Review Article

Bread and durum wheat tolerance under heat stress: A synoptical overview

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Abstract: Temperature and nutrition are two major components of environmental variation that provide significant limitations to a successful crop production. Increasing temperatures during grain filling interacts, at a metabolic level, with growth duration and filling rates, as well as with grain maturity and quality. At a nutritional level, temperature is also linked to uptake and translocation rates to roots and shoots tissues, which determines crop production. Nevertheless, these interacting effects are closely related to *Triticum* species and genotypes tolerance to heat stress, particularly during grain filling. In this context, the interactions of heat stress on the nutrient status and on the photosynthetic performance becomes determinant to the mobilization of photoassimilates to the grain and on the definition of its quality. In this review, an overview is presented on the tolerance of bread and durum wheat to heat stress, considering mineral nutrition, cellular membrane thermotolerance, the photosynthetic functioning, grain filling rate and duration and ultrastructure and biochemical traits of bread and durum wheat grains.

Keywords: Bread wheat, durum wheat, heat stress, thermotolerance.

ورقة استعراضية
قمح الخبز والقمح الخشن المتحمل للاجهاد الحرارى: لمحة شاملة

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الملخص: تعتبر درجة الحرارة والتغذية من المكونات الأساسية للتنوع البيئي الذي يوفر قيود مؤثرة على النجاح إنتاج المحاصيل الزراعية. ومع زيادة درجات الحرارة خلال فترة امتلاء الحبوب التي تتفاعل على مستوى التمثيل الغذائي ومعدلات النمو وكذلك مع نضج الحبوب والجودة الكلية. وعلى المستوى الغذائي ترتبط درجات الحرارة مع الامتصاص ومعدل إعادة تمركز في القطاع الجذري والخضري والتي تحدد الإنتاجية الكلية للمحاصيل. ومع ذلك تعتبر هذه التأثيرات المرتبطة بشكل كبير بالبناء على أنواع الأنماط الجينية (Triticum) والأصناف المتحملة للإجهاد الحراري وخاصة خلال فترة امتلاء وتعبئة الحبوب وفى هذا السياق نجد أن هذه التفاعلات بين الإجهاد الحراري على المواد الغذائية وعلى البناء الضوئي يصبح محددا مستوى المحفزات الضوئية وتعبئة الحبوب وتحديد نوعيته . وفى هذه الورقة الاستعراضية لمحة عامة لمدى تحمل قمح الخبز والقمح الخشن للإجهاد الحراري آخذا في الاعتبار التغذية المعدنية ومدى تحمل الأغشية الخلوية للإجهاد الحراري والتمثيل الضوئي والأداء ومعدل امتلاء الحبوب ومدتها والصفات البيوكيميائية من قمح الخبز والقمح الخشن.

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Introduction

When water is not a limiting factor, *Triticum* productions with late sowing (i.e., with high temperatures in the end of the cycle) have lower yields, mostly as a result of heat stress during grain filling (Maçãs et al., 2000). It has been reported (Sofield et al., 1977) that, during grain filling, increasing temperatures (between 15/10ºC and 21/16ºC day/night temperatures) counterbalances the diminished growth duration, augmenting the filling rate (although, only triggering a small variation of the grain weight). Caley et al. (1990) and Jenner (1994) further confirmed these data, and Shpiler and Blum (1986), working with field trials, also reported that grain maturity develops earlier, producing smaller and shrivelled grains, in heat stressed genotypes. Moreover, the heat stress effects after anthesis are complex since integrate wheat responses to periods with moderate high (25/32ºC) temperatures (Chinoy, 1947; Wardlaw et al., 1989) and plant behaviours to short periods with high (exceeding 32ºC) temperatures (Randall and Moss, 1990; Blumenthal et al., 1991; Stone and Nicolas, 1994). In this context, photosynthesis plays a pivotal role in grain production, as it determines, at different levels, the mobilization of photoassimilates (Enami et al., 1994; Sharkova and Bubolo, 1996; Çjánek et al., 1998; Yamane et al., 1998; Bukhov et al., 1999; Mohanty et al., 2002; Kouřil et al., 2004; Schrader et al., 2004; Sharkey, 2005).

It has long been known (Spiertz, 1974) that with high temperatures after anthesis, increasing leaf senescence is coupled to a significant increase in the respiration rates in the grain. Such a response, depending on its extent, might trigger decreased carbohydrate availability (Thornley, 1971), justifying the decline in grain weight. Jenner (1991a), further supported by Nicolas et al. (1984) in their work on sucrose concentrations (in the grain and endosperm) made a similar proposal, concluding that after anthesis heat stress affects wheat grain quality through changes in protein composition. During grain filling, under heat stress, the decreased grain weight (and therefore, the yield reduction) also diminishes wheat flour production (Guedira et al., 2002).

In this way, gluten strength and flour quality for breadmaking (for example, protein concentration), although highly linked to the genotype (Branlard and Dardevet, 1985), are also affected by environmental conditions (Rharrabti et al., 2001).

Additionally, considering that plant growth is metabolically driven, the general assumption is that the adjustment between the nutrient status and high temperature becomes collaterally over expressed if a feed-back inhibition can develop.

An overview is presented on tolerance and sensitivity of bread and durum wheat to heat stress, considering mineral nutrition, cellular membrane thermotolerance, photosynthetic functioning, grain filling rate and duration after anthesis and ultrastructure and biochemical traits of bread and durum wheat grains.

1. Mineral nutrition

During grain filling, in heat stressed bread wheat genotypes, Ca assimilation to the shoots and spikes can increase (Dias et al., 2009d), possibly accumulating in the citosol, alleviating heat injury (Biyaseheva et al., 1993; Palta, 1996; Gong et al., 1998; Jiang and Huang, 2001), increasing cellular survival (Bamberg et al., 1998; Gong et al., 1998) and limiting oxidative damage (Larkindale and Knight, 2002), namely Chl photodestruction, as also found by Jiang and Huang (2001), working with heat stressed *Festuca arundinacea* L. and *Poa pratensis* L. In bread wheat genotypes, Ca accumulation also seems to be linked with a higher tolerance to heat stress, possibly because this nutrient can shield chlorophylls from photodestruction (Jiang and Huang, 2001; Dias et al., 2009d) and maintain stomata functioning (Webb et al., 1996; Hare et al., 1998), thus attenuating the heat stress effects through transpiration (Palta, 1996). Nevertheless, although Ca bonds the phosphate and carboxylate groups of phospholipids and proteins, at the membranes surface of plant cells (Caldwell and Haug, 1981; Legge et al., 1982), this nutrient accumulation is not coupled with the maintenance of the selectivity

of membrane permeability (Dias et al., 2009d), as higher tolerance to heat stress in bread wheat follows a different pattern relatively to the Ca metabolisms in sugar beet and potato (Cooke et al., 1986; Coria et al., 1998). Calcium and Mg might also regulate cellular pH and cation-anion stability (Marschner, 1995), yet during plant growth of some plant species, Mg^{2+} uptake can be depressed by Ca^{2+} (Marschner, 1995), unbalancing photosynthetic carboxylations (Günther, 1981; Bergmann, 1992; Schoefs and Bertrand, 1997) and isoprenoids (Jiang and Huang, 2001) accumulation. In this context, Mg^{2+} strongly interacts with nucleophilic ligands (*i.e.*, phosphoryl groups) through ionic bonding (Günther, 1981), but under heat stress, although might stabilize the covalent bonds of chlorophylls, its depression might limit the synthesis of this molecule (Marschner, 1995). Nevertheless, it has been reported (Dias et al., 2009d) that, in the particular case of the life wheat cycle of most genotypes, Mg uptake is not significantly depressed by Ca and, therefore, an antagonistic interaction between these nutrients accumulations in the shoots is not expected to develop. Moreover, shoot Mg accumulation might display a synergistic pattern with chlorophylls accumulation during grain filling (Bergmann, 1992; Schoefs and Bertrand, 1997; Dias et al., 2009d), but at maturity, as the rate of Mg translocation from the roots tends to decrease (Dias et al., 2009d), the inhibition of chlorophylls accumulation might occur (Dias et al., 2009d). In durum wheat, further supporting a different extent of tolerance (Al-khatib and Paulsen, 1989; Maçãs et al., 1999, 2000; Dias et al, 2009d; Dias and Lidon, 2009a), at maturity Ca and Mg shoot accumulation in sensitive genotypes to heat stress might parallel with a diminishing chlorophyll content and a decreased net carbon assimilation rate (Dias et al., 2009d). This sensitivity to heat stress, follows a pattern previously described for *Pisum sativum* (Haldimann and Feller, 2005), being the inhibition of photosynthesis possibly due to efficiency losses in the use of photochemical energy and in the acyclic electron transport

(Dias et al., 2009d; Dias et al., 2010). Likewise, heat stress tolerance in bread and durum wheat, can be associated to the maintenance or an increasing stomatal conductance to water that favours the net carbon assimilation rates, in a process that is tied with the levels of Ca in the shoot (Dias et al., 2009d), probably coupling cellular turgescence (Hare et al., 1998) to an osmotic adjustment modulated by the symplast and apoplast Ca^{2+} levels (Palta, 1996). Furthermore, under heat stress such increased stomatal conductance to water is usually linked to a higher transpiration rate in tolerant genotypes (Dias et al., 2009d), allowing a better leaf cooling process that implicate evaporation (Fischer et al., 1998).

Although Na is not essential for plant species (Subbarao et al., 1999, 2000) it stimulates plant growth (Subbarao et al., 2003; Takahashi and Maejima, 1998), since it has a high capacity to exchange K^+ (Subbarao et al., 2003). Nevertheless, as most plants have a high selectivity to K^+ uptake (in the interface soil/roots), and translocation to the shoots (Subbarao and Johansen, 2002), the levels of Na are relatively low in grains (Subbarao et al., 2000; Subbarao and Johansen, 2002). The contents of Na, in the shoots and spikes, usually are considerably higher in the durum wheat genotypes (Dias et al., 2009c), but this effect is most effective in the shoot, since the mobilization of Na to the reproductive structures in wheat grain is low (Watt and Merrill, 1975; Dias et al., 2009c). This effect expresses a lower rate of Na accumulation independent of the growth of individual leaves and probably is regulated by some root process, and a compartmentation within leaves, which enhances the ability to tolerate high concentrations of Na in leaves (Schachtman and Munns, 1992; Dias et al., 2009c). When bread and durum wheat genotypes are submitted to heat stress after anthesis, facing a consistent period of moderate high temperatures, the levels of Na in the roots remain similar, relatively to the control, in both plant species, but expressing different genome characteristics (Schachtman et al., 1991; Dias

et al., 2009c). Indeed, although the ability to limit the accumulation of Na in leaves may be an important mechanism of salt tolerance, because the excessive accumulation of Na causes the premature senescence of leaves (Schachtman and Munns, 1992), in the heat stressed wheat species, during grain filling and at maturity, the levels of Na might became higher in durum wheat (Dias et al., 2009c).

Within plant tissues, the accumulation of K^+ is required for pH stabilization of the cytoplasm, to increase the osmotic potential in the vacuoles (Marschner, 1995), and to promote cellular growth, which determines higher yields (Lindhauer, 1983). Additionally, the inorganic P can also stimulate plant growth, as it regulates carbon flux between starch and sucrose biosynthesis (Terry and Rao, 1991; Usuda and Shimogawara, 1991) and phosphate distribution of photosynthates among tissues (Rao and Terry, 1989; Qiu and Israel, 1994). In non stressed wheat, as a general pattern, the concentrations of K decrease during the growth cycle in all tissues (Lásztity, 1987; Bergmann, 1992; Dias et al., 2009c). Moreover, under heat stress it has been reported that the levels of K might increase significantly in the roots and shoots, during grain filling and at maturity (Dias et al., 2009c). In general although heat stress affect the root uptake and shoot translocation kinetics of Na, P and K, tolerance to this stress does not seem to be linked to a selective accumulation of Na, K and P in durum and bread wheat.

Copper and Zn are microelements with important physiological functions in plants that act synergistically in wheat (Khurama and Chatterjee, 2000), but at high concentrations become toxic, leading to physiological and morphological disturbances and, eventually to a decreased yield (Agrawal and Sharma, 2006). Independently of heat stress tolerance, Cu concentrations in roots, during booting and grain filling, usually remain similar in all wheat genotypes, but at maturity bread and durum wheat genotypes might reveal significant differences (Dias and Lidon, 2009b). This effect can be linked to the ionic status of Cu that *in vivo* might occur with different oxidation states. During booting, Cu contents

in the shoot usually vary 5-9 μg/g (Bergmann, 1992; Dias and Lidon, 2009b) for *Triticum*. At maturity, the concentrations of Cu in the shoots of wheat, in control conditions, can be lower relatively to heat stressed plants (Davis et al. 1984; Dias and Lidon, 2009b). Under heat stress, the levels of Cu might increase in different plant tissues (Kabata-Pendias and Pendias, 1992; Garnett and Graham, 2005; Dias and Lidon, 2009b) without reaching the threshold of toxicity (20-30 μg/g). In bread wheat genotypes, the levels of Zn in the roots, which are mostly absorbed in the dicationic form, might be higher than those of durum wheat (Dias and Lidon, 2009b). This trend might not occur in the shoots, being a consistent drop usually detected during the plants cycle, which eventually became a sign of membrane permeability alteration (Pearson and Rengel, 1994; Dias and Lidon, 2009b). As a general trend, the concentration of Zn in the roots of both *Triticum* species is affected during all the life cycle by heat stress, probably indicating an higher membrane potential (Marschner, 1995; Dias and Lidon, 2009b) and being, in spite of some controversy (Moore, 1972), most likely metabolically controlled. Moreover, in the spike, heat stress does not affect significantly the levels of Zn, persisting asymptotic plant concentrations (Wheeler and Power, 1995; Dias and Lidon, 2009b). During booting, probably indicating a high capacity to synthesize stable complexes, the concentration of Zn usually does not change significantly between durum wheat genotypes, and in bread wheat genotypes only the shoots levels of Zn can vary, although persisting within the limits of non-phytoxicity (Marschner, 1995; Dias and Lidon, 2009b). Considering bread and durum wheat biomasses, under control conditions, the accumulation of Cu and Zn tends to increase from booting to grain filling, further indicating as already pointed, a high mobility (Marschner, 1995). In this period, among the genotypes, these nutrients can be translocated from the roots to the shoots in a similar proportion, being the accumulation rate in the spike higher from booting onwards (Dias and Lidon, 2009b). This pattern implicates an inhibitory effect on the excretion of Cu from root cells

into the xylem and phloem saps (Loneragan, 1981). Moreover, under heat stress, the lower mobility of Cu (Dias and Lidon, 2009b) is coupled to a slight drift from the aerial part of the plant to the spike (Kabata-Pendias and Pendias, 1992). In the heat stressed genotypes, the accumulation ratio of Cu in the spike can be higher (Dias and Lidon, 2009b) being, during grain filling, the decreased accumulation of Cu in the roots linked with a more efficient Cu translocation to the shoots (Dias and Lidon, 2009b). The ratio of total Zn in the grain of all the heat stressed wheat genotypes can be affected (Dias and Lidon, 2009b), mostly due to a remobilization from the shoot (Pearson and Rengel, 1994; Garnett and Graham, 2005; Dias and Lidon, 2009b), which might influence its protein composition (Peck at al., 2008; Dias et al., 2009a), or to a higher uptake and translocation by the roots and from the spike to the grain (Dias and Lidon, 2009b).

Iron and Mn are essential for plant growth being required appropriate contents at intracellular level, with ratios between them from 1.5 to 2.5 (Bergmann, 1992; Alvarez-Tinaut et al., 1980), due to its impact for the photosynthetic electron transfer, reduction of nitrites and sulphates, chlorophyll synthesis and on the nucleic acid metabolism (Boardman, 1975; Nicholas, 1975; Mengel and Kirkby, 1978; Price et al., 1972; Wild and Jones, 1988). However, under stress conditions, Fe and Mn uptake by the roots and the translocation to the shoot of most plant species shows opposite effects, leading to nutritional unbalancing (Alvarez-Tinaut et al., 1980; Brown and Devine, 1980; Terry, 1979). Under heat stress, during grain filling, the concentrations of Fe in the culm and leaves of bread wheat genotypes might decrease (Davis et al., 1984; Dias et al., 2009e). Concerning to durum wheat, with high temperature, the Fe levels of shoots displayed a different behaviour, as during grain filling Fe might increase. The heterogeneous patterns displayed by Fe accumulation in the shoot tissues point the occurrence, at a different extent, of a limiting factor linking the intensive growth of these cereals to the heat stress (Kabata-Pendias and Pendias, 1992). Eventually, the availability of citrates chelates, required for Fe transport in the xylem (Kabata-Pendias and Pendias, 1992) might change in heat stressed genotypes, becoming restricted at maturity. On the other hand, during grain filling, the contents of Mn, in the roots of several bread wheat genotypes might decrease with high temperatures (Dias et al., 2009e), while the opposite is observed in the durum wheat genotypes (Dias et al., 2009e). These effects suggest that Mn uptake is metabolically controlled (being the high temperature an interacting factor), apparently in a quite similar pathway to that of other divalent cations species such as Mg^{2+} and Ca^{2+}. The amount of Fe and Mn in the grain depends on the levels redistributed by the roots during grain development and the amount redistributed from the vegetative tissue via phloem (Garnett and Graham, 2005). In this context, considering the Fe/Mn antagonistic interactions (Alvarez-Tinaut *et al.*, 1980, Bergmann, 1992) the heat stress effects on shoot Mn content might be coupled to the changes on Fe contents (what is observed also in the grain filling stage). In non-stress conditions, during grain filling and at maturity, the Fe/Mn ratios usually show only a slight unbalance for Fe (Dias et al., 2009e). Yet, under stress this limiting factor increased during grain filling (Dias et al., 2009e), whereas became attenuated at maturity (*ca.* Fe/Mn ratios of about 0.8 and 1.3, respectively).

2. Cellular membrane thermotolerance

Cellular membranes are dynamic structures formed essentially by lipids and proteins, supporting many biophysical and biochemical traits, with emphasis in regulation and transport of ions and enzymatic activity. These permeable selective barriers allow the development of many biological responses, but they also are a main target of environmental stresses, therefore having an essential role in the adaptation to adverse conditions (Routaboul et al., 2000). As membrane fluidity is largely determined by the lipid class

composition, fatty acids unsaturation and chain length (Harwood, 1998; Sung et al., 2003), the induced changes by temperature in membrane fluidity are an immediate consequence of thermal stress, representing a potential place of perception and/or damage (Horváth et al., 1998). In this context, under heat stress (more than 35ºC), membrane fluidity changes, lipid peroxidation increases and membrane selectivity is often impaired (Saadalla et al., 1990; Shanahan et al., 1990; Bukhov et al., 1999). Accordingly, polyunsaturated fatty acid oxidation, particularly in the thylakoids (that constitute about 60–80 % of the total cellular membranes in the mesophyll tissues – Webb and Green, 1991), might induce a peroxidative chain reaction that increases ethylene synthesis (Lidon and Henriques, 1993) and minimizes thylakoid membrane functionality (Halliwell and Gutteridge, 1989; Mishra and Singhal, 1992). Nevertheless, during growth, genotypes tolerant to high temperatures can promote a higher fatty acid saturation and increase their polar lipids content enhancing membrane stability, particularly in the chloroplast lamellae (Berry and Björkman, 1980).

In *Triticum* species (Dias et al., 2009b) heat stress might also affect membrane stability, increasing the electrolyte leakage as a result of a loss of membrane selectivity. During grain filling, this effect can also be associated to the increased levels of lipid peroxidation (Jiang and Zhang, 2002; Balota et al., 2004; Dias et al., 2009b), coupled to higher ethylene synthesis. Nevertheless, at the end of grain filling, ethylene synthesis tends to decrease, which results in increased levels of linoleic (C 18:2) and linolenic (C 18:3) fatty acids and a lower oxidation rate.

In the heat-stressed tolerant bread wheat genotypes, acyl lipids peroxidation and ethylene might not change (Dias et al., 2009b), which supports the maintenance of membrane stability and fatty acids contents (Saadalla et al., 1990; Shanahan et al., 1990; Lidon and Henriques, 1993; Bukhov et al., 1999) in the middle term of grain filling. This high temperature-mediated effect can also be linked to the maintenance of a high content of C 18:2 (Dias et al., 2009b) which, according to

Halliwell and Gutteridge (1989) and Mishra and Singhal (1992), further justifies the maintenance of the photosynthetic light reactions at this stage. Indeed, galactolipids are the main lipid components representing 60 % (Harwood, 1998) to 80 % (Williams, 1998) of thylakoids, being the unsaturated fatty acids essential for the physical properties of the chloroplast lamellae (Quinn et al., 1989; Wada et al., 1994). Accordingly, thermostability of photosystem II is closely linked to fatty acid saturation of the chloroplast lamellae (Berry and Björkman, 1980; Thomas et al., 1986; Horváth et al., 1987; Mishra and Singhal, 1992). In this respect, the physical dissociation of its components is linked to an increasing permeability that modifies thylakoid stacking (Gounaris et al., 1984; Xu et al., 1995) and further changes fatty acid unsaturation during growth (Wada et al., 1994).

In durum wheat genotypes, heat stress induces lipid peroxidation, but that may not be attributed to the oxidation of C18:2 and C18:3, which somewhat can even increase (Dias et al., 2009b). A decreased peroxidative chain reaction of polyunsaturated fatty acid residues, also contribute to a decrease of ethylene synthesis (Lidon and Henriques, 1993) and to maintain membrane selectivity under heat stress (Dias et al., 2009b). As these fatty acids are also components of phospholipids and galactolipids that participate in the organization of the photosynthetic electron transport reaction centres (El-Shintinawy, 1999), photosynthetic electron transport might be shielded from thermal damage. Accordingly, in tolerant durum wheat genotypes, the high temperature exposed plants can show a decreased lipid peroxidation level, which contribute to the stability of membrane selectivity. However, that effect implicates slight reductions of C18:3 and C18:1t in the middle term of grain filling, which therefore implies a decreased membrane fluidity (Kunst et al., 1989; Murakami et al., 2000; Dias et al., 2009b). High temperatures might further increase fluidity of membrane lipids (Raison et al., 1982, Gounaris et al., 1984) promoting functional impairments and even thermal damages in the photosystem II (Berry and Björkman, 1980; Yordanov et al, 1986). In

this way, the increase of polyunsaturated fatty acids saturation possibly represents an adaptive advantage of tolerant genotypes under high temperature conditions, as it increases heat thermal stability (Raison et al., 1982; Thomas et al., 1986), favouring the photosynthetic light reactions (Berry and Björkman, 1980; Kunst et al., 1989) which probably allow thylakoid reorganization.

3. Photosynthetic functioning

In many plant species submitted to moderate heat stressed (35-45ºC) photosynthesis might become inhibited without damaging photosystem II (Schrader et al., 2004). Yet, when temperatures rise to ca. 45ºC (Wardlaw et al., 1989; Çjánek et al., 1998), the thermal damage of the photosynthetic oxygen evolving complex (Nash et al., 1985; Enami et al., 1994) affects the electron transport (Bukhov et al., 1990; Mohanty et al., 2002; Kouřil et al., 2004), increasing chlorophyll a fluorescence (Bukhov et al., 1990; Havaux 1992; Bukhov and Mohanty, 1993). In this context, heat stress affects the yield of the minimal fluorescence (Berry and Björkman, 1980; Smillie and Hetherington, 1983; Laash, 1987; Krause and Weis, 1991), which implicates the photochemical efficiency of photosystem II and the relative contributions of the non-photochemical quenching (Smillie and Hetherington, 1983; Laash, 1987). An increase of the minimal fluorescence has been attributed to the physical separation between the reaction centres of photosystem II and the associated antennae, resulting in energy transfer blocking (Bukhov et al., 1990). The non-photochemical quenching can result from several mechanisms associated to excess energy dissipation, essentially as heat, but can also include redistribution processes of excitation energy between photosystems II and I (Schreiber et al., 1986). Thus, a decrease of the non-photochemical quenching indicates a reduction of the transthylakoid proton gradient, resulting in a decreasing efficiency of photosystem II or in an alteration of the photosynthetic electron transport chain. Moreover, the increase of the non-photochemical quenching indicates that

ATP synthesized in the photochemical reactions is not being used in the Calvin cycle. The Stern-Volmer non-photochemical quenching coefficient is further associated to a non-radiant dissipation energy process that might shield photosystem II against over-excitation (Demmig-Adams, 1990).

As reported by Al-Khatib and Paulsen (1990), photosynthesis inhibition might vary significantly among wheat species, yet when heat stressed bread and durum wheat genotypes are compared, in general, the photosynthetic performance of durum wheat displays an higher tolerance (Dias et al., 2010). In general, in the heat stressed *Triticum*, a reversible photosynthetic inhibition and an alteration of the chloroplast structure (namely, grana stacking) has been reported (Sharkova and Bubolo, 1996). Under moderate high temperatures a thylakoid permeability deviation might also prevail, affecting the proton gradient (Bukhov et al., 1999; Schrader et al., 2004), the cyclic photophosphorylation and, eventually, the b6/f cytochrome complex (Sharkey, 2005). The structural changes in the thylakoids (Baker and Horton, 1987) and the inhibition of the photosynthetic electron transport (Krause and Weis, 1991) can, thereafter, decrease maximum photochemical efficiency of photosystem II essentially because of the variable fluorescence decay (Mishra and Singhal, 1992), resulting in a maximum fluorescence reduction and a gradual augmentation of minimal fluorescence (Al-Khatib and Paulsen, 1989; Genty et al., 1989). At a physiological level, these patterns point a reduction extend of the photochemical efficiency of photosystem II, resulting of an inefficient energy transfer from the light harvesting complex of photosystem II to the reaction centres. Eventually being a regulatory response, the inhibition of CO_2 assimilation can also occur synergistically with the photochemical reactions (Feller et al., 1998; Law and Crafts-Brandner, 1999; Salvucci and Crafts-Brandner, 2004a, b).

In the particular case of the heat stressed bread wheat, the decreasing of the net carbon assimilation rate might not be limited by the

internal CO_2 concentration (Dias et al., 2010). In this context, a significant increase of chlorophyll and carotenoids levels, coupled to the significant decrease of minimum and maximum fluorescence, might develop, pointing a higher efficiency of the excitation energy transfer from the photosystem II antennae, namely at the physical separation between the reaction centres and the associated antennae (Bukhov et al., 1990); the significant decrease of the non-photochemical quenching, Stern-Volmer non-photochemical quenching coefficient and the energy dependent quenching also can develop, indicating that the ATP synthesized in the photochemical reactions is being used in the Calvin cycle, whereas the related transthylakoid proton gradient decreases, shielding the photosystem II antennae from over-excitation (Dias et al., 2010). As in wheat genotypes stomata closure might not occur, the net carbon assimilation rate stability might prevail (Dias et al., 2010) and, in these circumstances, the variation of the stomatal conductance and transpiration rates further suggested that stomata aperture decrease leaves temperature through a cooling process implicating evaporation (Fischer et al., 1998; Dias et al., 2010). In general, in the heat stressed bread wheat genotypes, two patterns can develop (Dias et al., 2010): the inhibition of net carbon assimilation rate is not linked to stomata limitations and triggers an increasing inhibition of CO_2 assimilation, whereas the light reactions of the photosynthetic metabolism have an high efficiency energy transfer between the reaction centres of photosystem II and the associated antennae, but the transthylakoid proton gradient decreases, limiting ATP utilization in the Calvin cycle, justifying the increasing of the internal CO_2 concentration; the photosynthetic apparatus of is mostly limited, with a decreasing efficiency of the photochemical functioning of photosystem II, resulting of an inefficient energy transfer to the reaction centres, without inhibiting the net carbon assimilation rate.

In heat stressed durum wheat the variations of net CO_2 assimilation in most cases are not significant (Dias et al., 2010). Expressing different genomic characteristics, the variation of the internal CO_2 concentration in durum wheat, associated to the inhibitions of the net carbon assimilation rate and stomatal conductance, indicates that CO_2 concentrations limits the photosynthetic functioning. Moreover, the minimum fluorescence does not vary significantly and the maximum photochemical efficiency of photosystem II further indicates that the photosystem II functioning is only slightly affected by heat. In this context, during grain filling of the durum wheat genotypes, the alteration of maximum photochemical efficiency of photosystem II, due to a reduction of the variable fluorescence (Dias et al., 2010), probably results in an increasing energy dissipation (i.e., thermal energy) mediated by photoprotective mechanisms. The decrease of the non-photochemical quenching, in the heat stressed durum wheat, also points a reduction of the transthylakoid proton gradient linked to a decreasing efficiency of photosystem II. At this stage, the significant inhibition of the Stern-Volmer non-photochemical quenching coefficient further indicates that the thermal dissipation is lower, suggesting a decreasing rate of energy dissipation in the antennae of photosystem II, minimizing the protection of the photosynthetic apparatus (Demmig-Adams et al., 1996; Lu et al., 2001) and allowing an over-excitation of photosystem II reaction centres (Dias et al., 2010). In general, under heat stress, the photosynthetic performance of durum wheat genotypes might reveal three different parameters (Dias et al., 2010): stomatal conductance increases, but the net carbon assimilation rate and the internal CO_2 concentration are not affected; the opposite occurs for the internal CO_2 concentration and stomatal conductance without affecting net photosynthesis; considering that, under heat stress, the inhibitions of the photosynthetic light reactions might occur mostly at the photosystem II level, a significant fraction of the energy transfer of the light harvesting complex associated to photosystem II to the reaction centres is blocked.

4. Grain Filling Rate and Duration

During the crops growth cycle, the optimal mean temperature might vary between 15 and 18ºC (Chowdhury and Wardlaw, 1978),

with 20ºC being the best temperature for grain filling (Jenner, 1991b; Dupont and Altenbach, 2003). Several studies conducted in Australia and USA (Wardlaw and Wrigley, 1994) further indicated that, each year, crop production decreases about 10–15 %, mostly because of high temperatures during anthesis. It was also pointed out (Wardlaw et al., 1989) that a global reduction in crop production of about 3–4% occurs when the mean temperature increases by 1ºC above the optimum value. In this context, even when water is not a limiting factor, *Triticum* productions with late sowing in Mediterranean environments (thus, with high temperatures in the end of the cycle) have lower yields, mostly as a result of heat stress during grain filling (McDonald et al., 1983; Maçãs et al., 1999, 2000; Tewolde et al., 2006). Following this pattern, Sofield et al. (1977) showed that, during grain filling, high temperatures (between 15/10 and 21/16ºC) counterbalance a diminished duration of growth, by increasing the filling rate (triggering only a small variation on the grain weight). Yet, with higher temperatures, ranging between 21/16 and 30/25ºC, these authors also pointed that the grain filling rate did not display a compensatory increase when correlated with its duration period (thus, inducing a significant grain weight reduction at maturity). Wiegand and Cuellar (1981) and Jenner (1994) further confirmed these data, whereas Shpiler and Blum (1986) working with field trials also reported that grain maturity develops earlier, producing smaller and shrivelled grains, in heat stressed genotypes. Furthermore, it has long been known (Stoy, 1965; Spiertz, 1974) that with high temperatures after anthesis, increasing leaf senescence is coupled to a significant development of the respiration rates in the grain. These patterns, according to its extent, might trigger a decreasing carbohydrate availability for the grain (Thornley, 1971), justifying its weight decay. The experiments of Wardlaw et al. (1980), Jenner (1991a,b) and Nicolas et al. (1984) in their study on sucrose concentrations (in the grain and in the

endosperm), also attained these proposals, concluding that after anthesis heat stress affects wheat grain quality, reduces starch content and changes protein composition. In this context, it has also been reported that day/night temperatures, higher than optimal, ranging between 18/ 13 and 21/16ºC (Sofield et al., 1977; Chowdhury and Wardlaw, 1978) can decrease its size and the number of starch granules (Hoshikawa, 1962).

Variation for tolerance to high temperature stress among genotypes has been reported in wheat (Wardlaw et al., 1989; Viswanathan and Khanna-Chopra, 2001; Tahir and Nakata, 2005). During growth, the duration of the phenological phases of *Triticum* species reveal significant differences. Under controlled conditions, anthesis might develop later in the bread wheat genotypes, but the end of grain filling can take place earlier in comparison to durum wheat (Figure 1) (Dias and Lidon, 2009a). High temperatures significantly can shorten the grain filling period in all the bread and durum wheat genotypes, being significant the interaction of each genotype with temperature (Sofield et al., 1977; Chowdhury and Wardlaw, 1978; Wiegand and Cuellar, 1981; Shpiler and Blum, 1986; Gibson and Paulsen, 1999; Dias and Lidon, 2009a). The number of grains per spike usually remains constant among heat stressed and control genotypes, which is a well-known effect (Gibson and Paulsen, 1999; Dias and Lidon, 2009a). As seen by scanning electron microscopy, the increasing temperatures (from 25/14 to 31/20ºC), during grain growth, decreases grain size and promotes grain shrinking, thus implicating a reduction of individual grain weight (Dias and Lidon, 2009a). The individual grain weight became increasingly affected by high temperatures in both durum and bread wheat. Yet, in the heat stressed, genotypes tolerance and sensitivity is expressed by different grain weight, and therefore yield, mostly due to a significantly different potential grain weight and grain filling rate (Dias and Lidon, 2009a).
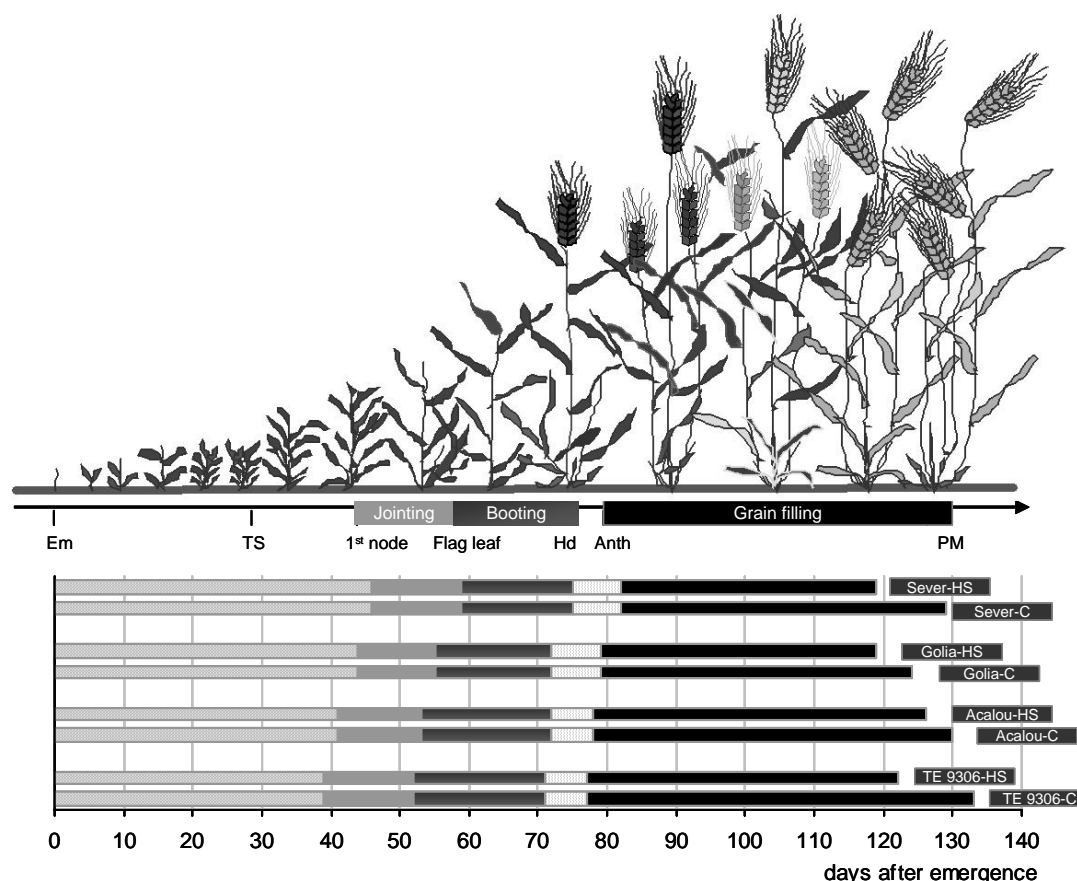
Figure 1. Duration of the phenological phases during the growth cycle for the different genotypes in both temperature situations. Sever and Golia – Bread Wheat; Acalou and TE9306-Durum Wheat. Em = emergence; TS = terminal spikelet; Hd = heading; Anth = anthesis; PM = physiological maturity; C = control; HS = heat stress.

Under controlled conditions, among *Triticum* genotypes, the differences found in the grain yield cannot be determined by the same yield components (Sofield et al., 1977; Dias and Lidon, 2009a). When significantly higher total grain weight/spike prevails, this trait can result essentially in a superior individual grain weight (Dias and Lidon, 2009a).

In the genotypes of durum wheat, the difference of total grain weight/spike can mostly result in variations in the number of grains/spike but not in the individual grain weight (Dias and Lidon, 2009a). Moreover, under heat stress, during grain growth, between bread and durum wheat, the differences in the yield/spike might result in the interactions between high temperatures and individual grain weight (Chowdhury and Wardlaw, 1978; Wardlaw et al., 1989; Tashiro and Wardlaw, 1990; Dias and

Lidon, 2009a). Additionally, the highly significant temperature x genotype interactions migh also suggests the occurrence of genetic variability to high temperature (Wardlaw et al., 1989; Hunt et al., 1991; Dias and Lidon, 2009a).

In bread and durum wheat tolerant genotypes to heat stress, the grain weight during the grain growth period, until maximum weight, can be significantly higher and, additionally, the difference of the mean grain filling rate can also be superior (Dias and Lidon, 2009a). Moreover, between anthesis and physiological maturity, in all the heat stressed wheat genotypes, the adjusted grain growth curves (in growing degree days) usually shows that grain weight remains lower when compared with the control genotypes (Dias and Lidon, 2009a). In spite of the high genetic variability

between *Triticum* genotypes (Bruckner and Frohberg, 1987; Darroch and Baker, 1990; Hunt et al., 1991; Dias and Lidon, 2009a), increasing temperature after anthesis might reduce the duration of the grain filling period (Dias and Lidon, 2009a). The mean grain filling rate estimated by the best fitting curves, and on duration basis (Julian days), does not increase significantly with high temperatures, but the patterns revealed among the genotypes can be different (Figure 2) (Dias and Lidon, 2009a).

In heat stressed *Triticum* species, probably the different grain filling rates between bread and durum wheat can also explain the weight variations. Indeed, Wardlaw and Moncur (1995) and (Dias and Lidon, 2009a) stated that the most tolerant cultivars (to heat stress during grain filling) had an increased grain filling rate.

Under heat stress, at the end of the growth cycle, the grain filling duration might decrease (Dias and Lidon, 2009a). As this trait is largely affected by high temperatures at the end of the growth, the final grain weight might become proportional to its filling rate (Bruckner and Frohberg, 1987; Wardlaw and Moncur, 1995). Accordingly, Wiegand and Cuellar (1981) and Dias and Lidon (2009a), indicated that genotype determines grain filling rate, whereas environmental factors, such as temperature, affect the duration of grain filling period (Panozzo and Eagles, 1999; Calderini and Reynolds, 2000; Dias and Lidon, 2009a). In general within bread and durum wheat genotypes, tolerance and sensitivity to heat stress is probably related with a pattern of grain filling including a fast grain growth (during a shorter growth period) that might contribute to a higher grain weight in environments with high temperatures after anthesis (Dias and Lidon, 2009a). In bread and durum wheat, in Mediterranean environments, Giunta and Motzo (2005) also found that higher grain weights are associated to higher dry matter accumulation rates. Additionally, the reports of Bruckner and Frohberg (1987),

Motzo et al. (1996) and Dias and Lidon (2009a) for durum and bread wheat in the Mediterranean environment, pointed significant synergistic correlations between the grain filling rates and the grain weight, but not between the grain filling duration and grain weight. In triticale, Santiveri et al. (2002) also described a similar relation type between the grain filling components and the grain weight.

The interactions between the grain filling components and grain weight can show a synergistic relation between the filling rate and the grain weight. Considering that these interactions were found in control and heat stress treatments, these data indicate that the genotypes with a high potential grain filling rate might reach a superior grain weight. Under heat stress, these interactions associated to a significant decrease in the grain filling rate, further reinforce the importance of the high grain filling rates in environments with high temperatures after anthesis. Several authors (Nicolas et al., 1984; Wardlaw and Moncur, 1995; Motzo et al., 1996; Calderini et al., 1999) described that longer grain filling periods are associated with smaller grain filling rates, when the duration of grain filling is measured in days.

The differences among *Triticum* genotypes, implicating heat stress sensibility, can also be associated to their grain filling rates. Indeed, the most tolerant genotypes to high temperatures show an increased grain filling rate with temperature (Hunt et al., 1991; Wardlaw and Moncur, 1995). Whan et al. (1996) also suggested that the grain filling rate might be a selection criterion to increase the grain weight and *Triticum* yield under Mediterranean conditions. This factor might be more important than the grain filling duration (as this is more affected by the environment). Therefore, the selection of genotypes showing a higher grain filling rate might be an efficient strategy to increase the grain weight (Bruckner and Frohberg, 1987), particularly for regions

having a grain filling duration restricted by high temperatures.

In the control treatment, the potential grain weight is strictly associated to the grain weight at physiological maturity and to the maximum grain weight, considering the grain filling period duration in Julian days or in thermal time, obtained in plants submitted to heat stress after anthesis (Dias and Lidon, 2009a).
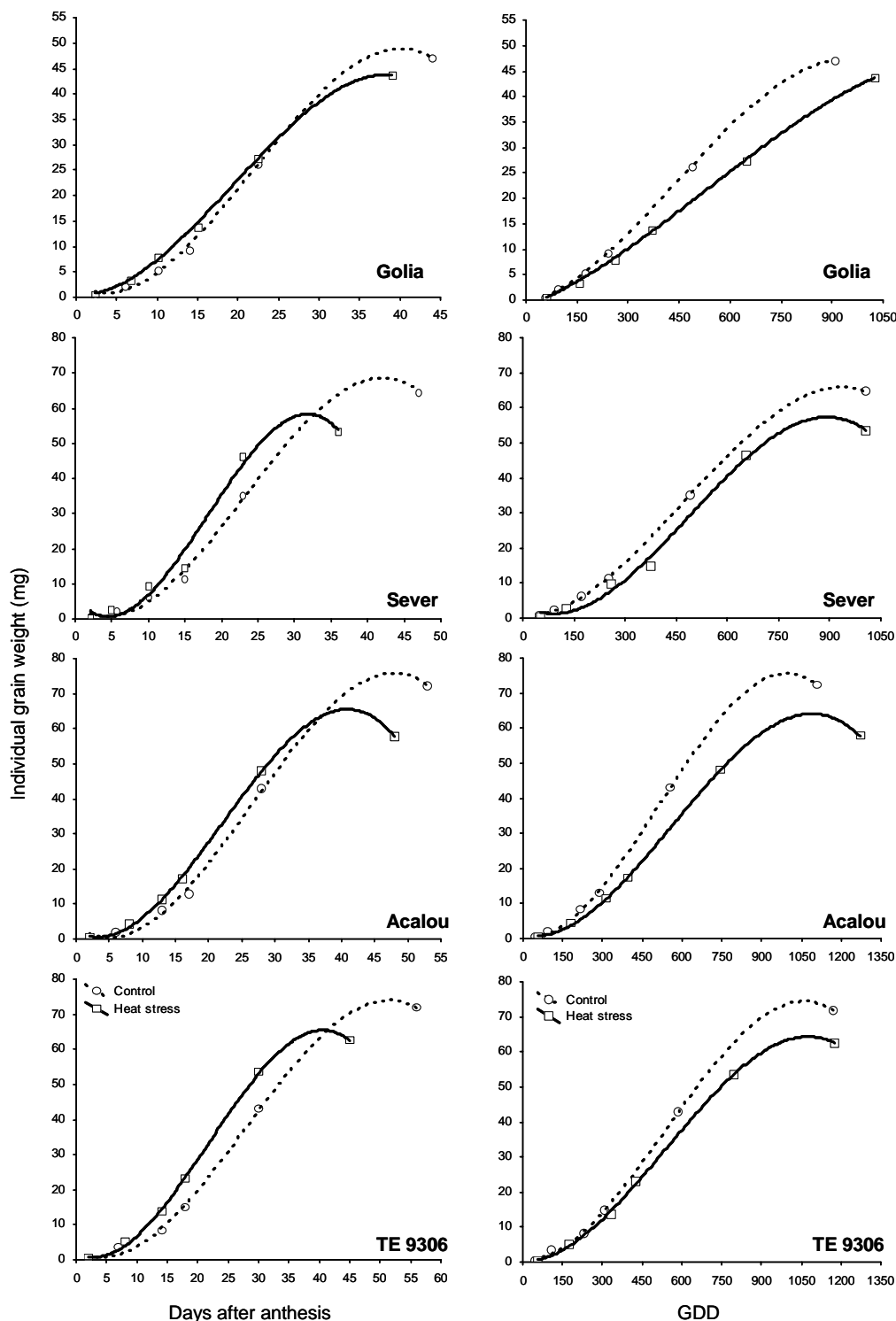
Figure 2. Grain filling curves for bread (Sever, Golia) and durum wheat (Acalou, TE9306) genotypes, in control and heat stress treatments, fitted to data obtained in a Julian days basis (left) and on a growing degree days (GDD) basis (right).

As a general pattern, a high potential grain weight (genetic characteristic) associated to a higher grain filling rate, under high temperatures, might be an advantage of the *Triticum* genotypes in the response of the grain weight to high temperatures, at the end of the life cycle of the plants.

5. Grains ultrastructure and biochemical traits

It has long been known (Spiertz, 1974) that at high temperatures after anthesis, increasing leaf senescence is coupled to a significant increase in the respiration rates in the grain. Such a response, depending on its extent, might trigger decreased carbohydrate availability (Thornley, 1971), justifying the decline in grain weight. Jenner (1991), further supported by Nicolas et al. (1984) in their work on sucrose concentrations (in the grain and endosperm) made a similar proposal, concluding that after anthesis heat stress affects wheat grain quality through changes in protein composition. Additionally, during grain growth, the high temperature might promote both, grain shrinkage and a decrease in weight (Dias et al., 2009a). The individual grain weight is more affected by high temperatures in the durum wheat genotypes as compared to bread wheat (Dias and Lidon, 2009a).

In the absence of heat stress, the unique aleurone layer of the wheat kernel presented large cells, surrounding a starchy endosperm (Bradbury et al., 1956; Dias et al., 2009a). After submitted to heat stress during grain filling, the shrunken grains of sensitive bread and durum wheat genotypes show an aleurone layer with disordered cells (Figure 3) (Dias et al., 2009a). Under heat stress, the endosperm of the kernels also might appear increasingly aggregated, with the starch granules embedded in the protein matrix and a dense cellular structure (Pyler, 1988; Dias et al., 2009a). Different types of starch granules can be found (Bechtel et al., 1986): A-type (lenticular shaped) starch granules, and B-type (spherical shaped). The grains developed under high temperatures can also reveal deformed starch granules in the endosperm with lower protein adherence (Shi et al., 1994; Dias et al., 2009a).

Genetic tolerance to high temperature (associated with drought) in wheat is observed at later phases of plant development, i.e., shooting and heading (Wiśniewski and Zagdańska, 2001). It is well known that soluble sugars play a complex essential role in plant metabolism as products of hydrolytic processes, substrates in biosynthetic processes and energy production as well as in a sugar sensing and signalling systems. It has been claimed that sugar flux may be a signal for metabolic regulation (Gibson, 2005), with the mobilization of storage reserves in the endosperm of cereal seeds being tightly regulated and having a primary pivotal role in the response to high temperatures associated with drought (Finkelstein and Gibson, 2001).

Although the concentrations of total sugars in bread and durum wheat during grain filling might not be significantly affected by high temperatures, the levels of reducing sugars can increase in tolerant genotypes, which might be a signal possibly developmentally regulated, modulated by the sugar pool and implying genetic variability in *Triticum* species (Leon and Sheen, 2003; Dias et al., 2009a).

Under heat stress, the protein content tends to increase significantly in wheat genotypes (Correll et al., 1994; Wardlaw et al., 1989; Guedira et al., 2002; Dias et al., 2009a). During grain filling, the modifications in the grain protein content, associated with high temperatures (more than 30ºC), have been related to reductions in the sedimentation index SDS (Graybosh et al., 1995) and seemed to promote a decrease in gluten strength. Data obtained

in several studies carried out in the field and confirmed under controlled environments (Blumenthal et al., 1993; Stone and Nicolas, 1994; Wrigley et al., 1994; Panozzo and Eagles, 2000), indicate that a few days of maximum daily temperatures surpassing 32ºC produce grains with weaker dough.
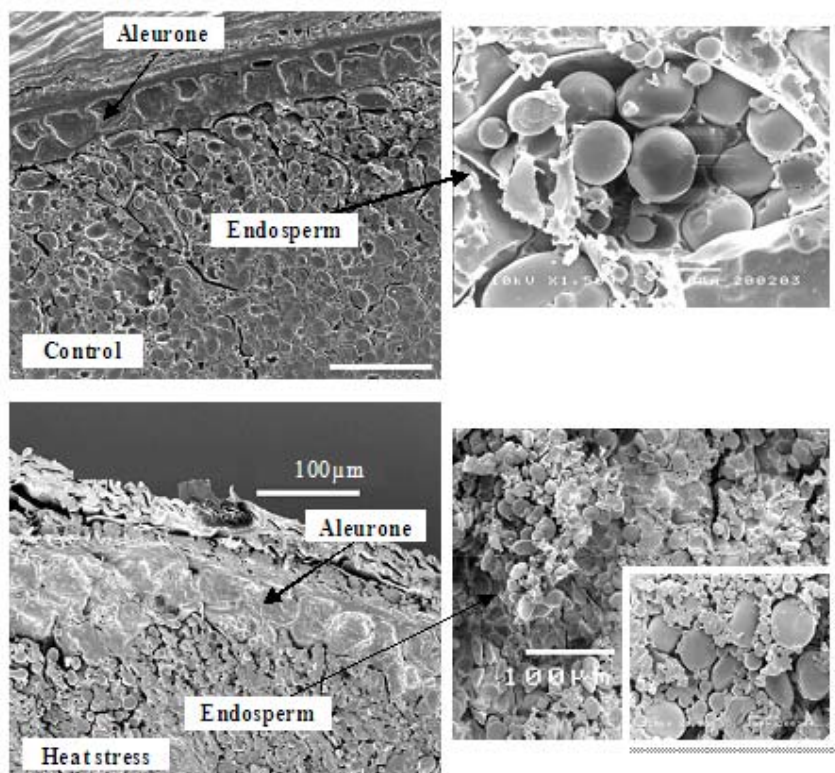
Figure 3. Scanning electron microscopy of kernels of control and heat stressed
Triticum aestivum.

This effect on the dough properties, involving modifications in the protein composition associated with high temperatures during grain growth has also been pointed out by several authors (Blumenthal et al., 1993; Wrigley et al., 1994). The lack of interaction genotype x treatment for protein content in the bread wheat, and also in SDS for the bread and durum wheat (Dias et al., 2009a), might indicate an absence of genetic variability in the response of these traits to high temperatures. In bread wheat, the grain hardness increase significantly with heat stress (Dias et al., 2009a) which, according to Guedira et al. (2002), might be an important factor for the wheat technological value. An increase in grain hardness might modify the milling quality, since greater energy will be required for

grain rupture procedures and the production of smaller particles (Finney et al., 1987). Additionally, this effect might also impair conservation and increase damage to starch grains during milling (Pomeranz and Williams, 1990).

The amino acid composition of proteins also might show that the stability of lysine is strongly affected under heat stress, whereas the levels of threonine, which is the second limiting amino acid (after lysine), tends to increase significantly with high temperatures (Dias et al., 2009a). Concerning nonessential amino acids of bread and durum wheat grains, only the contents of arginine and histidine usually vary significantly relative to controls (Dias et al., 2009a).

In general, under control and heat stress conditions, the nutrient contents of

the grains are not significantly different between genotypes of bread and durum wheat species (Calderini and Ortiz-Monasterio, 2003; Dias et al., 2009a).

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