Drought priming effects on alleviating the photosynthetic limitations of wheat cultivars (Triticum aestivum L.) with contrasting tolerance to abiotic stresses

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Table 1. Gas exchange parameters and leaf relative water content (LRWC) of two wheat cultivars: 'Gladius' and 'Paragon'. The parameters presented are: stomatal conductance (g_s), leaf transpiration rate (E), intercellular CO_2 (Ci), the ratio between CO_2 assimilation and transpiration rate (WUE_{leaf} = A/E) and the ratio between the maximum carboxylation of rubisco and the electron transport demand for RuBP (J/V_c). Measurements of non-primed and primed plants were taken on the flag leaf of the primary tiller after relative soil water content reached 25% (CD and PC). Heat stressed treatments (CH and PH) were measured after seven days of stress at heat temperature (32˚C); non-stressed and drought stress treatments (CC and PC; CD and PD) were measured at growth temperature (20˚C). All parameters are given at light level of 2000 µmol m^{-2} s^{-1} and [CO_2] of 407 ppm. Different lower letters indicate significant difference at $P<0.05$ within each cultivar for parameters with interaction between priming and stress, the absence of letters indicates no interaction between factors. Data represents mean values ± SEM, n = 3.

Parameters	Units	**CC**	**CD**	**CH**	**PC**	**PD**	**PH**
				'Gladius'			
LRWC	%	92.30±3.73	87.53±3.97	92.77±1.21	91.27±3.58	88.66±2.48	90.14±4.90
g_s	mmol m^{-2} s^{-1}	436.07 ± 49.22 [a]	221.19 ± 34.19 [b]	451.16 ± 47.02 [a]	349.53 ± 37.71 [a]	339.15 ± 8.32 [a]	369.26 ± 10.99 [a]
E	mmol m^{-2} s^{-1}	4.52 ± 0.26	2.66 ± 0.43	8.66 ± 0.69	3.64 ± 0.33	3.55 ± 0.05	7.64 ± 0.18
C_i	ppm	307 ± 10	261 ± 05	309 ± 04	287 ± 08	275 ± 10	294±01
WUE_{leaf}	µmol $mmol^{-1}$	4.88 ± 0.42	6.89 ± 0.0.33	2.38 ± 0.13	6.14 ± 0.42	6.70 ± 0.49	2.72 ± 0.01
J/V_c		2.29 ± 0.02	2.36 ± 0.08	1.55 ±0.04	2.36 ±0.05	2.279 ±0.04	1.68 ±0.04
				'Paragon'			
LRWC	%	93.44±0.63	90.38±0.66	89.93 ±3.03	92.41±1.17	88.10±3.68	89.46±2.54
g_s	mmol m^{-2} s^{-1}	327.29 ± 24.15	197.31 ± 8.25	324.28 ± 13.89	357.30 ± 8.86	223.82 ± 12.90	317.77 ± 18.52
E	mmol m^{-2} s^{-1}	3.36±0.18	2.22 ± 0.19	6.73 ± 0.20	3.74 ±0.10	2.59 ±0.09	6.78 ±0.33
C_i	ppm	275.48 ± 13.26	253.36 ±7.41	284.05 ±6.87	296.81 ±5.91	248.62 ±12.64	275.15 ±9.03
WUE_{leaf}	µmol $mmol^{-1}$	6.96 ± 0.67	7.85 ± 0.49	3.02 ± 0.14	5.63 ± 0.33	7.77 ± 0.51	3.19 ± 0.23
J/V_c		2.25 ± 0.02	2.11 ± 0.10	1.26 ±0.08	2.12 ±0.05	1.99 ±0.02	1.34 ±0.04

Table 2. Output of the two-way ANOVA of leaf relative water content (LRWC), maximum net photosynthetic rate (A_{max}), stomatal conductance (g_s), leaf transpiration rate (E), intercellular CO_2 (C_i), the difference between leaf and cuvette air temperature ($\Delta T = T_{leaf} - T_{cuvette}$), the ratio between CO_2 assimilation and transpiration rate ($WUE_{leaf} = A/E$), saturated net photosynthetic rate (A_{sat}), maximum carboxylation of Rubisco adjusted at 25˚C (Vc_{max25}), maximum photosynthetic electron transport rate adjusted at 25˚C (J_{max25}), the ratio between the maximum carboxylation of rubisco and the electron transport demand for RuBP (J/V_c), maximum quantum efficiency of PSII photochemistry (F_v/F_m) in dark adapted leaves, quantum efficiency of PSII ($F_{q'}/F_{m'}$), non-photochemical quenching (NPQ) and electron transport rate (ETR) based on absorbed light. Level of significance of each factor is indicated as*P<0.05, **P<0.01, ***P<0.0001. Different lower letters indicate significant difference at P<0.05 within each cultivar for parameters with interaction between priming and stress, ns indicates no statistically significant difference. The data is presented in figure 2, 3 and 4 and table 1.

Source of variation	LRWC	A_{max}	g_s	E	C_i	ΔT	WUE_{leaf}	A_{sat}	V_{cmax25}	J_{25}	J/V_c	F_v/F_m	F_q'/F_m'	NPQ	ETR
‘Gladius’															
Priming x Stress	ns	ns	*	ns	ns	**	ns	*	ns	ns	ns	ns	***	ns	**
CC	-	-	a	-	-	a	-	ab	-	-	-	-	a	-	a
CD	-	-	b	-	-	a	-	c	-	-	-	-	ab	-	a
CH	-	-	a	-	-	c	-	ab	-	-	-	-	c	-	b
PC	-	-	a	-	-	a	-	bc	-	-	-	-	c	-	b
PD	-	-	a	-	-	ab	-	bc	-	-	-	-	ab	-	a
PH	-	-	a	-	-	b	-	a	-	-	-	-	bc	-	b
Priming	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns
Control	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Priming	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stress	ns	ns	**	***	***	**	***	**	***	***	***	*	ns	ns	*
Non-stressed	-	-	a	b	a	b	b	b	b	a	a	a	-	-	ab
Drought stress	-	-	b	c	b	b	a	ab	b	a	a	ab	-	-	a
Heat Stress	-	-	a	a	a	a	c	a	a	b	b	b	-	-	b
‘Paragon’															
Priming x Stress	ns	*	ns	ns	ns	ns	ns	ns	*	*	ns	ns	**	ns	***
CC	-	a	-	-	-	-	-	-	a	a	-	-	a	-	a
CD	-	b	-	-	-	-	-	-	b	c	-	-	ab	-	b
CH	-	a	-	-	-	-	-	-	a	c	-	-	b	-	bc
PC	-	a	-	-	-	-	-	-	ab	bc	-	-	b	-	bc
PD	-	a	-	-	-	-	-	-	a	ab	-	-	b	-	c
PH	-	a	-	-	-	-	-	-	a	c	-	-	a	-	a
Priming	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	-	ns
Control	-	-	-	-	-	-	-	-	-	-	-	a	-	-	-
Priming	-	-	-	-	-	-	-	-	-	-	-	b	-	-	-
Stress	***	*	**	***	***	***	***	***	ns	*	*	***	ns	***	ns
Non-stressed	a	a	a	b	a	b	b	b	-	a	a	a	-	a	-
Drought stress	b	b	b	c	b	b	a	c	-	a	a	a	-	a	-
Heat Stress	a	a	a	a	a	a	c	a	-	b	b	b	-	b	-

Table 3

1. Results

1.1 Gas exchange

The temperature curve shape responded to e[CO_2] in both cultivar (Figure 2). When analysing T_{opt}, a positive interaction between [CO_2] and water regime was found for both cultivars (Figure 3a and b). Under e[CO_2], RW plants presented a higher $T_{opt,}$ independent of the temperature they were grown at, when compared to the respective treatment under a[CO_2]. In ‘Paragon’ e[CO_2], FW regime and elevated temperature increased the integrated carbon gain, however no interaction between factors was observed (Figure 3c). ‘Gladius’ data of integrated carbon gain did not fulfil the assumption of the parametric method, therefore it was compared using non-parametric Kruskal-Wallis test and no difference was observed between the correspondent treatments under e[CO_2], different temperatures or water regimes (Figure 3d).

In the temperature response curves, a linear decrease in WUE was observed as temperatures increased in ‘Paragon’ under a[CO_2] for all treatments. The same trend was observed under e[CO_2], but a more pronounced separation was noticed between treatments grown under different temperatures (18 C and 28 C), while plants under the same irrigation regime behaved similarly. In ‘Gladius’ a distinct WUE behaviour was observed at a[CO_2] for FW plants under 28C, a sharp increase followed by a sharp decrease of values of WUE was noted. Under e[CO_2], treatments presented the same inclination but a separation in the 28 C +RW treatment was observed.

1.2 Biomass accumulation and specific leaf area

The stress imposition reduced the leaf area of ‘Paragon’ and ‘Gladius’, showing a significant reduction in all stress treatments when compared to control. Dry weight (DW) accumulation in ‘Paragon’ was reduced by all stress impositions. In ‘Gladius’, an interaction between water regime and temperature and between temperature and [CO_2] was observed, with a significant decrease of DW of all treatments grown at 28℃ and e[CO_2], but a value similar to control in plants grown under reduced water and 18℃.

1.3 Photosynthetic pigments and C:N ratio

The C:N ratio in the leaves was affected by the water regime in ‘Gladius’, as reduced water increased the C:N values under both [CO_2]. In ‘Paragon’ the data for C:N in the leaves did not fulfil the assumption of the parametric method, therefore it was compared using non-parametric Kruskal-Wallis test, the treatments followed the same trend observed for ‘Gladius’.

‘Paragon’ pigment content analysis presented a three-factorial interaction to chlorophylls *a*, *b*, total chlorophylls and the ratios between Chl *a:b* and Chl:Car, while values of carotenoid contents showed a two-way interaction for water regime and [CO_2]. Chlorophyll *a* and total chlorophylls presented similar behaviour to stress imposition, all RW under e[CO_2] and the 28℃ +FW under a[CO_2] treatments presented a reduction to their pigments content. For the contents of chlorophyll *b*, a decrease in treatments at 18℃ + RW in in both [CO_2] was observed. Carotenoids values only decreased under RW in 18℃ in e[CO_2]. The ratio between Cehl *a:b* increased in RW under a[CO_2] and decreased under 28℃ under e[CO_2]. Chl:Car ratio decreased under 18℃ + RW in both [CO_2].

For ‘Gladius’, all pigments and pigments ratios showed a three-factorial interaction. Chl *a*, Chl *b*, total chlorophylls and carotenoids were not affected by e[CO_2] compared to control. Under a[CO_2] a the concentration of pigments in this cultivar responded to both temperature and water regime, while a decrease was observed for plants cultivated at 28 °C and FW, an increase of pigments content was noted for the treatment under stress combination (28 °C + RW). Compared to control, the Chl *a:b* ratio increased under RW at 18°C, while it decreased for the RW treatment under 28°C at a[CO_2]. The elevated temperature combined to e[CO_2] reduced the Chl a:b ratio independently of the water regime. Values of Chl:Car increased under stress combination (28°C + RW) at both [CO_2], but decreased elevated temperature and FW at a[CO_2].