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Multiple heat and drought events affect grain yield and accumulations of high molecular weight glutenin subunits and glutenin macropolymers in wheat

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ABSTRACT

Spring wheat plants were subjected to water deficit and/or high temperature episodes at spikelet initiation, anthesis or both stages. The stresses modified the early dough stage and maturity, shortened the kernel desiccation period and caused grain yield loss. Plants subjected to stress at the early growth stages had higher grain yields than the non-early-stressed plants when stress reoccurred at anthesis. Concentrations of high molecular weight glutenin subunits in grain were up-regulated by the single early drought, the early drought combined with late heat and the double drought stress treatments, but was down-regulated by the early heat and double heat stress events. Concentration of glutenin macropolymers was increased by the single early drought episode, the single late drought and heat events, as well as the early drought combined with the late heat stress, but was reduced by the early heat stress and double heat events.

1. Introduction

The frequency and extent of extreme drought and high temperature events are increasing more than anticipated due to global warming (IPCC, 2001). Heat and drought events are often occurring in parallel during crop growth, and long-period of high temperature will enhance leaf evapotranspiration and may result in secondary extreme water deficit (Plaut et al., 2004). In wheat, extremes of high temperature and water deficit during the critical grain filling period not only cause severe grain yield losses (Zhao et al., 2007), but also reduce grain quality (Gooding et al., 2003). Since wheat quality is of increasing importance for producers, it is necessary to understand the adverse effects of the interaction of these environmental constraints (Wollenweber et al., 2003).

The glutenin protein fraction is important in determining gluten quality and dough elasticity in wheat flour (Shewry et al., 2000). Glutenin is classified into two types of subunits according to their molecular weight, i.e. the high molecular weight glutenin subunits (HMW-GS) and the low molecular weight glutenin subunits (LMW-GS). HMW-GS links with LMW-GS via disulfide bonds and composes the so-called glutenin macropolymers (GMP), an SDS insoluble glutenin component which to a great extent determines wheat baking quality (Don et al., 2006). Thus, HMW-GS plays key roles in determining GMP accumulation in wheat grain and the consequent end-use quality such as bread-baking quality (Shewry et al., 2003).

It has been clear that composition of HMW-GS greatly affects bread-making quality. The subunits of 1 and 2*, pair of 7 + 8 or 7 + 9, and pair of 5 + 10 are associated with better baking performance (Pirozi et al., 2008). Meanwhile, high accumulation of the weak-dough associated subunit pair of 2 + 12 in wheat grain results in good bread-making quality (Zhu et al., 1999). In addition, overexpression of the Glu-B1 7x-subunit favors bread-making quality (Vawser and Cornish, 2004). High expressions of subunits 5 (Rakszegi et al., 2005) and 1 (Rakszegi et al., 2008) also greatly increase dough strength. Thus, the accumulation of HMW-GS in grain is a very important aspect in wheat quality formation.

It is noteworthy that HMW-GS composition is genetically controlled and stable in heredity. By contrast, the expressions or amounts of HMW-glutenin subunits and the proportion of each subunit (pair) to total subunit amount can be modified by environmental conditions, such as drought and waterlogging (Jiang et al., 2009), mineral nutrition and temperature (DuPont et al.,

Abbreviations: DAA, days after anthesis; GMP, glutenin macropolymers; GPC, grain protein concentration; HMW-GS, high molecular weight glutenin subunits; LMW-GS, low molecular weight glutenin subunits.

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2007). However, effects of stress interactions during wheat growth on accumulation of HMW-GS and GMP are not well documented.

Our previous report with the same experiment here indicated that a drought and/or high-temperature event applied at an early growth stage (terminal spikelet) affected another stress event at anthesis in affecting albumin and gliadin fractions (Yang et al., 2011). Here, we further reported the effects of water deficit and heat episodes at both growth stages on accumulations of HMW-GS and GMP. The aims of this study were to compare the differential responses of HMW-GS and GMP accumulation to a single drought or heat stress event at the vegetative or the reproductive stage or both, and, with the increased variability of climate in mind, to test the hypothesis that a drought and/or high-temperature event applied at terminal spikelet will modify grain glutenin accumulation under drought or heat stress occurring during grain filling.

2. Materials and methods

2.1. Experimental design

The experimental details have been described in Yang et al. (2011). In brief, a pot experiment was conducted at the facilities of the Research Center Flakkebjerg, Aarhus University, Denmark. Pots with depth and diameter of 25 cm were filled with 4.2 kg 1:2:1 (V:V:V) mixture of peat substrate, loamy soil and sand. A dose of 5.25 g K_2SO_4, 3.5 g $(NH_4)_2SO_4$, 4.67 g NH_4NO_3, 1.9 g $CaSO_4$, 1.9 g $MgSO_4$, 0.4 g $MnSO_4$, 0.4 g $CuSO_4$ and 11.67 g $CaCO_3$ per pot was mixed with the soil. Spring wheat (*Triticum aestivum* L. cv. Vinjett) was planted with a seedling rate of 5 per pot. An automatic irrigation system was used until the implementation of the water deficit treatment. The main shoot of each plant was labeled at the three-leaf stage. Thereafter, spike initiation of the main shoot was observed at an interval of two or three days until the spikelet initiation was identified by microscopic dissection.

Water deficit and high temperature were implemented during two growth stages, the end spikelet initiation stage (Stage A) and anthesis (Stage B). At Stage A, three treatments were separately implemented in three growth chambers, i.e. control (CTA), water deficit (WDA) and high temperature (HTA). At Stage B, each of the above treatments was further exposed to three treatments: control (CTB), water deficit (WDB) and high temperature (HTB). Thus, in total nine interactive stress treatments were implemented: CTA-CTB, CTA-WDB, CTA-HTB, WDA-CTB, WDA-WDB, WDA-HTB, HTA-CTB, HTA-WDB and HTA-HTB. Since the flowering date of the first heat event (27th of June) HTA-CKA, HTA-WDB and HTA-HTB was only one day earlier than WDA and CTA, the second heat event was implemented on the same day (28th of June). The experiment was a completely randomized block design with three replicates (pots) for each harvest.

The day/night temperature was set to 32°C/24 °C for the heat event at both treatment stages, while to 20°C/12 °C at Stage A and to 24°C/16 °C at Stage B for the non-heat treatments to simulate the actual temperature scenarios at the different growth stages. The drought treatment was achieved by withdrawing watering seven days earlier (three-leaf stage) and six days earlier (just after the spike emerged) at Stage A and Stage B, respectively, to provide the exact drought condition just before moving the pots into the growth chambers.

Uniform ears on the main stem and flowering on the same day were tagged for sampling. The tagged ears were sampled at 12 days after anthesis (DAA), 19 DAA, 26 DAA, 33 DAA and maturity.

2.2. Grain dry mass and water content

The harvested ears were put into liquid nitrogen. The frozen ears were quickly rubbed by hands in thick gloves to remove grains. The grains were weighed to get the fresh mass and then dried in a Heto Lyopro 6000 freeze drier (Heto-Holten A/S, Allerød, Denmark) to get the dry mass. The grain water content was calculated as (Fresh mass − Dry mass)/Fresh mass * 100%.

2.3. Grain protein concentration

The total N concentration of whole grain flour was determined using a Vario EL III CNS elemental analyzer (Elementar Analysaenaysteme GmbH, Hanau, Germany). N concentrations multiplied by 5.7 resulted in the grain protein concentration.

2.4. GMP and HMW-GS concentration

GMP and HMW-GS concentrations could be measured out from 19 DAA. GMP concentration was measured by the method of Weegels et al. (1996). In brief, grain samples (50 mg) were suspended in 1 ml of 1.5% SDS solution and centrifuged at 15,500 g for 30 min at 20 °C. The nitrogen concentration of the sediment measured with the Biuret reagent (Gornall et al., 1949) was taken as the GMP concentration. HMW-glutenin subunits were separated by SDS-PAGE, and quantification of each individual subunit was performed according to our previous method, and total HMW-GS concentration was the sum of each individual subunit (Yue et al., 2007).

2.5. Statistical analysis

All data were subjected to one-way analysis of variance (ANOVA) using the SAS statistical analysis procedures (SAS Institute, USA). The Duncan's multiple *t*-test was used to compare the difference between treatments. The SYSTAT SigmaPlot Suite V 12.0 (SYSTAT Software Inc., Chicago USA) was used to analyze correlation between grain water content and DAA, and to calculate the date of the early dough stage for each treatment. The relationship between contents of HMW-GS and GMP was also analyzed using the SYSTAT SigmaPlot Suite V 12.0, and the *t*-test was used to check the significance.

3. Results

3.1. Phenology and grain yield

The maturity date but not the flowering date was essentially altered by the stress events (Table 1). Compared with the non-

Table 1
The flowering date, time of stages of early dough and harvest ripening under each treatment.

Treatments	Anthesis date	Early dough (DAA)	Harvest ripening (DAA)	Kernel desiccation period (*d*)
CTA-CTB	28-June	33	42	9
WDA-CTB	28-June	34	42	8
HTA-CTB	27-June	34	39	5
CTA-WDB	28-June	34	39	5
CTA-HTB	28-June	33	37	4
WDA-WDB	28-June	35	40	5
WDA-HTB	28-June	34	41	7
HTA-WDB	27-June	35	40	5
HTA-HTB	27-June	32	36	4

Note: CT, WD and HT indicate control, water deficit and high temperature, respectively. A and B means treatment applied at end of spikelet initiation stage and flowering stage, respectively. The early dough development stage (Stage 83 in the Zadoks Scale, with grain water content of ca. 44%) and the hard kernel stage (harvest ripening, i.e. Stage 92 in the Zadoks Scale, with grain water content of ca. 20%) were determined according to the corresponding trend curve (regression curve) of grain water content vs. DAA of each treatment in Fig. 1. DAA indicates days after anthesis. Kernel desiccation period is the days between Stage 83 and Stage 92 in the Zadoks Scale.