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Review

# New insights into the effects of high temperature, drought and post-anthesis fertilizer on wheat grain development

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ABSTRACT

Temperature, water and fertilizer have complex and interacting effects on wheat grain development, yield and flour quality. Transcript and protein profiling studies have provided insight into molecular processes in the grain and are now being used in conjunction with controlled growth experiments to decipher the effects of specific environmental variables on grain development. These studies are complicated because environmental treatments such as high temperature and drought shorten the duration of grain development and because effects of high temperature and drought on gene expression and protein accumulation are superimposed upon those of post-anthesis fertilizer. The integration of data from recent proteomic and transcriptomic studies is an important step in identifying genes and proteins that respond to environment and affect yield and flour quality. Such information is needed to develop wheat better able to adapt to global climate change.

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## 1. Introduction

Climate model projections suggest that higher seasonal temperatures will become commonplace in many parts of the world by the end of the century (Battisti and Naylor, 2009). Periods of drought also are likely to become more frequent and more severe. Wheat is one of the major crops grown in many different environments worldwide and is an important source of calories for human nutrition. High temperatures and drought already limit wheat productivity in many parts of the world and recent modeling studies indicate that increases in average growing season temperatures are likely to cause further reductions in wheat grain production, potentially threatening global food security (Asseng et al., 2011). Environmental factors also affect wheat flour quality and thus are a major concern for end-users of wheat.

Relationships between the environment and yield and quality of wheat are complex (Triboï and Triboï-Blondel, 2002). In the field, unfavorable environmental conditions can occur at any time in the life cycle of the wheat plant, can vary in intensity and duration, and can affect diverse processes during either vegetative or reproductive phases of the plant. The plant has devised numerous mechanisms to cope with environmental stress with the ultimate goal of producing a viable seed. These mechanisms involve changes at the molecular, cellular and physiological levels that vary with genotype and are further influenced by the nutritional status of the plant. Ultimately, changes are manifested in the grain where they influence the accumulation of starch and protein. Starch is a major component of the grain and is the most important factor for yield while both the amount and composition of protein are critical for quality.

Several excellent reviews discuss the effects of high temperatures and drought on wheat and other cereals (Barnabás et al., 2008; Dupont and Altenbach, 2003; Yang and Zhang, 2006). Controlled environment studies have been essential for unraveling the effects of individual environmental factors on wheat grain development. They also have made it possible to utilize proteomic and transcriptomic approaches to evaluate the effects of environment on proteins and genes that may be involved in determining yield and flour quality. However, each study provides only a small glimpse of a complex picture. While other reviews in this issue provide updates on the effects of environment on starch production and the formation of glutenin polymers in the grain, this review focuses on results

*Abbreviations:* 2-DE/MS, two-dimensional gel electrophoresis/mass spectrometry; DPA, days post-anthesis; EST, expressed sequence tag; GADPH, glyceraldehyde-3-phosphate dehydrogenase; HMW-GS, high molecular weight glutenin subunit; HSP70, 70 kDa heat shock protein; LEA, late embryogenesis abundant; LMW-GS, low molecular weight glutenin subunit; LTP, lipid transfer protein; MS, mass spectrometry; MS/MS, tandem mass spectrometry; NPK, nitrogen:phosphorous:potassium fertilizer; PMF, peptide mass fingerprinting; qRT-PCR, quantitative reverse transcription polymerase chain reaction; RT-PCR, reverse transcription polymerase chain reaction.

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from recent proteomic and transcriptomic studies aimed at uncovering molecular mechanisms in the response of the developing grain to temperature, water and fertilizer.

## 2. Wheat grain development

The mature wheat grain consists of the endosperm that makes up about 89% of the grain, the embryo that comprises less than 3%, and various outer layers of dead maternal tissues that make up about 9% of the grain (Evers and Millar, 2002). The endosperm provides most of the commercial value of the wheat grain and consists of the starchy endosperm, in which starch granules are embedded in a matrix of protein, surrounded by the aleurone, a single cell layer. Wheat grain development is a complex process that involves coordination among a number of different tissues (reviewed by Evers and Millar, 2002). Grain development is often described on the basis of morphological characteristics (Rogers and Quatrano, 1983). However, to relate genes and proteins to processes that occur during grain development, it is perhaps simpler to consider wheat grain development in three stages: cell division, cell expansion/filling and desiccation. Grain development begins with fertilization followed by a period of rapid cell division and differentiation into the endosperm, embryo and testa. The endosperm cells then expand and begin to accumulate large quantities of starch and protein. Finally, protein and starch deposition cease, the grains undergo a period of maturation and rapidly lose moisture, and the endosperm tissue undergoes apoptosis.

## 3. Effects of environment on the timing of grain development

Understanding how environmental treatments affect the timing of developmental processes in the grain provides an essential framework for determining molecular changes that occur as a result of environment. Several recent controlled environment studies, each comparing a number of different environmental treatments, illustrate how high temperatures and drought accelerate grain development.

Altenbach et al. (2003) evaluated grain development in the spring wheat cv. Butte 86 under three different temperature regimens. They defined physiological and molecular transition points that allowed them to demonstrate that high temperatures and high temperatures combined with drought advanced and compressed the timing of key events during grain development. Under each regimen, the onset and cessation of protein and starch accumulation, the time of maximum water content, maximum dry weight and harvest maturity and the onset of apoptosis were used as developmental benchmarks. The time from anthesis to harvest maturity spanned 44 days under a 24/17 °C day/night regimen, 35 days under a 37/17 °C regimen and 26 days under a 37/28 °C regimen (Fig. 1A). The imposition of drought stress under a 37/17 °C regimen further shortened the duration of grain development from 35 to 28 days. The application of post-anthesis fertilizer affected the accumulation of protein in the grain, but did not influence the duration of grain development under any of the temperature regimens.

Shah and Paulsen (2003) compared grain development in the spring wheat cv. Len under three temperature regimens with and without drought stress applied from one week after anthesis to maturity. As observed in the previous study, increased temperatures decreased the duration of grain development. The time from anthesis to harvest maturity was 47 days under a 15/10 °C regimen, 31 days under a 25/20 °C regimen and 23 days under a 35/30 °C regimen when plants were well watered (Fig. 1B). Drought also shortened grain development, but had the most dramatic effect under the low temperature regimen. The duration of grain filling was reduced to 26 days under a 15/10 °C regimen, 24 days under a 25/20 °C regimen and 21 days under a 35/30 °C regimen under drought conditions.

While the previous studies applied environmental treatments from anthesis to harvest maturity, Gooding et al. (2003) evaluated the effects of drought stress applied during specific stages of grain development. The winter wheat cv. Hereward was subjected to drought stress from 1 to 14 days post-anthesis (DPA), 15 to 28 DPA and 29 to 42 DPA at 23/15 °C, corresponding roughly to the cell division, cell expansion/grain filling and maturation phases, respectively, and the time to 37% moisture content was measured. The effects of drought on the timing of grain development were most pronounced when the stress occurred during the first 14 days after anthesis (Fig. 1C). When drought was combined with a 28/20 °C heat treatment from 15 to 28 DPA, the effects were additive. High temperatures shortened the time to the end of grain filling by 4.5 days relative to the 23/15 °C regimen and water stress reduced it by another 1.1 days.

Changes in the timing of grain development in response to environmental factors have also been documented using

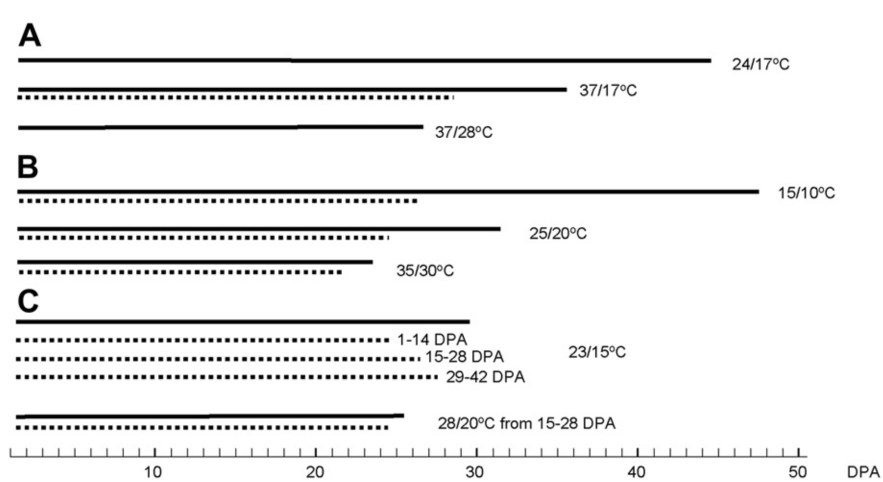


**Fig. 1.** Duration of grain development under different temperature and water regimens. In each panel, solid lines denote grain development with adequate water and dashed lines denote grain development under drought conditions. Temperature and drought treatments were applied from A) anthesis to maturity B) one week after anthesis to maturity or C) various 13-day periods during grain development. The times from anthesis to harvest maturity are shown in panels A and B while the times to 37% moisture content are indicated in panel C. Data in panel A is summarized from Altenbach et al. (2003), B from Shah and Paulsen (2003), and C from Gooding et al. (2003).