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Short communication

EFFECT OF TERMINAL DROUGHT ON YIELD AND SOME PHYSIOLOGICAL TRAITS OF WINTER WHEAT

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Terminal drought i.e. drought during grain-filling phase is the most devastating environmental stress to wheat production. In present study the effect of terminal drought on physiological traits and its influence on yield and yield components in two winter wheat varieties (Kuna and Karla) were investigated. Terminal drought stress was applied from the beginning of anthesis by installing mobile plastic roof above the crops. Leaf gas exchange parameters, chlorophyll content index (CCI), relative water content (RWC), and nitrogen (N) content were measured three times during grain-filling phase, at early milk maturity (EMM), late milk maturity (LMM), and at early wax maturity (EWM). Grain yield and 1000 grain weight were measured by harvesting of each plot at crop maturity. Terminal drought enhanced leaf senescence and caused reduction of RWC, CCI, net photosynthetic rate (A), stomatal conductance (g_s), and transpiration rate (E) as well as, grain yield and all measured yield components. However, grain yield and grain weight per ear were less affected in Karla indicating enhanced tolerance to terminal drought compared to Kuna variety. Higher tolerance to terminal drought in Karla is based on stay-green strategy. Stay-green strategy in Karla was characterized by retention of CCI at early wax maturity, which contributed to higher E and lower intercellular CO_2 concentration compared to Kuna under terminal drought. Stay-green strategy as trait that enhanced terminal drought tolerance in Karla should be used in breeding programs and utilized to ensure maximum economic yields under terminal drought conditions.

Key words: gas exchange; chlorophyll content; relative water content; stay-green strategy

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More than 50% of the area under wheat production is affected by periodic drought (PFEIFFER *et al*., 2005). Wheat production in Croatia experience late season drought stress known as terminal drought that occurs during reproductive and grain-filling growth phases (REYNOLDS *et al*., 2005). Reproductive and grain-filling phases are considered as most sensitive to drought (PASSIOURA, 2012), and prolonged terminal drought can cause significant reduction in wheat yield (FAROOQ *et al*., 2014). Both, terminal drought tolerance and grain yield represent complex traits and a comprehensive understanding of physiological responses under terminal drought are needed.

Therefore, the objective of this study was to investigate the effect of terminal drought conditions on physiological traits and yield and yield components in two winter wheat varieties.

Field experiment was conducted at the Faculty of Agriculture (Zagreb, Croatia) during the 2009-2010 growing season. Previous crop was soybean (*Glycine max* L. Merr.). Soil type at the experimental site is silt loam. Before sowing 400 kg ha^{-1} of N-P-K (7:20:30) was applied. Additional nitrogen (N) fertilization was applied as KAN (27% N) by topdressing 150 kg ha^{-1} at GS 25 and 100 kg ha^{-1} at GS 32 (ZADOKS *et al*., 1974). Two winter wheat cultivars (Kuna and Karla) of different morphology and plant stature, which had previously been found to differ in drought susceptibility index (Barić personal communication), were sown at 400 seeds m^{-2} on 16 October 2009, within optimal sowing time for this region. Terminal drought stress (Stress treatment) was applied from the beginning of anthesis (GS 61) to maturity (GS 92) by installing mobile plastic roof above the crops. To prevent heat stress, roofs were installed only during rainfall events and removed afterwards. Control plots (field conditions) were left uncovered and received normal rainfall precipitation. Total amount of precipitation until the moment of drought stress induction was 483.8 mm, and during the stress treatment the total amount of precipitation on control plots was 504.7 mm (until GS 73), 521.2 mm (until GS 77), and 541.3 mm (until GS 83). The experiment was set out as Randomized Complete Block Design with three replications. Plot size was 3 rows, 1 m long, with 20 cm row space. Leaf gas exchange parameters, chlorophyll content index (CCI), relative water content (RWC), and nitrogen (N) content were measured three times during grain-filling phase, at early milk maturity (EMM) (GS 73), late milk maturity (LMM) (GS 77), and at early wax maturity (EWM) (GS 83), respectively. Leaf gas exchange parameters (net photosynthetic rate (A), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i)) were measured on cloud-free days, twice a day, during morning period (between 9:30 and 11:00 h) and during afternoon period (between 14:00 and 15:30 h), by the LCpro portable photosynthesis system (ADC, Bio Scientific Ltd., UK). Measurements were carried out at 1100 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) and 380±5 μmol mol^{-1} CO_2 concentration. The instantaneous water use efficiency (WUE) and intrinsic water use efficiency (WUEi) were calculated as WUE = A/E, and WUEi = A/g_s, respectively. CCI was measured by chlorophyll content meter, CCM-200 (Opti-Sciences Inc., Hudson, USA), on the same leaves as gas exchange parameters. Measurement of flag leaf RWC was conducted according to Tas and Tas (2007). RWC were calculated using the equation (BEADLE *et al*., 1993): RWC = ((fresh weight - dry weight) / (turgid weight - dry weight)) × 100. Flag leaf N content was determined by Kjeldahl procedure (AOAC, 1995). All measurements were performed on flag leaf on three plants per Variety × Stress treatment × Replication combination and mean values per plot were calculated. At anthesis (GS 60) 10 plants per plot were manually defoliated. All leaf lamina of the plants were removed. Stem reserves were estimated based on percent reduction in 1000 grain weight for each genotype (BLUM, 1998). Ten spike-bearing tillers were randomly chosen from each plot to measure the grain number per spike and grain weight per spike. Grain yield and 1000 grain weight were measured by harvesting of each plot at crop maturity.

For the data analysis Mixed model ANOVA was performed using SAS 9.3 statistical package (SAS Institute Inc., 2011). Repeated measures analysis was used for traits that were repeatedly measured during grain-filling phase (CCI, A, E, g_s, C_i, WUE, WUEi, RWC, and N content). Pairwise differences between levels of factors that were estimated as significant were tested using Tukey – Kramer method.

Results of this experiment showed that all measured physiological parameters decreased, and the intercellular CO_2 concentration increased during the measurements, from EMM to EWM, which is caused by natural leaf senescence and concomitant increase of respiration rate (Figure 1 and Figure 2). However, terminal drought enhanced leaf senescence as could be noticed from the significant reduction in RWC, CCI (Figure 1), A, g_s, and E (Figure 2). In contrast, WUEi slightly (not significant) or WUE significantly (during morning measurement period) increased under terminal drought (Figure 2i, 2j, 2k and 2l), due to faster decrease in g_s and E compared to A. Similar increase in WUE and WUEi under drought stress were reported for wheat seedlings (WANG *et al*., 2016). The flag leaf is the major source of assimilates for grain-filling (LARBI, 2004), therefore stay-green strategy which combines delaying senescence, maintaining leaf chlorophyll content, sustaining transpiration, and photosynthetic rate (VADEZ *et al*., 2011) represents one of the key factors that contributes to embodiment of yield potential under terminal drought stress. Results of this study show that variety Karla had higher average flag leaf N content (Figure 1), A, g_s, E, WUE, WUEi, and lower C_i values compared to Kuna (Figure 2). Moreover, at the EWM there was no differences in CCI between control and terminal drought treatment grown Karla, which indicate stay-green strategy of the Karla variety. Stay-green strategy in maize (*Zea mays* L.) is related to enhanced N use (BLUM, 2006), and in sorghum (*Sorghum bicolor* L. Moench) to root traits which enable water uptake from the deeper soil layers (MACE *et al*., 2012). Although Karla has higher average N content compared to Kuna, the fact that terminal drought did not affect flag leaf N content for both varieties, it seems that stay-green strategy in Karla relies on the root features which enabled enhanced water uptake. Although root features were not measured in this experiment, further support of possible root feature basis of stay-green strategy in Karla lies in fact that under terminal drought Karla retain higher E and lower C_i compared to Kuna (Figure 2). All these indicate better water status of the variety Karla, which sustained higher transpiration rate and lower photorespiration under terminal drought conditions. Terminal drought decreased average grain yield as well as all measured yield components (Table 1). DOLFERUS *et al*. (2011) stated that yield reduction under terminal drought could be more accounted to decrease in grain number compared to grain size. However, drought after anthesis has no effect on grain number but it reduces yield due to shortening of grain-filling period (PLAUT *et al*., 2004). In present experiment, terminal drought caused strongest reduction of grain weight per spike, which indicate that severe drought stress occurred after anthesis, and again that remaining soil moisture after applying stress treatments delayed effect of terminal drought treatment. In addition, grain yield and grain weight per spike were less affected in Karla variety (Table 1). It has been shown that remobilization of water soluble carbohydrates from the stem can mitigate negative effect of terminal drought on grain-filling and yield (BLUM *et al*., 1994). Relative contribution of water soluble carbohydrates to wheat grain yield ranges from 6-100% (BLUM *et al*., 1994). Stem reserves were estimated based on percent reduction in 1000 grain weight by defoliation for each genotype (BLUM, 1998), and results indicate that Kuna (66.9%) and Karla (67.1%) have similar capacity for remobilization of stem carbohydrates to developing grains (Table 2).

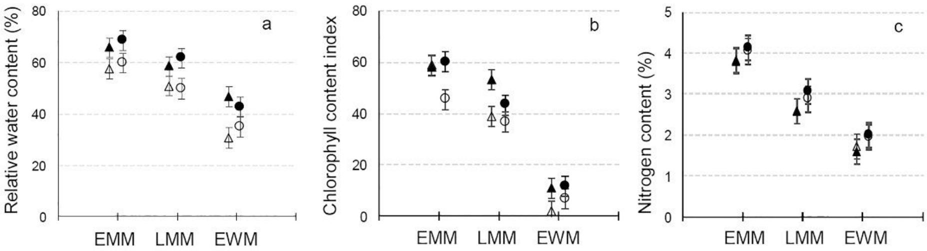

Figure 1. Flag leaf relative water content (a), chlorophyll content index (b), and nitrogen content (c) of two winter wheat varieties, Kuna (△, ▲) and Karla (○, ●), measured at early milk maturity (EMM), late milk maturity (LMM), and early wax maturity (EWM) under terminal drought treatment (△, ○) and control treatment (▲, ●). Data are represented as means ± double standard errors of the mean (n=3).

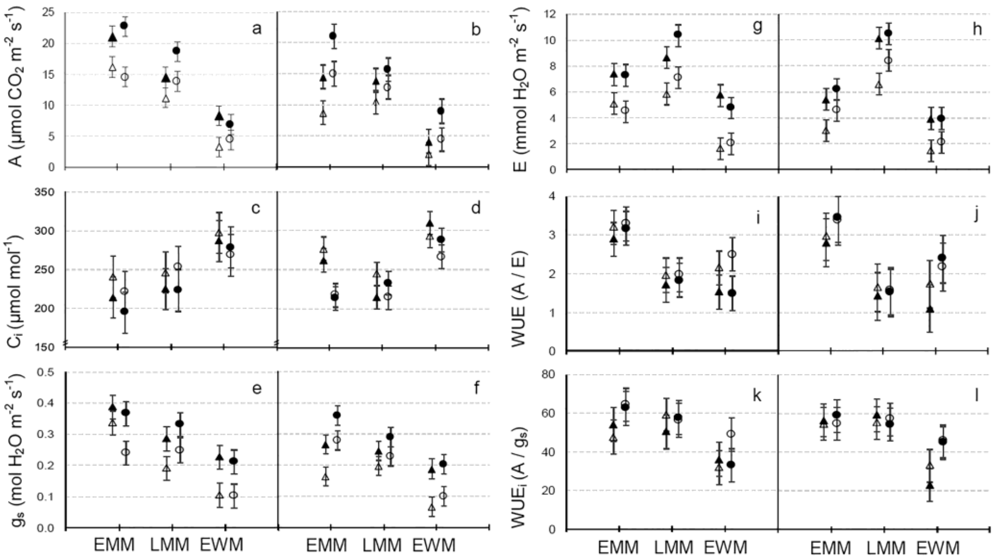

Figure 2. Flag leaf net photosynthetic rate (a, b), transpiration rate (c, d) intercellular CO_2 concentration (e, f), stomatal conductance (g, h), instantaneous water use efficiency (i, j), intrinsic water use efficiency (k, l), of two winter wheat varieties, Kuna (△, ▲) and Karla (○, ●), measured during morning (a, c, e, g, i, k) and afternoon (b, d, f, h, j, l) measurement period at early milk maturity (EMM), late milk maturity (LMM), and early wax maturity (EWM), under terminal drought treatment (△, ○) and control treatment (▲, ●). Data are represented as means ± double standard errors of the mean (n=3).

Table 1. Means (± standard error of a mean) for grain yield and yield components of two winter wheat varieties grown under terminal-drought and control treatment.

Treatment/variety	Grain yield (t ha^{-1})		Grain weight per spike (g)		Grain number per spike		1000-kernel weight	
	Kuna	Karla	Kuna	Karla	Kuna	Karla	Kuna	Karla
Control	9.2±0.16^a	8.5±0.16^a	2.2±0.06^a	2.0±0.06^a	52.2±1.0^a	48.5±1.0^a	42.3±1.6^a	41.7±1.6^a
Terminal-drought	7.3±0.16^b	7.4±0.16^b	1.5±0.06^b	1.6±0.06^b	42.7±1.0^b	43.1±1.0^b	36.0±1.6^b	38.3±1.6^b
$\overline{x}$	8.3±0.12	7.9±0.12	1.8±0.04	1.8±0.04	47.5±0.7	45.8±0.7	39.2±1.2	40.0±1.2

Different letters indicate Stress treatment means differences within a Variety (*P*=0.05).

Table 2. Means (± standard error of a mean) for yield components of defoliated and non-defoliated winter wheat varieties.

Treatment/variety	Grain weight per spike (g)		Grain number per spike		1000-kernel weight	
	Kuna	Karla	Kuna	Karla	Kuna	Karla
Non-defoliated	2.2±0.07^a	2.0±0.07^a	52.2±1.9^a	48.5±1.9^a	42.3±1.0^a	41.7±1.0^a
Defoliated	0.9±0.07^b	1.0±0.07^b	31.7±1.9^b	34.7±1.9^b	28.3±1.0^b	28.0±1.0^b
$\overline{x}$	1.5±0.07	1.5±0.07	42.0±1.6	41.6±1.6	35.2±0.8	35.0±0.8

Different letters indicate Stress treatment means differences within a Variety (*P*=0.05).

Our results showed that terminal drought enhance leaf senescence and cause significant reduction in CCI, RWC, g_s, E which led to reduction in A and consequently reduction of grain number, grain weight, and grain yield. However, terminal drought caused lower grain yield reduction of Karla variety, due to stay-green strategy which delayed flag leaf senescence and prolonged the grain-filling period. These valuable trait should be used to ensure maximum economic yields under terminal drought conditions and should be included in future breeding programs.

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UTICAJ TERMINALNE SUŠE NA PRINOS I FIZIOLOŠKE KARAKTERISTIKE OZIME PŠENICE

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Izvod

Terminalna suša tj. suša tokom faze nalevanja zrna predstavlja najvažniji okolinski stresni faktor u proizvodnji pšenice. U ovom radu istraživan je uticaj terminalne suše na fiziološke karakteristike te na prinos i komponente prinosa kod dve sorte pšenice (Kuna i Karla). Tretman terminalne suše primenjen je od početka klasanja postavljanjem plastične folije iznad useva. Parametri izmene gasova, indeks sadržaja hlorofila (CCI), relativni sadržaj vode u listu (RWC) i koncentracija azota u listu (N) mereni su tri puta tokom faze nalevanja zrna, u ranoj mlečnoj zrelosti (EMM), kasnoj mlečnoj zrelosti (LMM) i ranoj voštanoj zrelosti (EWM). U tehnološkoj zrelosti određen je prinos i masa 1000 zrna. Terminalna suša ubrzala je proces senescencije lista te izazvala redukciju RWC, CCI, neto fotosinteze (A), stomatalne provodljivosti (g_s) i transpiracije (E), kao i prinos i sve merene komponente prinosa. Međutim, terminalna suša manje je uticala na smanjenje prinosa zrna i mase zrna po klasu kod sorte Karla u odnosu na sortu Kuna, što ukazuje na prisutnost određene tolerantnosti kod ove sorte. Tolerantost sorte Karla na terminalnu sušu temelji se na "stay green" strategiji. Ova karakteristika sorte Karla imaj potencijal za korištenje u oplemenjivačke svrhe sa ciljem stvaranja sorata sa većom potencijalnom rodnošću u uvetima terminalne suše.

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