



Critical Reviews in Food Science and Nutrition

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/bfsn20>

Stress-Induced Changes in Wheat Grain Composition and Quality

M. Ashraf^a

^a University College of Agriculture, University of Sargodha , Sargodha , 40100 , Pakistan

Accepted author version posted online: 24 May 2013. Published online: 28 Feb 2014.

To cite this article: M. Ashraf (2014) Stress-Induced Changes in Wheat Grain Composition and Quality, Critical Reviews in Food Science and Nutrition, 54:12, 1576-1583, DOI: [10.1080/10408398.2011.644354](https://doi.org/10.1080/10408398.2011.644354)

To link to this article: <http://dx.doi.org/10.1080/10408398.2011.644354>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

Stress-Induced Changes in Wheat Grain Composition and Quality

M. ASHRAF

University College of Agriculture, University of Sargodha, Sargodha 40100, Pakistan

Abiotic stresses such as drought, salinity, waterlogging, and high temperature cause a myriad of changes in the metabolism of plants, and there is a lot of overlap in these changes in plants in response to different stresses such as drought and salinity. These stress-induced metabolic changes cause impaired crop growth thereby resulting in poor yield. The metabolic changes taking place in several plant species due to a particular abiotic stress have been revealed from the whole plant to the molecular level by researchers, but most studies have focused on organs such as leaf, stem, and root. Information on such stress-induced changes in seed or grains is infrequent in the literature. From the information that is available, it is now evident that abiotic stress can induce considerable changes in the composition and quality of cereal grains including those of wheat, the premier staple food crop in the world. Thus, the present review discusses how far different types of stresses, mainly salinity, drought, high temperature, and waterlogging, can alter the wheat grain composition and quality. By fully uncovering the stress-induced changes in the nutritional values of wheat grains it would be possible to establish whether balanced supplies of essential nutrients are available to the human population from the wheat crop grown on stress-affected areas.

Keywords Abiotic stresses, salinity, drought, waterlogging, high temperature, wheat flour quality, grain starch, grain protein, nutrients

INTRODUCTION

Stressful environments such as drought, salinity, waterlogging, extremes of temperature, deficiency or excess of mineral nutrients, and ozone, cause a multitude of changes in the metabolism of plants, although these changes overlap considerably in plants in response to different stresses. These metabolic changes certainly lead to impaired growth and hence poor yield. The metabolic changes taking place in different plants due to a particular stressful environment have been revealed to a great extent by the researchers working from whole plant to the molecular level, but most studies have been carried out on leaf, stem, and root. However, information on such stress-induced changes in seed/grains cannot be frequently obtained from the literature. The rationale of assessing the stress tolerance mechanism in different plant parts excluding seed or grains seems to be plausible as the plant has to sustain itself and grow well under stress conditions so as to produce reasonable biomass and seed or grain yield. Due to this reason, the premier focus of research

in most studies on plant stress tolerance has been on uncovering metabolic changes taking place in other parts of a plant thereby ignoring elucidation of stress-induced changes taking place during seed development and affecting seed composition. For example, it has been noted that the early pollen development stage in most cereals is highly sensitive to abiotic stress (Dolferus et al., 2011). The impairment in this early reproductive phase may lead to improper grain development and hence considerable fluctuations in the components of grains. However, there are a few earlier studies which indicate that subjecting crops to different types of stress affects the level of several compounds within grains. For example, in triticale (*Triticum* × *Secale*), grain protein was negatively related to the rainfall that occurred during the entire crop growth period (Garcia del Moral et al., 1995). This was ascribed to water deficit induced reduction in starch accumulation as well as grain yield during the grain filling stage. Similarly, while investigating the effect of drought simulated by a senescing agent (KI) on triticale grain composition, Fernandez-Figares et al. (2000) reported that grain dry weight, carbohydrates, and protein decreased considerably due to KI application. This may have forced the grain to acquire carbohydrates produced before anthesis.

Address correspondence to University College of Agriculture, University of Sargodha, Sargodha 40100, Pakistan. E-mail: ashrafbot@yahoo.com

Heat stress can also cause considerable changes in grain composition. While assessing the effect of high temperature on the grain composition and quality of bread (*Triticum aestivum*) and durum (*Triticum turgidum*) wheats, Corbellini et al. (1997) observed that high-temperature application at all grain filling stages induced changes in the rheological properties. For example, a consistent increase in soluble polymeric proteins and low molecular weight gliadins, and a contrasting decrease in insoluble polymeric proteins were observed following heat shock treatment. Like drought and heat stress, salinity is also known to alter the grain composition of wheat. For example, in durum wheat salinity stress increased grain protein content by 18%, wet gluten by 3%, and dry gluten by 8% (Houshmand et al., 2005).

All the above reports clearly show that stress can induce considerable changes in wheat grain composition. Thus, the present review discusses how far different types of stresses mainly salinity, drought, high temperature, and waterlogging can alter the wheat grain composition and quality. By determining the stress-induced changes in the nutritional values of wheat grains it would be possible to ascertain whether balanced supplies of essential nutrients are available to the human population using grains of wheat crop grown in stress-affected regions.

WHEAT GRAIN COMPOSITION

The wheat grain comprises three parts, bran (outer layer), endosperm (site of most food reserves), and germ (embryo). The main constituent of endosperm is starch which varies from 60 to 75% on a dry weight basis. The protein content of wheat grain (dry) falls within 10–18%. The most common protein fractions are albumins (water soluble due to being low molecular weight), globulins (water insoluble due to being relatively high molecular weight), gliadins (monomeric), and glutenins (polymeric). Both latter fractions are of high molecular weight and comprise about 75% of the total grain protein. Gliadins are further categorized into α , γ , and ω units, whereas glutenins occur in low and high molecular weight subunits (Flagella et al., 2010). Dough elasticity and extensibility, the rheological properties, mainly depend on glutenin content.

Grain lipid content is around 1.5% which contains the essential fatty acids in varying amounts. For example, high amount of linoleic acid (C18:2) but low levels of palmitic acid (C16:0) and oleic acid (C18:1) are present in the wheat grain fat (Cornell, 2003). Minerals in the wheat grain are also around 1.5%, although like many other cereals wheat grain is deficient in some minerals including Fe, Zn, Se, Ca, and Mg (Šramková et al., 2009). In fact, Fe and Zn deficiency has been considered as the major risk factor for human health (Welch and Graham, 2004). The wheat grain is deficient in the essential amino acids lysine, tryptophan, and threonine (Bicar et al., 2008).

Despite a variety of desirable nutrients, there are some undesirable compounds such as phytates (Lopez et al., 2001). It is now evident that most of the grain inorganic phosphorus is stored as phytate, which forms complexes with inorganic nutri-

ents such as Fe^{3+} , Zn^{2+} , Ca^{2+} , and Mg^{2+} thereby impairing their bioavailability. Wheat grain is also a fair source of important vitamins such as thiamin, niacin, and riboflavin (<http://www.wheatfoods.org/UrbanWheatfield-29/Index.htm>). It also contains tocopherols (tocopherols and tocotrienols) which are generally referred to as vitamin E.

WHEAT FLOUR/DOUGH QUALITY PARAMETERS

Composition of wheat flour depends on the grain composition of types of wheat or cultivar. Dough rheology is, in fact, the assessment of stress and strain in dough because the dough transforms into visco-elastic mass after mixing with water. However, the main rheological parameters commonly measured are absorption/hydration of flour, and resistance, extensibility, mixing tolerance and stability of the dough. In addition, physical parameters such as particle size distribution and starch damage are also important to determine the quality of grains, particularly the degree of milling. Falling number, a chemical parameter, is also an important parameter which indicates sprout damage (α -amylase activity), though it does not directly measures the enzyme activity. It indicates the extent to which starch has been hydrolyzed in the grain. High falling number indicates good viscosity and processing characteristics, whereas a low falling number reflects a high quantity of amylases naturally present in the grain. Sedimentation value (Zeleny value) is a measure of the baking quality of flour, which depends on the wheat protein (gluten) content. Higher Zeleny values indicate the slower rate of sedimentation and relates to a higher content and quality of gluten. Wheat with Zeleny values ranging from 22 to 30 mL is generally considered of good quality (<http://foodquality.wfp.org/Glossary/tabid/200/Default.aspx?PageContentMode=1>; Rakszegi et al., 2008). A typical flour possesses the following characteristics: absorption (at 14% moisture content), 61.8%; tolerance index, 475 BU; stability, 17 minutes; falling number, 497 seconds; particle size, 76.6 μm ; starch damage, 9.8% (<http://www.iaom.info/asia/04reddygenmills.pdf+wheat+dough+quality+parameters&cd=1&hl=en&ct=clnk&gl=pk>).

EFFECTS OF ENVIRONMENTAL STRESSES ON WHEAT GRAIN COMPOSITION AND QUALITY

Environmental stresses cause impairment in the processes involved in plant growth and development. These impaired processes not only cause reduction in seed yield, but also bring about alteration in composition and quality of seed or grain. However, different types of stresses and their intensity have differential effects on grain composition and quality.

Drought

Shortage of water imposes multiple effects on plant growth and development. The major effects of drought stress on plants

are osmotic effects, imbalance in uptake and accumulation of nutrients, hormonal imbalance, and oxidative stress caused by the production of reactive oxygen species such as superoxide, singlet oxygen, hydroxyl radical, and hydrogen peroxide. All these drought-induced effects not only cause stunted growth and reduced seed yield, but also bring about considerable changes in grain composition and quality. For example, while assessing the influence of drought stress on the grain quality of some salt-tolerant genotypes of durum wheat, Houshmand et al. (2005) reported that although drought stress decreased significantly grain weight and test weight of the genotypes, it resulted in increased SDS sedimentation volume (an indicator of bread-making quality) by 31%, protein content by 12%, wet gluten content by 20%, and dry gluten content by 20%.

From the previous section, it is evident that carbohydrates are the major constituents of wheat grains. However, changes in the proportions of specific carbohydrates significantly affect the quality of grain composition and these changes frequently take place due to a variety of environmental factors. For example, drought stress is known to reduce contents of carbohydrates including sucrose and starch in cereal grains, the latter being 65% of cereal kernels (Jenner, 1994; Barnabás et al., 2008). Starch content in cereal grains is positively correlated with sucrose content and the activity of sucrose synthase (SuSy) and other related enzymes (Yan et al., 2008). Thus, starch accumulation depends on sucrose content and activities of the enzymes involved in starch synthesis (Balla et al., 2011). Labuschagne et al. (2009) reported that dough quality depends on the amylose-to-amylopectin ratio.

It is now known that the process of starch accumulation in cereal grains is mediated by enzymes including SuSy, ADP-glucose pyrophosphorylase (AGPase), soluble starch synthase (SSS), and starch branching enzyme (Morell et al., 2001; Barnabás et al., 2008). The activities of these enzymes have been correlated with starch synthesis in wheat grains under water-limited conditions. For example, Ahmadi and Baker (2001) reported that drought-induced reduction in AGPase activity was the main cause of cessation in grain growth under severe water deficit conditions.

Generally, it is known that drought-induced reduction in crop grain yield is associated with an increase in protein content (Garrido-Lestache et al., 2005; Dupont et al., 2006; Flagella et al., 2010). A study carried out in several regions of Spain showed moisture stress caused by low rainfall resulted in a significant increase in protein content in the grains of durum wheat (Rharrabti et al., 2003). Another study conducted by Garrido-Lestache et al. (2004) in southern Spain showed maximum values of alveograph index *W* (which indicates the quality of finished products made from cereal flour) during the period when rainfall was lowest.

Although drought stress applied at any developmental stage adversely affects the grain composition and quality, in view of a number of reports it is evident that drought stress application, particularly at the grain filling stage has a substantial effect on wheat grain quality. Although it might appear intuitively that

drought stress should have an adverse effect on grain quality, this is certainly not always the case, especially if the stress is applied at the grain filling stage. For example, drought stress applied during wheat grain development considerably reduced the SDS sedimentation volume and this was found to be mainly dependent on the timing of stress imposition (Gooding et al., 2003).

The major gliadin and glutenin storage proteins are vital for maintaining the rheological properties, with glutenins particularly responsible for the elasticity and extensibility of wheat flours (Shewry et al., 1995). In some field trials conducted in Victoria, Australia, Panozzo et al. (2001) found no difference between irrigated and nonirrigated treatments in terms of the gliadin/glutenin ratio, although the fraction of polymeric proteins was higher in the nonirrigated treatment (Table 1). Similar results were observed by Daniel and Triboï (2002) in bread wheat when they observed no change in the rate of accumulation of soluble and insoluble proteins per degree day, although the polymer insolubilization started earlier due to water-deficit conditions. Contrarily, Singh et al. (2008) reported a substantial effect of drought stress imposed during the grain filling stage on the contents of different dimethyl formamide-soluble and insoluble proteins.

Changes in flour protein composition are reported to be linked to increases in protein content (Saint Pierre et al., 2008). The proportion of monomeric proteins increases more than that of the polymeric proteins to cause an increase in flour protein content. For example, Hajheidari et al. (2007) reported a progressive increase in the amount of gliadins in three bread wheat cultivars with a consistent increase in protein content under water-deficit conditions (Table 1). The same authors detected 121 proteins in seeds, which showed considerable changes in response to the stress, of which they were able to identify only 57 proteins. Most of the identified proteins were found to be linked to thioredoxin, showing the association between drought and oxidative stress. In another study with wheat (Fan et al., 2004) drought stress applied at the postanthesis stage significantly increased grain gliadin content. Drought stress also increased the wet and dry gluten content in the grains.

From the above contrasting reports, it can be inferred that the varying effects of drought stress on wheat grain quality and protein composition depend on the variation in environmental conditions in which the studies had been conducted, intensity of stress, development stage at which stress was imposed, different protocols employed to appraise grain or flour quality, and different wheat varieties.

Salinity

Salinity of soil or water imposes effects on plants similar to those imposed by drought stress except with an additional salinity-induced effect, i.e., specific ion effect. However, all salinity-induced effects on plants cause growth suppression thereby reducing seed/grain yield. Although the effects of

Table 1 Effect of stress environments on wheat grain composition and quality

Stress	Stress-induced changes in wheat grain	Reference
Drought	Grain weight decreased; SDS sedimentation increased by 31%, protein content by 12%, wet gluten content by 20%, and dry gluten content by 20%	Houshmand et al., 2005
	Cessation in grain growth due to reduced AGPase activity Grain protein content increased Maximum values of alveograph index <i>W</i> SDS sedimentation decreased No change in gliadin/glutenin ratio	Ahmadi and Baker, 2001 Rharrabti et al., 2003 Garrido-Lestache et al., 2004 Gooding et al., 2003 Panozzo et al., 2001; Daniel and Triböi, 2002
Salinity	Total grain proteins and gliadins increased Grain gluten and gliadin contents increased	Hajheidari et al., 2007 Fan et al., 2004
	Grain weight decreased; SDS sedimentation volume increased by 66%, protein content by 18%, wet gluten content by 3%, and dry gluten content by 8%. A marked decrease in grain protein and starch content; perturbation in grain glutenin/gliadin and amylase/amylopectin ratios	Houshmand et al., 2005 Zheng et al., 2009a
Heat stress	A salt tolerant cultivar of winter wheat resisted changes in pasta quality parameters such as water absorption, wet gluten content, dough development time and dough stability time at lower levels of salinity, i.e. up to 100 mM NaCl, whereas in contrast, in a salt sensitive cultivar all the pasta quality attributes were adversely affected at both low and high salinity levels	Zheng et al., 2009b
	In wheat plants subjected to 24/17°C transcripts of gluten appeared 8 d after anthesis, whereas in those subjected to relatively high temperature (37/17°C) accumulation of the gluten transcripts started earlier but continued for a relatively shorter period	Altenbach et al., 2002
	Down-regulation of a number of proteins involved in starch metabolism and the induction of heat shock proteins (HSPs) in wheat grains	Majoul et al., 2004
	A reduction in the glutenin/gliadin ratio takes place due to heat stress which has a negative effect on flour quality	Bencze et al., 2004
	Exposure of developing wheat seed to heat stress after anthesis showed a considerable change in the relative proportions of glutenins (both high and low molecular weight) and gliadins as well as a change in the quality of the flour	Stone, 2001
	A 3–5 fold increase in the quantity of different HSPs occurred in the developing seeds of bread and durum wheats under heat stress	Perrotta et al., 1998; Treglia et al., 1999
	Over-expression of HSP70 and HSP26 proteins in durum wheat grains due to heat stress	Laino et al., 2010
	High temperature (37/17°C) applied to wheat plants from anthesis to maturity resulted in a marked reduction in starch accumulation period (21 days earlier than in the control) in developing wheat grains	Hurkman et al., 2003
Waterlogging	Caused a marked reduction in grain yield and protein content. In contrast, total grain starch and amylose content increased significantly in plants subjected to waterlogged conditions. However, waterlogging resulted in reduced processing quality of the wheat grain.	Fan et al., 2004
	Caused a substantial decline in grain protein and starch content	Zheng et al., 2009a

salinity stress on plants have been explored substantially, not much information on salinity-induced effects on grain composition and quality can be deciphered from the literature. A few studies reported in the literature clearly show that salinity can bring about considerable change in wheat grain composition and quality. For example, Houshmand et al. (2005) investigated the effect of salinity stress on the grain quality of some salt-tolerant genotypes of durum wheat. They found a significant reduction in grain weight and test weight of the genotypes under saline stress. Furthermore, they observed a salinity-induced increase in SDS sedimentation volume by 66%, protein content by 18%, wet gluten content by 3%, and dry gluten content by 8%. In contrast, Zheng et al. (2009a) reported a marked decrease in grain protein and starch content due to salt stress. They also reported a perturbation in the grain glutenin/gliadin and amylase/amylopectin ratios due to saline stress (Table 1).

In another study, while assessing the effects of salt stress on the grain composition of plants of two winter wheat cultivars, Zheng et al. (2009b) also reported a salt-induced increase in grain protein in both cultivars differing in salt tolerance, al-

though there was a marked salinity-induced decrease in flour yield in both cultivars. It was interesting to note that the salt tolerant cultivar (DK 961) resisted salt-induced changes in pasta quality parameters such as water absorption, wet gluten content, dough development time, and dough stability time at lower levels of salinity, i.e., up to 100 mM NaCl, whereas in contrast, in the salt sensitive cultivar (JN17), all the pasta quality attributes were adversely affected at both low and high salinity levels of the growth medium (Table 1). This shows that salt tolerant cultivars can maintain their grain yield as well as the grain quality under saline conditions. Thus, salt tolerant wheat cultivars are the best option for attaining high grain yield and better quality on salt affected fields.

Heat Stress

In terms of temperature requirement wheat is categorized into winter (low-temperature requirement) and spring (mild-temperature requirement) wheat. The spring wheat requires

much lower temperature than does the rice for its normal growth and development. Heat stress is considered more injurious to plants compared to other abiotic stresses including salinity, drought, and nutrient deficiency/excess. For wheat, high temperature becomes especially injurious at the reproductive stage, resulting in a markedly reduce grain yield and poor grain quality. In addition, wheat plants exposed to extremely high temperatures can undergo a sudden death.

For end-use quality, proteins are the key components of wheat grains. The gluten proteins, glutenins and gliadins, play an important role to maintain the quality of dough (Balla et al., 2011). Although albumins and globulins have little effect on the dough quality, they are nutritionally very important because of the fact that most of them contain essential amino acids for human nutrition (Gupta et al., 1992; Balla et al., 2011). Despite the fact that cereal grain composition, including that of wheat, depends principally on the genetic make-up of the cultivar or line, it is also considerably influenced by environmental factors (Triboi et al., 2003). Evidence shows that the heat-induced changes in protein composition under high-temperature conditions could be mainly due to change in the amount of N accumulated during grain filling (Triboi et al., 2003). This statement is supported by a study in which postanthesis application of N fertilizers mitigated the effect of heat stress on the storage protein composition of wheat grain (as described in Dupont and Altenbach, 2003). For example, in wheat plants subjected to 24/17°C (day and night) and well supplied with water and nutrients, transcripts of gluten appeared 8 days after anthesis, whereas in wheat plants subjected to relatively high-temperature (37/17°C) accumulation of the gluten transcripts started earlier but continued for a relatively shorter period (Altenbach et al., 2002). This shows that kernel development speeds up under high-temperature regimes (Barnabás et al., 2008). Majoul et al. (2004) have noted the down-regulation of a number of proteins involved in starch metabolism and the induction of heat shock proteins (HSPs) in wheat grains (Table 1).

The accumulation of proteins active in biosynthesis and metabolism results in shifts in favor of storage proteins and of those involved in defense against biotic and abiotic stress factors. Specific protein responses depend on whether high temperature is experienced during the early or middle phase of grain filling (Hurkman et al., 2009). It is widely reported that the protein content of grains exposed to heat stress after anthesis rose significantly in response to the stress (Balla and Veisz, 2007; Labuschagne et al., 2009). Despite the heat-induced increase in grain protein content, a reduction in the glutenin/gliadin ratio takes place (Table 1), which has a negative effect on flour quality (Bencze et al., 2004).

High temperature is capable of causing substantial changes in the accumulation level of gluten proteins during grain filling. For example, while assessing the effects of heat shock during grain filling on the grain composition of bread and durum wheat Corbellini et al. (1997) reported that continuous exposure of plants of both wheat types to very high temperatures from 27 days after pollination to maturity adversely affected the

rheological properties of the wheat flour including a significant change in the level of protein aggregation. For example, increase in the intensity of heat stress resulted in increased soluble polymeric proteins and low molecular weight gliadins, whereas in contrast, it caused a marked decrease in insoluble polymeric proteins. Thus, heat stress generally favors the synthesis of gliadins, but glutenin decreases. Heat stress-induced reduction in glutenins and a relative increase in gliadins in the grains have been widely reported in wheat grains and are considered potential indicators of poor bread making quality under high temperatures (Bencze et al., 2004; Spiertz et al., 2006; Laino et al., 2010; Balla et al., 2011).

Bread-making quality of wheat flour primarily depends on the presence of high-molecular-weight glutenin in grains (MacRitchie, 1984; Laino et al., 2010). For example, exposure of developing wheat seed to high temperature after anthesis caused a considerable change in the relative proportions of glutenins (both high and low molecular weight) and gliadins as well as a change in the quality of the flour (Stone, 2001). However, the maintenance of wheat flour quality depends on the temperature to which developing wheat seed has been subjected. For example, it has been reported that a moderately high temperature during the grain filling stage enhanced the flour protein content, which is beneficial for making good quality bread (Stone, 2001). There is a general consensus that wheat bread-making quality improves at growth temperatures up to 30°C (Randall and Moss, 1990) and decreases above 35°C (Blumenthal et al., 1993; Stone and Nicolas, 1995). However, HSPs which occur in the developing grains due to heat stress have long ago been suggested to decrease bread-making quality (Blumenthal et al., 1990; Majoul et al., 2004). A 3 to 5-fold increase in the quantity of different HSPs has been observed in the developing seeds of bread and durum wheats under high-temperature stress (Perrotta et al., 1998; Treglia et al., 1999). Similarly, and more recently, Laino et al. (2010) have reported the overexpression of HSP70 and HSP26 in durum wheat grains due to heat stress (Table 1). However, the role of HSPs in bread-making quality is still not clear.

High temperature has also been reported to cause an adverse effect on cereal grain carbohydrates. For example, Hurkman et al. (2003) reported that high temperature (37/17°C) applied to wheat plants from anthesis to maturity resulted in a substantial decline in the starch accumulation period (21 days earlier than in the control) in developing wheat grains compared with plants subjected to a milder temperature (24/17°C). Furthermore, high temperatures have been reported to increase starch content, whereas modest temperatures decrease it in wheat flour, which adversely affects bread quality (Williams et al., 1994). Of the four enzymes involved in starch synthesis reported earlier, AGPase and SSS have been reported to be the most sensitive to heat stress, particularly at temperatures above 34°C (Hurkman et al., 2003).

In view of the number of reports cited above, it is clear that the effects of temperature on wheat grain composition and quality have been relatively more investigated than those of other

stresses. This is because the wheat crop from different regions of the world has been grown at considerably different temperatures and there has been an economic imperative to understand this factor. As has been noticed, a slight change in temperature may have a large effect on the wheat grain quality and composition. It is crucial to have the knowledge to be able to take measures to ameliorate this problem and maintain high-quality wheat grain and flour production.

Waterlogging

Waterlogging of soil can be due to a variety of factors including climate change, deforestation of hilly areas, intensive irrigation of cultivable lands, and poor soil porosity. One of the prominent effects of waterlogging is the depletion of oxygen from the rhizosphere which is the primary cause of damage to the roots and then the shoots of most plants (Vartapetian and Jackson, 1997). Furthermore, waterlogging also causes the accumulation of gases such as ethylene and CO₂, which can ultimately impede root growth and function (Arshad and Frankenberg, 1990) thereby adversely affecting shoot growth and hence yield. In fact, when grain/seed yield of a crop is affected, the quality and composition of the seed is also altered. The support for this statement can be reinforced by some reports. For example, while assessing the effect of waterlogging on some wheat cultivars grown in southern China, Fan et al. (2004) reported that waterlogging caused a substantial reduction in grain yield and protein content. In contrast, total starch and amylose content increased markedly in grain from plants grown under waterlogged conditions (Table 1). However, waterlogging resulted in reduced processing quality of the wheat grain. Similarly, Zheng et al. (2009a) reported that waterlogging resulted in decreasing protein and starch content in the grains of the two wheat cultivars, Yangmai 12 and Huaimai 17, but with different effects on the grain proteins (Table 1). Waterlogging caused an increase in grain glutenin and albumin in Huaimai 17, but a decrease in globulin and gliadin contents, as well as a decrease in all protein components in cv. Yangmai 12.

Since waterlogging-induced effects on wheat grain composition and quality have so far been examined in a very few studies, it is not yet possible to draw sound inferences on these effects. This merits further consideration to uncover the putative role of waterlogging in altering the wheat grain composition and quality.

Conclusions and Future Prospects

Most crops including wheat are prone to a variety of natural or man-made environmental stresses. All these stresses alter physiological and biochemical processes in plants which ultimately lead to poor growth and low crop yield. The stress-induced low crop yield particularly in a grain crop like wheat may be due to either low number of grains developed in spikes or reduced

size/weight of grains in the plants subjected to stress. However, in both cases, the processes operative during the grain filling stage, the most crucial stage of grain development, are hampered due to a stress which impede the transport of assimilates to the developing grains. Thus, any type of stress (salinity, drought, extremes of temperature, waterlogging) during the grain filling stage may cause reduced grain yield and hence altered composition and quality of grains.

It is imperative to elucidate the metabolic processes that are functional at the grain filling stage and which are perturbed due to a stress. Furthermore, each type of stress has its specific effects on grain development, altering specific components of the grains. As yet it is not clear which components of wheat grains are specifically affected by a specific stress because in all four stresses described in the present review all major grain components such as carbohydrates, protein, and fat undergo changes due to each type of stress. Further studies need to be conducted to ascertain whether an individual stress has a specific or general effect on grain composition.

From a number of reports, it is evident that the proportions of different types of carbohydrates and proteins in wheat grains are affected to a varying extent due to the nature, intensity, or duration of a stress. However, from the existing literature it is not yet clear to what extent a specific stress and its intensity or duration can alter the contents of different types of carbohydrates, protein or fat.

In most cases, the wheat crop is exposed naturally to a combination of different types of abiotic stresses. For example, in most arid and semi-arid regions drought, salinity and high temperature occur concurrently and pose an integrative harmful effect to the wheat crop. Under such circumstances it is not easy to identify the harmful effects of an individual stress on grain composition and quality.

Based on temperature and day-length requirements, wheat is categorized into winter and spring types. Compared with spring wheat, the winter type can tolerate temperatures below freezing but the opposite is true for the response of the two types to high temperatures. Thus, in winter wheat a slight increase in temperature may have a deleterious effect on grain quality. However, from the existing literature it is not yet apparent to what degree grain composition and quality is altered at the same temperature in these two different types of wheat.

The information on the effects of different stresses on the parameters of wheat grain composition and flour/dough quality described earlier is not much. For example, how far the four different stresses alter vitamin and mineral content of wheat grain as well as flour/dough and its effect on human nutrition and health is not much known from the literature. Thus, there are major gaps in this area of research from the nutritional perspective which need to be filled with more research in this area.

From the very few studies reported here on the effects of different abiotic stresses on wheat grain composition and quality, it is not possible to answer the question posed in the introduction section of the present review that whether or not balanced

supplies of essential nutrients are available to the human population using grains of wheat crops grown in stress-affected regions. Some reports clearly show that composition of wheat grain and its processing properties undergo changes under stress environments, but whether all these changes really affect the nutritional quality, and are these changes sufficient to affect the human diet are not explicit due to lack of appropriate literature.

The effects of different types of stresses on wheat plant growth and physiology have been extensively studied, as is evident from a plethora of the literature available at all sources. In contrast, there are only a few reports on the effects of these stresses on wheat grain composition and quality, as cited in the earlier sections of this paper. This comparison clearly shows that the area of research concerning the effects of different abiotic stresses on wheat grain quality and composition has been of lesser priority to researchers.

Currently, a few efforts have been made wherein advanced molecular tools have been employed to uncover the stress-induced alterations in cereal grains including those of wheat. Such studies could provide detailed information on the underlying mechanisms involved in reducing yield and hampering grain quality due to stress conditions.

Since studies exploring the stress-induced effects on wheat grain composition and quality are few, so it is not yet possible to draw sound inferences on any changes in wheat grains due to different types of stresses. Thus, this area of research merits the future focus of researchers.

ACKNOWLEDGMENTS

The author is grateful to Dr. Meriel Jones, Institute of Integrative Biology, University of Liverpool, UK, for critically reading the manuscript.

REFERENCES

- Ahmadi, A. and Baker, D. A. (2001). The effect of water stress on the activities of key regulatory enzymes of the sucrose to starch pathway in wheat. *J. Plant Growth Regul.* **35**:81–91.
- Altenbach, S. B., Kothari, K. M. and Lieu, D. (2002). Environmental conditions during wheat grain development alter temporal regulation of major gluten protein genes. *Cereal Chem.* **79**:279–285.
- Arshad, M. and Frankenberger, W. T. (1990). Production and stability of ethylene in soil. *Biol. Fert. Soil.* **10**:29–34.
- Balla, K., Rakszegi, M., Li, Z., Békés, F., Bencze, S. and Veisz, O. (2011). Quality of winter wheat in relation to heat and drought shock after anthesis. *Agric. Res. Inst. Hung. Acad. Sci.* **29**:117–128.
- Balla, K. and Veisz, O. (2007). Changes in the quality of cereals in response to heat and drought stress. *Acta Agron. Óváren.* **49**:451–455.
- Barnabás, B., Jäger, K. and Fehér, A. (2008). The effect of drought and heat stress on reproductive processes in cereals. *Plant Cell Environ.* **31**:11–38.
- Bencze, S., Veisz, O. and Bed, Z. (2004). Effects of high atmospheric CO₂ and heat stress on phytomass, yield and grain quality of winter wheat. *Cereal Res Commun.* **32**:75–82.
- Bicar, E. H., Woodman-Clkeman, W., Sangtong, V., Peterson, J. M., Yang, S. S., Lee, M. and Scott, M. P. (2008). Transgenic maize endosperm containing a milk protein has improved amino acid balance. *Transgenic Res.* **17**:59–71.
- Blumenthal, C. S., Barlow, E. W. R. and Wrigley, C. W. (1993). Growth environment and wheat quality: The effect of heat stress on dough properties and gluten proteins. *J. Cereal Sci.*, **18**:3–21.
- Blumenthal, C., Batey, I. L., Wrigley, C. W. and Barslow, E. W. R. (1990). Gliadin genes contain heat-shock elements: Possible relevance to heat-induced changes in grain quality. *J. Cereal Sci.* **11**:185–188.
- Corbellini, M., Canevar, M. G., Mazza, L., Ciaffi, M., Lafiandra, D. and Borghi, B. (1997). Effect of the duration and intensity of heat shock during grain-filling on dry matter and protein accumulation, technological quality and protein composition in bread and durum wheat. *Aust. J. Plant. Physiol.* **24**:245–260.
- Cornell, H. (2003). The chemistry and biochemistry of wheat. In: Bread Making, Improving Quality, p. 31. Cauvain, S. P., Ed., CRC, Woodhead Publishing Limited, Cambridge, England.
- Daniel, C. and Tribou, E. (2002). Changes in wheat protein aggregation during grain development: Effects of temperatures and water stress. *Eur. J. Agron.* **16**:1–12.
- Dolferus, R., Ji, X. and Richards, R. A. (2011). Abiotic stress and control of grain number in cereals. *Plant Sci.* **181**:331–341.
- Dupont, F. M. and Altenbach, S. B. (2003). Molecular and biochemical impacts of environmental factors on wheat grain development and protein synthesis. *J. Cereal Sci.* **38**:133–146.
- Dupont, F. M., Hurkman, W., Vensel, W., Tanaka, C., Kothari, K., Chung, O. and Altenbach, S. (2006). Protein accumulation and composition in wheat grains: Effects of mineral nutrients and high temperature. *Eur. J. Agron.* **25**:96–107.
- Fan, X. M., Jiang, D., Dai, T. B., Jing, Q. and Cao, W. X. (2004). Effects of post-anthesis drought and waterlogging on the quality of grain formation in different wheat varieties. *Acta Phytoecol. Sin.* **28**:680–685.
- Fernandez-Figares, I., Marinetto, J., Royo, C., Ramos, J. M. and Garcia del Moral, L. F. (2000). Amino-acid composition and protein and carbohydrate accumulation in the grain of triticale grown under terminal water stress simulated by a senescing agent. *J. Cereal Sci.* **32**:249–258.
- Flagella, Z., Giuliani, M. M., Giuzio, L., Volpi, C. and Masci, S. (2010). Influence of water deficit on durum wheat storage protein composition and technological quality. *Eur. J. Agron.* **33**:197–207.
- Garcia del Moral, L. F., Boujenna, A., Yanez, J. A. and Ramos, J. M. (1995). Forage production, grain yield and protein content in dual purpose triticale grown for both grain and forage. *Agron. J.* **87**:902–908.
- Garrido-Lestache, E. L., Lopez-Bellido, R. J. and Lopez-Bellido, L. (2004). Effect of N rate, timing and splitting and N type on bread-making quality in hard red spring wheat under rainfed Mediterranean conditions. *Field Crops Res.* **85**:213–236.
- Garrido-Lestache, E. L., Lopez-Bellido, R. J. and Lopez-Bellido, L. (2005). Durum wheat quality under Mediterranean conditions as affected by N rate, timing and splitting, N form and S fertilization. *Eur. J. Agron.* **23**:265–278.
- Gooding, M. J., Ellis, R. H., Shewry, P. R. and Schofield, J. D. (2003). Effects of restricted water availability and increased temperature on the grain filling, drying and quality of winter wheat. *J. Cereal Sci.* **37**:295–309.
- Gupta, R. B., Batey, I. L. and MacRitchie, F. (1992). Relationships between protein composition and functional properties of wheat flours. *Cereal Chem.* **69**:125–131.
- Hajheidari, M., Eivazi, A., Buchanan, B. B., Wong, J. H., Majidi, I. and Salekdeh, G. H. (2007). Proteomics uncovers a role for redox in drought tolerance in wheat. *J. Proteome Res.* **6**:1451–1460.
- Houshmand, S., Arzani, A., Maibody, S. A. M. and Feizic, M. (2005). Evaluation of salt-tolerant genotypes of durum wheat derived from in vitro and field experiments. *Field Crops Res.* **91**:345–354.
- Hurkman, W. J., McCue, K. F., Altenbach, S. B., Korn, A., Tanaka, C. K., Kothari, K. M., Johnson, E. L., Bechtel, D. B., Wilson, J. D., Anderson, O. D. and Dupont, F. M. (2003). Effect of temperature on expression of genes encoding enzymes for starch biosynthesis in developing wheat endosperm. *Plant Sci.* **164**:873–881.

- Hurkman, W. J., Vensel, W. H., Tanaka, C. K., Whitehand, L. and Altenbach, S. B. (2009). Effect of high temperature on albumin and globulin accumulation in the endosperm proteome of the developing wheat grain. *J. Cereal Sci.* **49**:12–23.
- Jenner, C. F. (1994). Starch synthesis in the kernel of wheat under high temperature conditions. *Aust. J. Plant Physiol.* **21**:791–806.
- Labuschagne, M. T., Elago, O. and Koen, E. (2009). The influence of temperature extremes on some quality and starch characteristics in bread, biscuit and durum wheat. *J. Cereal Sci.* **49**:184–189.
- Laino, P., Shelton, D., Finnie, C., De Leonardis, A. M., Mastrangelo, A. M., Svensson, B., Lafiandra, D. and Masci, S. (2010). Comparative proteome analysis of metabolic proteins from seeds of durum wheat (cv. Svevo) subjected to heat stress. *Proteomics* **10**:2359–2368.
- Lopez, H. W., Krespine, V., Guy, C., Messenger, A., Demigne, C. and Remesy, C. (2001). Prolonged fermentation of whole wheat sourdough reduces phytate level and increases soluble magnesium. *J. Agric. Food Chem.* **49**:2657–2662.
- MacRitchie, F. (1984). Baking quality of wheat flours. *Adv. Food Nutr. Res.* **29**:201–277.
- Majoul, T., Bancel, E., Tribol, E., Hamida, J. B. and Branlard, G. (2004). Proteomic analysis of the effect of heat stress on hexaploid wheat grain: Characterization of heat-responsive proteins from non-prolamin fraction. *Proteomics* **4**:505–513.
- Morell, M. K., Rahman, S., Regina, A., Appels, R. and Li, Z. (2001). Wheat starch biosynthesis. *Euphytica* **119**:55–58.
- Panozzo, J. F., Eagles, H. A. and Wootton, M. (2001). Changes in protein composition during grain development in wheat. *Aust. J. Agric. Res.* **52**:485–493.
- Perrotta, C., Treglia, A. S., Mita, G., Giangrande, E. P., Rampino P., Ronga, G., Spano, G. and Marmioli, N. (1998). Analysis of mRNAs from ripening wheat seeds: The effect of high temperature. *J. Cereal Sci.* **27**:127–132.
- Rakszegi, M., Boros, D., Kuti, C., Láng, L., Bedo, Z. and Shewry, P. R. (2008). Composition and end-use quality of 150 wheat lines selected for the HEALTHGRAIN diversity screen. *J. Agric. Food Chem.* **56**:9750–9757.
- Randall, P. J. and Moss, H. J. (1990). Some effects of temperature regime during grain filling on wheat quality. *Aust. J. Agric. Res.* **41**:603–617.
- Rharrabti, Y., Villegas, D., Royo, C., Martos-Núñez, V. and García del Moral, L. F. (2003). Durum wheat quality in Mediterranean environments. II. Influence of climatic variables and relationships between quality parameters. *Field Crops Res.* **80**:133–140.
- Saint Pierre, C., Peterson, C. J., Ross, A. S., Ohm, J. B., Verhoeven, M. C., Larson, M. and Hoefer, B. (2008). Winter wheat genotypes under different levels of nitrogen and water stress: Changes in grain protein composition. *J. Cereal Sci.* **47**:407–416.
- Shewry, P. R., Tatham, A. S., Barro, F., Barcelo, P. and Lazzeri, P. (1995). Biotechnology of breadmaking: Unraveling and manipulating the multi-protein gluten complex. *Nat. Biotechnol.* **13**:1185–1190.
- Singh, S., Singh, G., Singh, P. and Singh, N. (2008). Effect of water stress at different stages of grain development on the characteristics of starch and protein of different wheat cultivars. *Food Chem.* **108**:130–139.
- Spiertz, J. H. J., Hamer, R. J., Xu, H., Primo-Martin, C., Don, C. and Van der Putten, P. E. L. (2006). Heat stress in wheat (*Triticum aestivum* L.): Effects on grain growth and quality traits. *Eur. J. Agron.* **25**:89–95.
- Šramková, Z., Gregová, E. and Šturdík, E. (2009). Chemical composition and nutritional quality of wheat grain. *Acta Chim. Slov.* **2**:115–138.
- Stone, P. J. (2001). The effects of heat stress on cereal yield and quality. In: *Crop Responses and Adaptation to Temperature Stress*, pp. 243–291. Basra, A. S., Ed., Food Products Press, Binghamton, NY.
- Stone, P. J. and Nicolas, M. E. (1995). Effect of timing of heat stress during grain filling on two wheat varieties differing in heat tolerance. I. Grain growth. *Aust. J. Plant Physiol.* **22**:927–934.
- Treglia, A., Spano, G., Rampino, P., Giangrande, E., Nocco, G., Mita, G., Di Fonzo, N. and Peppotta, C. (1999). Identification by in vitro translation and Northern blot analysis of heat shock mRNAs isolated from wheat seeds exposed to different temperatures during ripening. *Cereal Sci.* **30**:33–38.
- Tribol, E., Martre, P. and Trioi-Blondel, A. M. (2003). Environmentally-induced changes of protein composition for developing grains of wheat are related to changes in total protein content. *J. Exp. Bot.* **54**:1731–1742.
- Vartapetian, B. B. and Jackson, M. B. (1997). Plant adaptations to anaerobic stress. *Ann. Bot.* **79**(Suppl. A):3–20.
- Welch, R. M. and Graham, R. D. (2004). Breeding for micronutrients in staple food crops from a human nutrition perspective. *J. Exp. Bot.* **55**:353–364.
- Williams, M., Shewry, P. R. and Harwood, J. L. (1994). The influence of the “greenhouse effect” on wheat (*Triticum aestivum* L.) grain lipids. *J. Exp. Bot.* **45**:1379–1385.
- Yan, S. H., Yin, Y. P., Li, W. Y., Li, Y., Liang, T. B., Wu, Y. H., Geng, Q. H. and Wang, Z. L. (2008). Effect of high temperature after anthesis on starch formation of two wheat cultivars differing in heat tolerance. *Acta Ecol. Sinica* **28**:6138–6147.
- Zheng, C. F., Jiang, D., Dai, T. B., Jing, Q. and Cao, W. X. (2009a). Effects of salt and waterlogging stress at post-anthesis stage on wheat grain yield and quality. *Ying Yong Sheng Tai Xue Bao* **20**:2391–2398.
- Zheng, Y., Xu, X., Li, Z., Yang, X., Zhang, C., Li, F. and Jiang, G. (2009b). Differential responses of grain yield and quality to salinity between contrasting winter wheat cultivars. *Seed Sci. Biotechnol.* **3**:40–43.