (B2) induced in three different stages of development (end of tillering stage, flag leaf stage, end of grain filling stage) has caused significant decrease (P≤0.01) in GYP, BWP, HI, WUEb and WUEg in the average for all tested genotypes (Table 2; Fig 1a, 1b, 1d, 1e and 1f).



Values designated with blank markers and asterisk *(P≤0.05); **

Figure 1. Grain yield per pot (GYP) (A), biomass weight per pot (BWP) (B), water use (WU) (C), water use efficiency for biomass (WUEb) (D), water use efficiency for grain yield (WUEg) (E), harvest index (HI) (F), yield stability index (YSI) and stress tolerance index STI (G) for winter wheat cultivars (A1-A10) and average of all cultivars (Avg) in well-watered (B1) and drought stress (B2) treatments.

Table 2. The analysis of variance and "F-test" for winter wheat cultivars, treatments and interaction in the trial with well-watered (B1) and in moderate short-terms drought stress conditions (B2).

	F-test							
	B1+B2				B1		B2	
Source of variability	Cultivar	Treatment	Interaction	Error MS	Cultivar	Error MS	Cultivar	Error MS
Degree of freedom (df)	9	1	9	38	9	18	9	18
GYP	9.76**	101.34**	0.85	7.707	4.33**	6.070	10.91**	5.089
BWP	3.60**	173.78**	1.44	20.445	3.46*	20.85	2.62*	11.820
HI	17.78**	13.50**	1.07	4.9571	14.99**	2.4896	8.47**	6.6329
WU	4.66**	435.51**	1.73	0.2456	7.64**	0.1705	0.99	0.2678
WUE_G	10.30**	42.19**	0.95	0.0061	6.12**	0.0042	12.34**	0.0035
WUE_B	3.83**	48.35**	1.07	0.0156	3.65**	0.0474	3.57**	0.0293

*(P≤0.05); **(P≤0.01) – significance of F-test

Significant differences (P≤0.05 and P≤0.01) were also determined between cultivars in both treatments (B1 and B2) for GYP, BWP, HI, WUEg and WUEb, except for WU in treatment B2 (Table 2). There was no significant interaction between cultivar and treatment for any one of the specified traits of wheat cultivars (Table 2).

Cultivars A2, A3 and A5 are characterized by significantly (P≤0.05 and P≤0.01) higher GYP, WUEg and HI in both treatments (B1 and B2) compared to the average value of all cultivars in the same treatments (Fig 1a, 1e and 1f). In contrast, cultivars A9 and A10 had significantly lower GYP, WUEg and HI in the same comparison. Significantly higher BWP and WUEb in both treatments had cultivar A5 compared to average values of all cultivars in treatment (Fig 1b and 1d). Cultivars A9 and A10 had significantly higher water use (WU) in the B1 treatment while in the same treatment cultivar A4 had significantly lower (WU) (Fig 1c). Cultivars A2, A3 and A5 also had significantly better STI, while cultivars A9 and A10 had significantly lower STI (P≤0.05) in relation to the average of all cultivars (Figure 1g).

Photosynthetic efficiency parameters of winter wheat cultivars

Significant differences between cultivars of winter wheat (P≤0.01) were found for all 12 parameters of photosynthetic efficiency based on OJIP test and measured in the stage of full tillering (a) (Table 3). In the same stage (a), treatment had significant impact on most of the examined parameters (ET_0/ABS, ET_0/RC, ABS/CS_0, ET_0/CS_0, DI_0/CS_0, RC/CS_0, ET_0/(TR_0-ET_0) and PI_{ABS}) while the interaction between treatment and cultivars was also significant for ET_0/ABS, ABS/RC, TR_0/RC, ET_0/RC, RC/CS_0 and ET_0/(TR_0-ET_0) (Table 3).

In the flag leaf stage (b) photosynthetic efficiency parameters showed significant differences between cultivars for parameters ABS/RC, TR_0/RC, ET_0/RC, ABS/CS_0, ET_0/CS_0, DI_0/CS_0 and RC/CS_0 (Table 3).

Treatments and interaction of treatments and cultivars showed no significant effect on any of the 12 parameters of photosynthetic efficiency measured in the flag leaf stage (Table 3). Particularly distinctive differences (F-test > 30) between cultivars were recorded for the parameters ABS/CS_0, ET_0/CS_0 and RC/CS_0 in the full tillering stage, which was also confirmed for the same parameters in the flag leaf stage (F-test > 8) (Table 3). For the parameters ABS/RC, TR_0/RC, ABS/CS_0, ET_0/CS_0 and RC/CS_0 significant differences (P≤0.01) between cultivars were found in both phases of development (a and b) and in both treatments (B1 and B2) (Table 3).

Table 3. The analysis of variance and "F-test" for the photosynthetic parameters observed in tillering (a) and flag leaf (b) stages of growth in well-watered (B1) and moderate short-term drought stress conditions (B2).

	F-test								F-test for cultivars			
	Tillering stage (a)				Flag leaf stage (b)				Tillering stage (a)		Flag leaf stage (b)	
Photosynthetic parameters	Cultivar	Treat.	Interac.	MS Error	Cultivar	Treat.	Interac.	MS Error	B1a	B2a	B1b	B2b
n-1	9	1	9	158	9	1	9	158	9	9	9	9
TR_0/ABS	3.01**	2.37	1.12	0.00008	0.90	0.01	0.74	0.00094	1.06	3.49**	1.04	0.70
ET_0/ABS	8.52**	37.83**	2.62**	0.00043	1.44	0.00	1.20	0.00125	7.67**	4.23**	1.34	1.38
ABS/RC	9.75**	0.11	2.33*	0.01267	5.59**	2.79	0.51	0.01996	4.86**	7.69**	3.14**	3.04**
TR_0/RC	9.65**	0.03	2.73**	0.00771	5.48**	2.76	1.01	0.01241	6.17**	6.92**	3.80**	3.26**
ET_0/RC	13.47**	26.27**	3.82**	0.00581	2.15*	1.32	1.86	0.00778	11.51**	6.38**	2.17*	1.81
DI_0/RC	5.26**	1.53	1.09	0.00168	1.33	0.22	0.60	0.01202	1.28	3.46**	1.04	0.76
ABS/CS_0	49.50**	20.56**	1.82	418.075	11.13**	0.01	0.60	2164.643	26.08**	29.26**	13.84**	4.04**
ET_0/CS_0	32.87**	4.15*	1.04	151.454	8.18**	0.09	0.87	456.331	24.35**	12.31**	6.97**	3.04**
DI_0/CS_0	13.91**	9.61**	1.69	53.717	2.12*	0.01	0.60	587.400	6.03**	11.02**	2.01*	1.07
RC/CS_0	34.36**	13.97**	2.32*	50.929	9.62**	0.64	0.92	227.369	18.52**	18.97**	9.95**	4.06**
ET_0/(TR_0-ET_0)	9.06**	44.85**	2.26*	0.01134	1.47	0.01	1.14	0.02459	8.87**	4.02**	1.06	1.66
PI_{ABS}	5.92**	27.32**	1.94	0.06689	1.65	0.31	0.84	0.23411	3.11**	4.68**	1.30	1.16

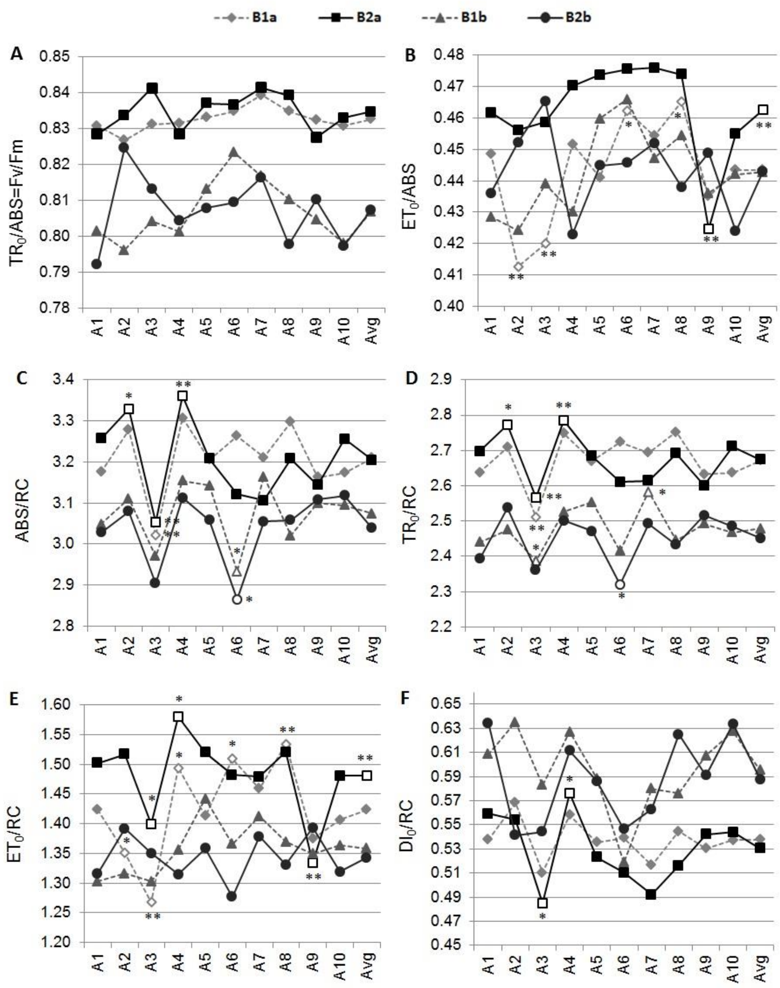
*(P≤0.05); **(P≤0.01) – significance of F-test for cultivars, treatments and interaction

In the interpretation of photosynthetic parameters, values of every cultivar were compared to average of all studied cultivars in the same treatment and growth stage (B1a, B2a, B1b, B2b). All studied winter wheat cultivars in both treatments had higher TR_0/ABS (F_v/F_m), ABS/RC and TR_0/RC in the full tillering stage (B1a and B2a) compared to the flag leaf stage (B1b and B2b) (Fig 2a, 2c and 2d). Values of DI_0/RC, DI_0/CS_0 and RC/CS_0 were lower in both treatments in the full tillering stage compared to the flag leaf stage (Fig 2f, Fig 3c and 3d).

In the well-watered treatment at the full tillering stage (B1a) cultivar A2 had significantly (P≤0.01) lower values of parameters ET_0/ABS, ET_0/(TR_0-ET_0) and PI_{ABS} (Fig 2b; Fig 3e and 3f), and higher ABS/CS_0 (Fig 3a) in relation to the average of all cultivars for mentioned parameters. In the same treatment (B1a), cultivar A3 had significantly lower (P≤0.01) values of parameters ET_0/ABS, ABS/RC, TR_0/RC, ET_0/RC and ET_0/(TR_0-ET_0) (Fig 2b, 2c, 2d, 2e; Fig 3b, 3e). Cultivar A5 also had significantly lower (P≤0.01) values of parameters ABS/CS_0, ET_0/CS_0, DI_0/CS_0 and RC/CS_0 than the average of all cultivars in the same treatment (Fig 3a, 3b, 3c, 3d). Cultivar A8 had significantly (P≤0.01) higher values of parameters ET_0/RC, ET_0/CS_0 and ET_0/(TR_0-ET_0) than the average of all cultivars (Fig 2e; Fig 3b and 3e), while cultivar A10 had significantly (P≤0.01) higher than the average values of parameters ABS/CS_0 and RC/CS_0 (Fig 3a and 3d).

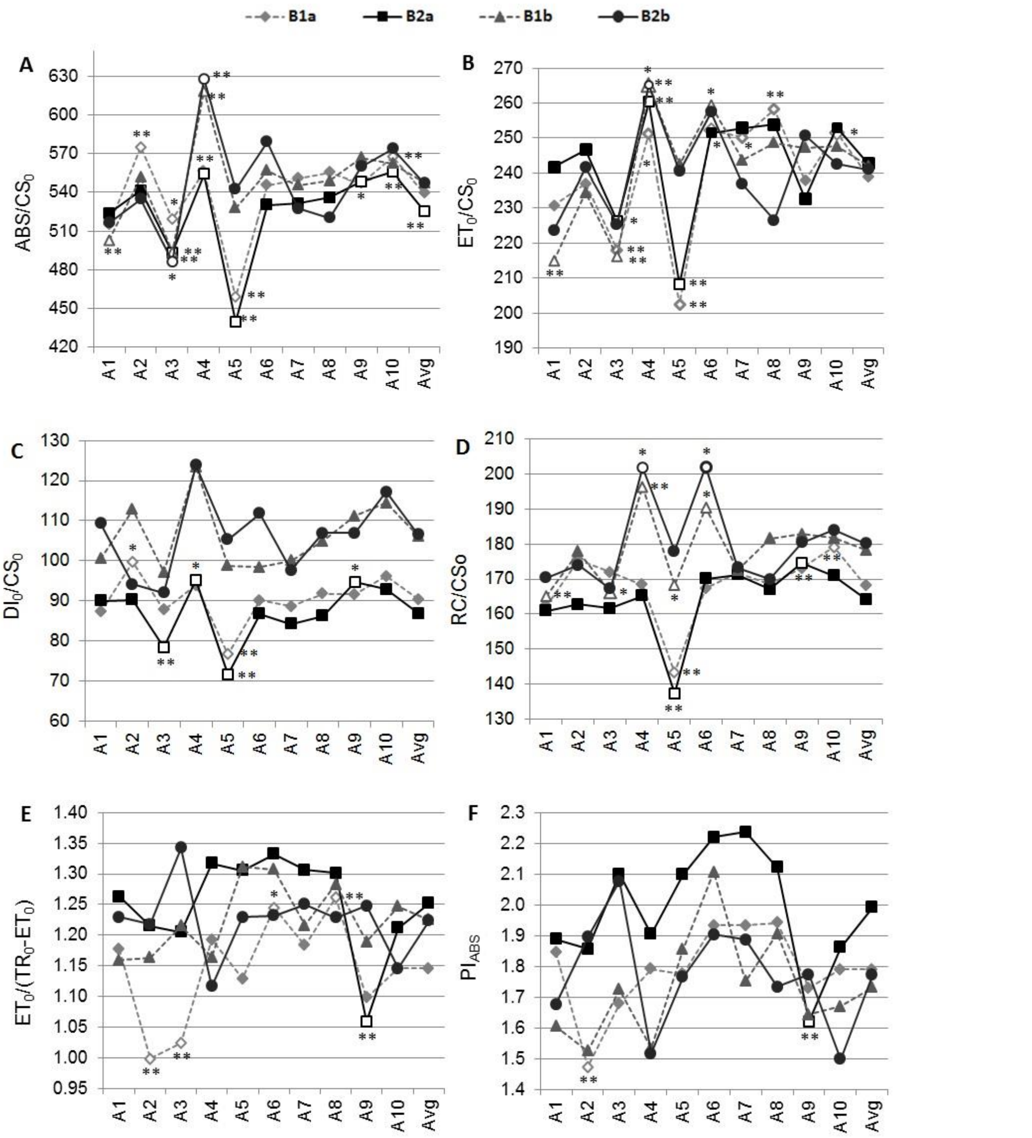
In the moderate short-term drought stress treatment at the full tillering stage (B2a) cultivar A3 had significantly lower (P≤0.01) than average values of the parameters ABS/RC, TR_0/RC (Fig 2c, 2d), ABS/CS_0 and DI_0/CS_0 (Fig 3a, 3c), while cultivar A4 had significantly (P≤0.01) higher than average values of the parameters ABS/RC, TR_0/RC, ABS/CS_0 and ET_0/CS_0 (Fig 2c, 2d; Fig 3a, 3b). Cultivar A5 had, as well as in the treatment B1a, significantly (P≤0.01) lower than average values of parameters ABS/CS_0, ET_0/CS_0, DI_0/CS_0 and RC/CS_0 (Fig 3a-3d).

Cultivar A9 had significantly ($P \leq 0.01$) lower than average values of parameters ET_0/ABS, ET_0/RC, $ET_0/(TR_0\text{-}ET_0)$ and PI_{ABS} (Fig 2b, 2e; Fig 3e, 3f) and significantly higher than average value of parameter RC/CS_0 (Fig 3d) while cultivar A10 had a significantly ($P \leq 0.01$) higher than the average value of the parameter ABS/CS_0 (Fig 3a).



*Values designated with blank markers and asterisk *(P≤0.05); ** (P≤0.01) represent significant differences of cultivars in relation to average of all cultivars (Avg) in the same treatment.*

Figure 2. Photosynthetic parameters of winter wheat cultivars (A1-A10) detected in well-watered (B1) and moderate short-term drought stress (B2) treatments in the tillering (B1a; B2a) and flag leaf stages of growth (B1b; B2b): TR_0/ABS or F_v/F_m - maximum quantum yield of photosystem II (A), ET_0/ABS - quantum yield for electron transport (B), ABS/RC - absorption flux per active reaction centre (RC) (C), TR_0/RC - trapping energy flux per active RC (D), ET_0/RC - electron transport flux per active RC (E) and DI_0/RC - dissipation energy flux per active RC (F).



*Values designated with blank markers and asterisk *(P≤0.05); ** (P≤0.01) represent significant differences of cultivars in relation to average of all cultivars (Avg) in the same treatment.*

Figure 3. Photosynthetic parameters of winter wheat cultivars (A1-A10) detected in well-watered (B1) and moderate short-term drought stress (B2) treatments in the tillering (B1a; B2a) and flag leaf stages of growth (B1b; B2b): ABS/CS_0 - absorption flux per excited cross section (CS_0) (A), ET_0/CS_0 - electron transport per excited CS_0 (B), DI_0/CS_0 - dissipation energy flux per excited CS_0 (C), RC/CS_0 - density of the active reaction centres per CS_0 (D), $ET_0/(TR_0-ET_0)$ - electron transport beyond primary acceptor Q_A (E) and PI_{ABS} - photosynthetic performance index (F).

In the well-watered treatment at the flag leaf stage (B1b) OJIP test showed that cultivar A1 had a significantly ($P \leq 0.01$) lower than the average values of parameters ABS/CS_0, ET_0/CS_0 and RC/CS_0 (Fig 3a, 3b, 3d) and cultivar A3 also had significantly ($P \leq 0.01$) lower than average values of parameters ABS/CS_0 and ET_0/CS_o (Fig 3a, 3b). Cultivar A4 had significantly ($P \leq 0.01$) higher than average values of parameters ABS/CS_0, ET_0/CS_0 and RC/CS_0 (Fig 3a, 3b, 3d).

In moderate short-term drought stress treatment in the flag leaf stage (B2b), cultivar A4 achieved a similar results with a significantly ($P \leq 0.01$) higher than average value of parameter ABS/CS_0 and on significance level $P \leq 0.05$ parameters ET_o/CS_o and RC/CS_o (Fig 3a, 3b, 3d).

Correlation of agronomic traits and photosynthetic efficiency parameters

Correlation coefficients were estimated between 12 photosynthetic efficiency parameters for ten cultivars in the tillering stage of growth (a) and flag leaf stage (b) in well-watered (B1) and moderate short-term drought stress (B2) treatments, and GYP, WUEg, YSI and STI of the examined cultivars (Table 4).

Table 4. Correlation coefficients of photosynthetic parameters observed in well watered (B1) and moderate short-terms drought stress (B2) treatments in the tillering (a) and the flag leaf stage (b) with agronomic traits of winter wheat cultivars in B1 and B2 treatments.

Photosynthetic parameters	Growth stages	B1 treatment in the tillering stage (a) and the flag leaf stage (b)				B2 treatment in the tillering stage (a) and the flag leaf stage (b)			
		GYP	WUEg	YSI	STI	GYP	WUEg	YSI	STI
TRo/ABS	a	-0.14	-0.09	-0.35	-0.24	0.46	0.45	0.39	0.46
	b	0.26	0.27	0.04	0.19	0.46	0.45	0.29	0.50
ETo/ABS	a	-0.32	-0.28	-0.49	-0.44	0.28	0.29	-0.01	0.35
	b	0.21	0.17	0.22	0.23	0.59	0.59	0.60	0.56
ABS/RC	a	0.00	0.04	-0.31	-0.13	-0.18	-0.17	-0.26	-0.14
	b	-0.14	-0.13	-0.44	-0.25	-0.53	-0.55	-0.45	-0.53
TRo/RC	a	-0.02	0.03	-0.36	-0.17	-0.10	-0.10	-0.21	-0.06
	b	-0.02	0.00	-0.43	-0.16	-0.31	-0.33	-0.31	-0.29
ETo/RC	a	-0.21	-0.17	-0.48	-0.36	0.08	0.09	-0.18	0.16
	b	0.10	0.08	-0.12	0.04	0.10	0.08	0.18	0.08
DIo/RC	a	0.09	0.10	-0.05	0.04	-0.35	-0.34	-0.36	-0.33
	b	-0.28	-0.28	-0.22	-0.27	-0.63	-0.63	-0.45	-0.66
ABS/CSo	a	-0.44	-0.38	-0.48	-0.51	-0.74	-0.75	-0.68	-0.74
	b	-0.31	-0.27	-0.58	-0.44	-0.41	-0.41	-0.55	-0.35
ETo/CSo	a	-0.54	-0.47	-0.67	-0.66	-0.62	-0.61	-0.70	-0.57
	b	-0.19	-0.17	-0.43	-0.30	-0.22	-0.21	-0.38	-0.15
DIo/CSo	a	-0.36	-0.32	-0.34	-0.39	-0.75	-0.74	-0.67	-0.74
	b	-0.40	-0.37	-0.48	-0.46	-0.56	-0.55	-0.58	-0.53
RC/CSo	a	-0.48	-0.43	-0.38	-0.49	-0.69	-0.70	-0.58	-0.70
	b	-0.26	-0.22	-0.43	-0.36	-0.21	-0.19	-0.39	-0.14
ETo/(TRo-ETo)	a	-0.31	-0.28	-0.47	-0.42	0.21	0.22	-0.09	0.29
	b	0.23	0.17	0.36	0.30	0.51	0.51	0.61	0.45
PI_{ABS}	a	-0.31	-0.28	-0.44	-0.41	0.38	0.39	0.17	0.43
	b	0.23	0.20	0.28	0.43	0.64	0.64	0.60	0.62

Significance of correlation coefficient: $r \geq 0.632$ (≤ -0.632) for $p \leq 0.05$; $r \geq 0.765$ (≤ -0.765) for $p \leq 0.01$

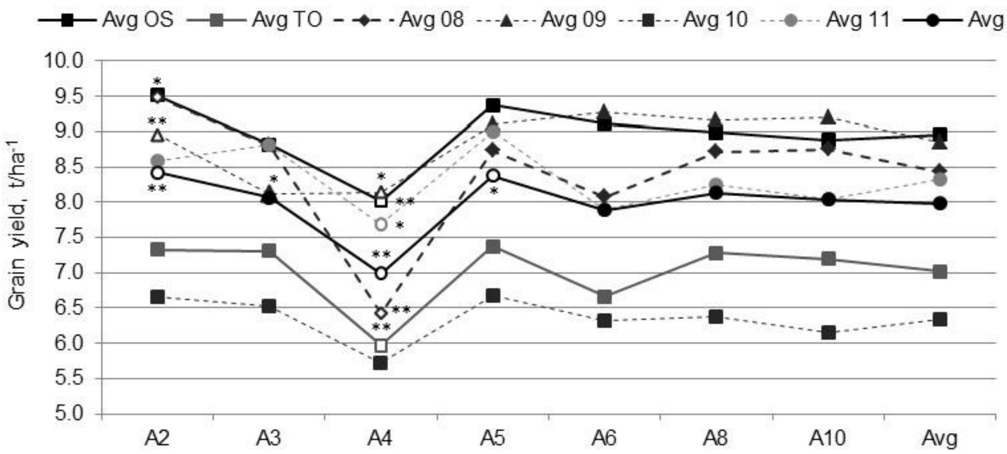
In well-watered treatment at the tillering stage of growth (B1a) only parameter ET_0/CS_0 had significantly ($P \leq 0.05$) negative correlation with YSI (-0.67) and STI (-0.66) (Table 4). ET_0/CS_0 detected in moderate short-term drought stress treatment (B2a) was also in significantly ($P \leq 0.05$) negative correlation with YSI (-0.70).

In the moderate short-term drought stress treatment at the tillering stage (B2a) parameters ABS/CS_0, DI_0/CS_0 and RC/CS_0 were in significant negative correlation with GYP (-0.74, -0.75 and -0.69), WUEg (-0.75, -0.74 and -0.70) and STI (-0.74, -0.74, -0.70). ABS/CS_0, ET_0/CS_0 and DI_0/CS_0 were also correlated with YSI (Table 4).

In the flag leaf stage and water stressed treatment (B2b) significantly ($P \leq 0.05$) negative correlation coefficients were recorded between parameter DI_0/RC and agronomic traits GYP, WUEg and STI (-0.63, -0.66) (Table 4). In the same treatment positive correlation coefficients were estimated for PI_{ABS} with GYP (0.64) and WUEg (0.64) (Table 4).

Multi-environmental field trials

In multi-environmental field trials with seven winter wheat cultivars performed during four years at two locations in the Republic of Croatia, cultivars A2 and A5 achieved, in average for all years and locations of testing, significantly ($P \leq 0.01$ and $P \leq 0.05$) higher yield than the average of all cultivars, while cultivar A4 in the same experiment, had significantly ($P \leq 0.01$) lower grain yield compared to the average yield of all wheat cultivars (Fig 4). Analysis of variance for grain yield of winter wheat cultivars in multi-environmental field trials detected significant ($P \leq 0.01$) impact of cultivars, years, locations and interactions (cultivars x years, cultivars x locations and locations x years) (Table 5).



*($P \leq 0.05$); **($P \leq 0.01$) - Significant difference of average grain yield of cultivars for locations and years and total average for 2 locations and 4 years in relations to average grain yield of all cultivars in the same groups of trials.

Figure 4. Average grain yield of seven wheat cultivars (A2-A10) for years 2008, 2009, 2010 and 2011 and locations Osijek (OS) and Tovarnik (TO) and average grain yield of total results.

Table 5. Analysis of variance for grain yield of winter wheat cultivars in multi-environmental field trials (7 cultivars, 4 years, 2 locations).

	Repet.	Combin.	Error (E)	Cultivar (C)	Year (Y)	Location (L)	Interactions			
							C*Y	C*L	Y*L	C*Y*L
n-1	3	55	165	6	3	1	18	6	3	18
MS	0.568	10.292	0.445	7.264	70.034	211.204	1.699	0.868	17.809	0.665
F-test	1.28	23.13**		16.32**	157.38**	474.61**	3.82**	1.95**	40.02**	1.50

DISCUSSION

Drought stress and agronomic traits of winter wheat cultivars

As expected, drought stress treatment in three different stages of growth significantly reduced average values of GYP, BWP, WUEb, WUEg and HI in all tested genotypes. BIESAGA-KOŚCIELNIAK *et al*. (2014) also reported a statistically significant decrease of GYP in 18 and WUE in all 20 of the tested wheat varieties caused by drought stress, when compared to the properly watered controls.

Cultivars with significantly higher average GYP in the B2 treatment were more rational in using water for grain yield formation. They also had significantly higher WUEg and HI in relation to the average values of all cultivars in the corresponding treatments. Opposite situation was found for cultivars with lower GYP values (Fig 1a and 1e). This interrelationship of traits is consistent with the results of AKHTER *et al*. (2008), SHAMSI *et al*. (2010) and YONG'AN *et al*. (2010), who also found a very strong correlation between WUE and grain yield.

Long-term presence in production as well as the distribution in the wider georgarphic area of Southeast Europe confirms the stability of tested cultivars and could explain the absence of G x E interaction for all agronomic traits in short term moderate drought stress conditions.

Amount of water used by a crop while creating biomass, as described by its WUE, may have an impact on how it copes with drought stress, therefore, WUE can be a good indicator for plant production in water-limited conditions (PASSIOURA, 1977; REYNOLDS *et al*., 2007; ARAUS *et al*., 2008; BLUM, 2009; YONG´AN *et al*., 2010).

Drought stress and photosynthetic efficiency parameters of winter wheat cultivars

Drought stress treatment also influenced photosynthetic parameters of wheat cultivars and resulted in significant differences between cultivars in both stages of growth. Differences between cultivars were more pronounced when measured in the full tillering stage, in relation to the same measurments performed in the flag leaf stage (Table 3). One of the reasons for this could be the lower values of error observed in the tillering stage for all calculated parameters compared to the higher error observed in the flag leaf stage, which also caused the absence of significant interaction of cultivars and treatments in the same phase. (Table 3).

Tillering stage of growth is considered to be the critical period of wheat responses to soil water deficits (MUNNS, 2002; PLAUT, 2003) and SHAO *et al*. (2005) also discovered that different developmental phases significantly affect wheat drought resistance and photosynthetic parameters. HARDING *et al.* (1990) and AL-KHATIB and PAULSEN (1994) reported that the different degree of leaf senescence could be the problem in the study of physiological properties.

We considered measuring of chlorophyll *a* fluorescence (OJIP-test) in the early stage of development (a) to be more reliable based on significance of F test for all photosynthetic parameters in cultivars and treatments and overall lower values of error variance (Table 3) in tillering stage compared to flag leaf stage.

The majority of tested winter wheat cultivars had higher values of ET_0/ABS, ET_0/RC, $ET_0/(TR_0-ET_0)$ and PI_{ABS} in the moderate short-term drought stress conditions in the early stage of development (a), when compared to well-watered treatment (Fig 2b and 2e, Fig 3e and 3f). This increase in photosynthetic electron transport in the early stage of development can be linked to the activation of mechanisms responsible for drought tolerance. Accordingly, LOGGINI *et al.* (1999) reported that higher total rate of photosynthetic electron transport of drought-tolerant wheat variety, in response to drought stress, was probably sufficient to prevent the build-up of excess energy in PSII. KOVAČEVIĆ *et al*. (2013) reported higher grain yield and better grain yield stability in winter wheat cultivars with the increased values of F_v/F_m, ET_0/ABS and PI_{ABS} in moderate short-term drought stress treatment, when compared to well-watered conditions in the early stage of growth (full tillering). Similar results were also presented in the research of BALOUCHI (2011) who reported increasing F_v/F_m values in eight Australian wheat cultivars after drought stress was induced in the early stage of growth. However, KOCHEVA *et al*. (2005) reported no significant variation in the F_v/F_m ratio between control and drought stress treatments of two barley cultivars, suggesting that the efficiency of the quantum yield of PSII was unaffected and that the photosynthetic apparatus is resistant to water deficit which was also confirmed by some authors (CHAVES *et al*., 2002, CORNIC and FRESNEAU, 2002). Lack of sensitivity of the F_v/F_m under drought stress conditions was also observed in other cereals (KOCHEVA *et al*., 2004; HURA *et al*., 2007).

Correlation of agronomic traits and photosynthetic efficiency parameters

Significant correlation between parameters of photosynthetic efficiency ABS/CS_0, ET_0/CS_0 and DI_0/CS_0 (Fig 3a, 3b, 3c) and agronomic traits of winter wheat cultivars indicate that higher ABS/CS_0 and ET_0/CS_0 values in some cultivars cause an increased dissipation (DI_0/CS_0), which negatively impacts GYP, WUEg, YSI and STI (Fig 1a, 1e, 1g). Accordingly, decreased DI_0/CS_0 measured at the tillering stage in the drought stress treatment, could be used to identify cultivars A3 and A5 as genetic material with desirable agronomic traits, while cultivar A4, with markedly higher DI_0/CS_0 did not have desirable values for GYP, WUEg, YSI and STI (Fig 1a, 1e, 1g). On the other hand, positive correlations were found for PI_{ABS} with GYP and WUEg at the flag leaf stage in the drought stress treatment (Table 4) which was earlier reported by FRANIĆ *et al*. (2015) who discovered low (r=0.36), but statistically significant correlation between performance index (PI_{ABS}) and grain yield per plot in the trial with increasing plant density of maize IBM population. TR_0/ABS (F_v/F_m) also had a tendency to be in a positive correlations with GYP and WUEg, in both stages of growth in drought stress treatment (Table 4) which was previously recorded by ARAUS *et al*. (1998) on a larger set of genotypes where significant ($P \leq 0.001$) positive correlation coefficients between TR_0/ABS and grain yield were found on 144 wheat varieties in flag leaf stage in the rain-fed and 124 varieties in irrigated treatment.

Multi-environmental field trials and pot experiment

Field trials with seven out of ten winter wheat cultivars used in pot experiment were performed during four years at two locations in order to confirm pot experiment results regarding grain yield. Cultivars A2 and A5 had significantly higher grain yield than the trial average, and cultivar A4 had the lowest yield, which is common for both pot and field experiment. Considering that multi-environmental field trials (year, location, agro-technical measures) are irreplaceable for final selection of economically valuable cultivars, pot experiments could be used as an effective method for preliminary selection of desirable traits among numerous genotypes and consequently, for the reduction of genotypes tested in extensive field experiments.

CONCLUSIONS

According to higher values of GYP, WUEg, HI, and STI, cultivars A2, A3 and A5 were singled out as the genetic material with a favourable set of traits which could be used in further breeding for drought stress tolerance.

Lower values of ABS/CS_0, ET_0/CS_0 and DI_0/CS_0 and higher values of PI_{ABS}, measured on wheat genotypes (cultivars) in the tillering stage of growth and drought stress conditions of pot trial, could indicate higher tolerance on drought stress conditions.

Higher values of ABS/CS_0 and ET_0/CS_0 in some cultivars cause an increased dissipation (DI_0/CS_0), which then has a negative impact on GYP, WUEg, YSI and STI. This is also confirmed by the strong negative correlations between parameters of photosynthesis and agronomic traits. Results of the studied photosynthetic efficiency parameters of wheat cultivars were also the good predictor for important agronomic traits, especially, when they were detected in the early stage of growth.

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PARAMETRI FOTOSINTETIČKE EFIKASNOSTI KAO INDIKATORI AGRONOMSKIH OSOBINA ZIMSKE PŠENICE U RAZLIČITIM VODENIM ZEMLJIŠNIM USLOVIMA

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Izvod

U cilju iznalaženja oplemenjivačkih metoda za poboljšanje toleratnosti na stres suše i prinos, 12 parametara fotosintetske efikasnosti je mereno na 10 sorti zimske pšenice (*Triticum aestivum* L.), uporedno sa efikasnosti korišćenja vode, komponentama prinosa, indeksom stabilnosti prinosa (YSI) i indeksom toleratnosti na stres (STI) u vegetativnom ogledu sa kontrolom (B1) i tretmanom na stres (B2). Stres sušom indukovan u tri različite faze razvoja je uzrokovao smanjenje efikasnosti korišćenja vode na osnovu biomase (WUEb) (B1:2.94 g L^{-1}; B2:2.71 g L^{-1}) i prinosa zrna (WUEg) (B1: 1.03 g L^{-1}; B2: 0.89 g L^{-1}), kao i prinosa (GYP) i težine biomase. Performans indeks (PI_{ABS}) meren u uslovima suše u fazi lista zastavičara je bio u značajnoj pozitivnoj korelaciji sa GYP i WUEg (r=0.64). Niže vrednosti absorcionog fluksa po ekcitiranoj ukrštenoj sekciji (ABS/CS_0), elektron transporta po ekcitiranoj CS (ET_0/CS_0) i fluks energije po ekcitiranoj CS (DI_0/CS_0) i visoke vrednosti PI_{ABS}, mereni na genotipovima pšenice u uslovima stresa suše, mogu ukazati na visoku toleranciju na uslove stresa suše.

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