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Insight into heat tolerance and grain yield improvement in wheat in warm rainfed regions of Iran

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ABSTRACT

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Terminal heat and drought are the main constraints for wheat production in the vast and diverse semi-tropical rainfed regions of Iran. High temperature stress during wheat's reproductive stage is particularly detrimental, reducing both individual kernel weight and kernel number. Identification of adapted genotypes can improve grain yield and its stability under heat stress conditions. Selection to improve grain yield and adaptation to abiotic stress is difficult, making the use of indirect selection for grain yield attractive to plant breeders. Experimental results in diverse environments have indicated remarkable variation for canopy temperature and a significant negative correlation with grain yield, particularly in warmer environments. There is also evidence that adapted wheat genotypes are able to maintain high individual kernel weight despite heat stress. Two recently released wheat cultivars for warm rainfed regions of Iran have shown high grain weight and cooler canopy temperature under different environmental conditions. Therefore, it is concluded that plump grain and cooler canopy temperature are essential traits for the adaptation of wheat genotypes in warm rainfed regions of Iran.

Key words: canopy temperature, drought, grain-filling period, source-sink limitation, thousand-kernel weight

INTRODUCTION

The total area of Iran is around 164.8 million hectares, of which about 18.5 million hectares are used for agriculture. The country's climate is generally semi-arid or arid, except in the Caspian Sea region. Wheat is harvested on a total of more than 6.7 million hectares; of these, about 2.6 million hectares (40%) are irrigated and about 4.1 million hectares (60%) are rainfed (Jalal Kamali *et al*., 2012).

Iran's dryland areas are classified into three distinct agro-ecological zones: cold, warm and temperate. Warm rainfed areas, about 1.2 million hectares, are characterized by a Mediterranean climate, winter rainfall pattern, mild winters, short springs and warm-to-hot summer temperatures. This agro-climatic zone includes Khouzestan, Boushehre, Golestan, parts of Kermanshah, Ilam, Lorstan, Kohgilouieh and Boyrahmad, and Fars Province. Wheat, the major crop, is grown in rotation with fallow; however, lentil and canola were recently included in this rotation.

Variable rainfall in successive years and the irregularity of its distribution within each season are important climatic features of this agro-climatic zone. Rain usually begins in mid to late autumn but falls mostly from December to March. Spring rains account for about 15-25% of annual rainfall, but in some years, there is no rain in spring. Climatic parameters such as rainfall and temperature show significant variation (Fig. 1) depending on geographic location and altitude (<1000 masl). Rainfall decreases to less than 200 mm or exceeds 800 mm in some years. Low (<300 mm) and moderate (500 mm) rainfall areas in warm dryland regions comprise about 6.5% and 23.5%, respectively, of total dryland wheat growing areas. Average absolute minimum temperature is -5ºC with about 15 days of freezing temperatures.

Thirty years ago, improved seed, research recommendations for fertilizer application, planting date, plant density and other crop management practices were non-existent in Iran's rainfed wheat growing areas. Seed was broadcast on the soil surface and incorporated into the soil using a plow, which resulted in soil erosion and land degradation, as well as poor plant stand. Gradually, breeding and agronomy research was initiated in the cereal research department of the Seed and Plant Improvement Institute (SPII), followed by the

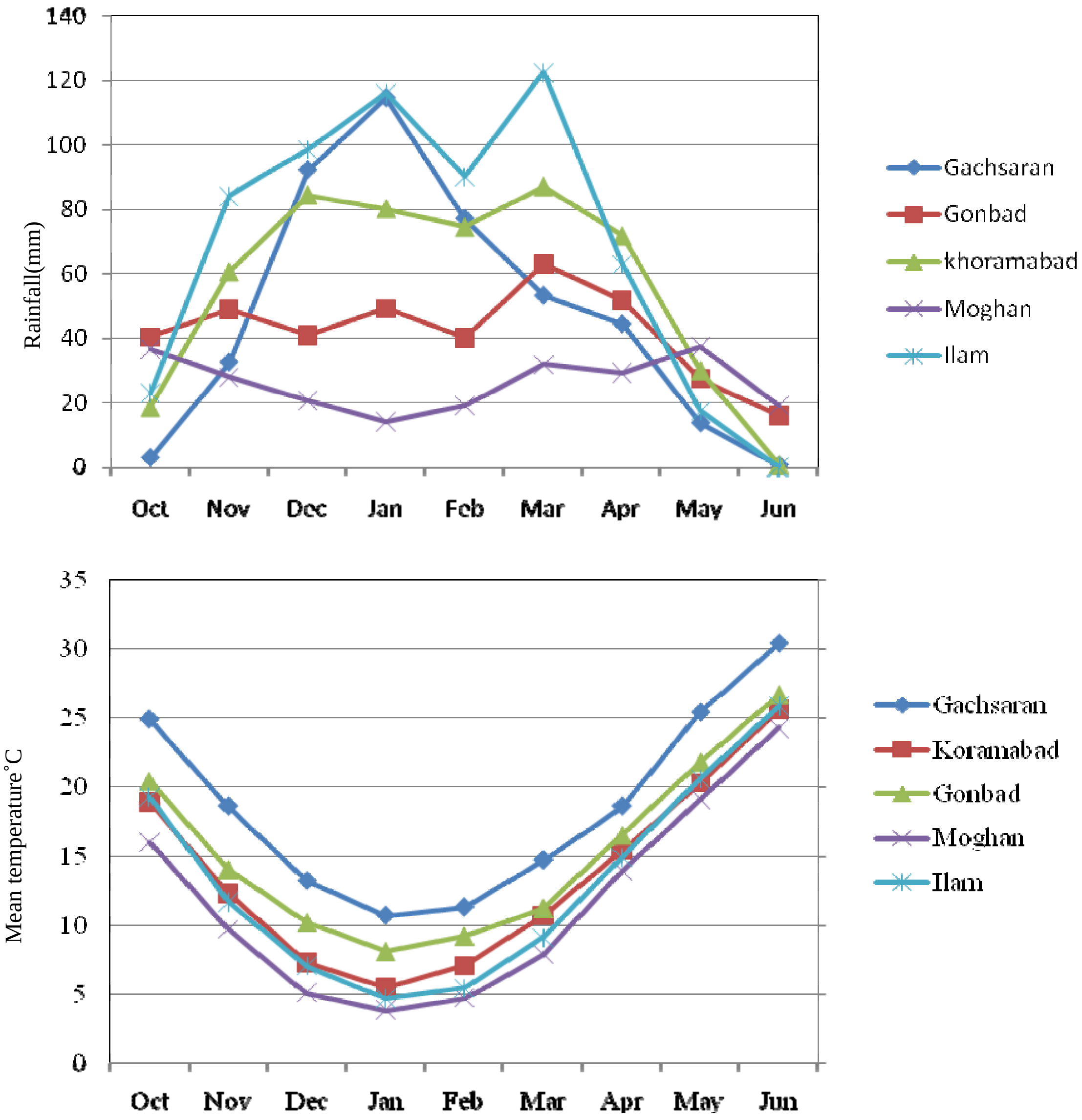

Fig. 1. Long-term monthly average rainfall (top) and mean temperature (bottom) at the five main agricultural research stations in warm rainfed regions of Iran.

Dryland Agricultural Research Institute (DARI) in the early 1990s.

Impacts of heat stress on wheat production

Heat and drought are the major abiotic constraints that determine wheat yield and quality in the warm dryland areas of Iran. Studies on losses associated with abiotic, biotic and socio-economic constraints to wheat production indicate that heat is an environmental factor that affects large areas, but water constraints are associated with the largest economic losses (Kosina *et al*., 2007).

Terminal heat stress caused by high temperatures during wheat grain development is an important constraint to wheat production (Rane *et al*., 2000; Sharma *et al*., 2007). In most wheat growing regions and especially in Mediterranean environments, plants are subjected to several physical and biotic stresses during grain-filling. Grain-filling often occurs when temperatures are rising and the moisture supply is decreasing. It has been reported that high temperatures drastically shortened the grain-filling period, particularly under delayed seeding (Sharma, 1992).

Heat stress during grain-filling is a major constraint to wheat yield in Iran's warm dryland areas. Evidence shows that climate change is occurring in Iran as in other parts of the world. Winter temperatures are becoming milder (Jalal Kamali *et al.*, 2012). It has been estimated that precipitation will decline by 9% and temperature will increase by 0.5-1.5 °C in Iran due to the changing climate (Sharifi and Bani-Hashemi, 2010). For example, during 2007-2011 at Gachsaran Dryland Agricultural Research Station in southwestern Iran, mean temperatures in March, April and May increased by 1.3, 1.2 and 0.9 °C, respectively, over long-term averages.

The number of days from heading to maturity decreased by 7.5 days for each degree centigrade of increase in mean temperature (Mohammadi, 2012). Terminal heat stress during anthesis and grain-filling accelerates crop maturity and significantly reduces grain size and grain weight. In a study on the effect of heat stress on grain yield of 16 bread wheat genotypes, Mohammadi (2001) reported that heat stress from double ridge to anthesis stages reduced grain number per unit area by 5.6% for each degree centigrade of temperature increase.

About 40% of the wheat crop in Iran's subtropical dryland areas is sown belatedly and suffers from terminal heat stress, which causes significant yield losses. To maintain wheat production under delayed sowing, emphasis has been given to developing heat tolerant genotypes with a shortened life cycle. Field experiments were carried out to evaluate the adaptation of some wheat genotypes and identify adaptive traits in terminal heat and drought stress environments. It has been estimated that, on average, wheat yield loss is 1.7% per each day sowing is delayed from the optimum window in warm dryland areas (Mohammadi, 2001).

Since wheat is a temperate crop, its productivity decreases under high temperatures. Wheat's optimal growing temperature during its reproductive stage is 15˚C, and for each 1˚C above this optimum, a 3-4% reduction in yield has been reported (Wardlaw *et al*., 1989). Exposure to higher than optimal temperatures reduces wheat yield and grain quality (Fokar *et al*., 1998; Maestri *et al*., 2002; Wardlaw *et al*., 2002). Research in the Yaqui Valley, Mexico, has demonstrated that high wheat yields are strongly associated with low average temperatures and, especially, low average minimum temperatures (Lobell *et al*., 2005).

Grain yield is affected by changes in grain number, which is determined starting 30 days before flowering (or anthesis) until shortly after anthesis, and grain size, which is determined during grain-filling. Towards the end of the season, when hot conditions are common in many regions, the most pronounced effect of warming is to shorten the duration of grain-filling (Lobell *et al*., 2012; Tashiro and Wardlaw, 1989). It seems that extending grain development duration by a few days could be important in improving grain yield under heat stress, which is in contrast to drought conditions.

High temperatures can increase the grain-filling rate, but only slightly at temperatures above 20 ˚C, which fails to compensate for the shortened duration and leads to an overall reduction in grain size (Wardlaw and Wrigley, 1994; Asseng *et al.*, 2011; Wardlaw and Mancur, 1995). Mohammadi (2012) reported that grain-filling rate increased from 0.9 to 1.0 mg/grain/day when conditions were 2.1˚C warmer. Warming can also slow grain-filling rates, partly because the photosynthetic apparatus of the leaf can be damaged under extreme canopy temperatures, accelerating senescence (Lobell *et al*., 2012). Radmehr (1997) reported that increasing the temperature from 21.1 to 25.9 ˚C caused the grain-filling rate to decrease from 1.06 to 0.97 mg/grain/day, while thousand-grain weight and grain-filling period were reduced from 44.7 to 30.9 g and from 42 to 32 days, respectively (Table 1).

Table 1. Effect of high temperature on grain-filling period and yield components in Ahwaz.

Sowing time	Absolute maximum temperature	Average temperature during grain-filling (°C)			Grain-filling (days)	1000 grain weight (g)	Grain-filling rate (mg/g/day)	Grain yield (g/m2)
		Minimum	Maximum	Daily				
Normal (20th Nov.)	38.6	15.3	26.6	21.1	42	44.7	1.06	430
Late (25th Jan.)	36.0	20.0	31.9	25.9	32	30.9	0.97	170
% reduction from normal					24	31.0	9	61
Very late (20th Feb.)	41.0	22.0	33.5	27.9	32	28.8	0.90	130
% reduction from normal					24	36.0	15	70

Farmers in warm dryland areas of Iran typically select wheat varieties with phenological adaptation to local climatic conditions. That is, they complete their growth stage and reach anthesis while temperatures are favorable, attaining physiological maturity before high temperatures begin. However, seasonal temperature fluctuations can cause significant reductions in wheat grain yield, despite adapted wheat varieties. For example, a recent study showed that in an unfavorable (late-sown) environment that was 2.1 ˚C warmer than average during the grain-filling period, wheat grain yield decreased by 24.1% in comparison with yield in a favorable (timely sown) environment, with no differences in rainfall and irrigation (Mohammadi, 2012).

A study on nine bread wheat genotypes under different heat and drought levels showed that the genotypes' productivity diminished more due to the combined effects of both stresses (Mohammadi, 2012). However, the study concluded that the combined effects of heat and drought are not necessarily additive. According to this interpretation, high temperature reduced grain-filling duration but increased grain-filling rate, thus decreasing the adverse effect of post-anthesis drought (Mohammadi, 2012). Wardlaw (2002) also reported that high temperature had a compensating effect on grain growth parameters.

Breeding

Over the last 50 years, wheat production has increased at the rate of nearly 1% per annum (Trethowan *et al*., 2002), and tolerance to high temperature stress has been identified as an important contributing factor to this increase. Despite these advances, increasing wheat's yield potential and yield stability in marginal environments remains a priority, particularly in areas with low production and high malnutrition, and in areas with increasing environmental instability created by the changing global climate (Reynolds *et al*., 2007).

Many regions in the world need wheat cultivars that are high yielding under favorable conditions, but produce stable yields when conditions are unfavorable. These cultivars should have high yield potential in both favorable and high temperature environments (Yang *et al*., 2002). However, it should be noted that wheat planting may be delayed by late harvesting of previous crops in systems where wheat is rotated (for example, with rice or maize), or in general, planting may be delayed due to inadequate planters or continuous rainfall. Also, in many regions, wheat's reproductive stage coincides with high temperatures due to late planting. Wheat genotypes may express a differential response to chronic heat as well as heat shock (Hays *et al*. 2007; Yang *et al*., 2002; Mohammadi *et al*., 2009, 2012).

Until 1990, wheat cultivars grown in the warm dryland areas of Iran were mainly landraces (such as Seiah Ryshak, Shahyvndy, Ghareh-Sonbol, Sareh Bughda, Sorkh Turkman and Orooji) or a mixture of different wheat varieties known as Chahar Tokhm, as well as varieties imported from neighboring countries, such as Sholeh from Iraq. Since then, national wheat breeding programs, in close collaboration with international research centers such as CIMMYT and ICARDA, have released several improved wheat cultivars for warm dryland areas of Iran (Table 2).

Table 2. Agronomic characteristics of wheat cultivars released for warm dryland areas of Iran, 1993-2011.

Cultivar	Origin	Wheat type	Year of release	PH (cm)	DM (day)	TGW (g)	GY (kg/ha)
Maroon	Iran	BW	1993	80-105	130-135	37	3300
Zagros	CIMMYT	BW	1997	77-100	134-139	36	3450
Niknejad	CIMMYT	BW	1997	75-105	137-145	34	3500
Gahar	CIMMYT	BW	1997	73-95	139-150	31	3850
Seimareh	ICARDA	DW	1997	77-100	137-140	36	3350
Koohdasht	CIMMYT	BW	2001	90-95	133-138	37	3500
Dehdasht	ICARDA	DW	2008	75-95	135-138	39	3700
Karim	ICARDA	BW	2011	75-90	130-135	39	3700

BW: bread wheat; DW: durum wheat; PH: plant height; DM: days to maturity; TGW: 1000-grain weight; GY: grain yield.

Multidisciplinary research at CIMMYT, including germplasm enhancement and crop physiology, has led to a physiological trait-based approach for developing wheat germplasm tolerant to abiotic stress. This approach has merit compared to breeding for yield *per se*, for it increases the probability of successful crosses resulting from additive gene action. Advances have already been made in the drought-breeding program, and this strategy is being used to breed wheat for heat-stressed environments (Reynolds and Borlaug, 2006; Ortiz *et al*., 2007). However, there is always uncertainty associated with the inherent genetic and environmental complexity, especially in water-limited environments (Lopes and Reynolds, 2010).

Physiological research activities

The quantitative nature of heat tolerance and the unpredictability of heat stress in the field makes it difficult for breeders to effectively select for the target traits. However, any genetic advance in yield in a stress environment is based on physiological traits. Under water-limited conditions, the efficiency of selecting for genotypes tolerant to drought/heat is restricted, based on empirical selection for yield *per se*, by the low heritability of yield, as well as by large genotype × environment interaction (Trethowan *et al*., 2002). In addition, yield evaluation in early generations is difficult because yield per plant may not be related to crop yield. Progress in plant breeding has been achieved by using physiological traits as selection criteria to complement conventional breeding for yield (Araus, 2003; Condon *et al*., 2002; Richards, 1996; Richards *et al*., 2002).

If our physiological understanding of yield is adequate, we can identify traits that are most likely to improve yield in a given environment. Physiological traits can be used to dissect stress adaptation into some of its components. Based on successful experiences, two important criteria, canopy temperature and source/sink limitation, are explained below.

Canopy temperature

Leaf temperature is depressed below air temperature when water evaporates; therefore, canopy temperature (CT) is an indirect measure of (instantaneous) transpiration at the whole-crop level (Reynolds, 2002) and of plant water status (Araus, 2003). Canopy temperature also reflects the leaf's energy balance, which is determined by the environment and physiological traits (Balota *et al*., 2008). However, genotypic variation for CT has been reported in wheat (Amani *et al*., 1996; Blum *et al*., 1989; Fischer *et al*., 1998; Reynolds *et al*., 1994).

Studies have shown that low CT is associated with increased wheat yield in warm irrigated environments (Amani *et al*., 1996; Reynolds *et al*., 1994; Reynolds, 2002; Fischer *et al*., 1998), and in dryland environments (Araus *et al*., 2002; Araus, 2003; Blum *et al*., 1989; Condon and Richards, 1992; Olivares-Villegas *et al*., 2007; Balota *et al*., 2007). Given that canopy temperature does not mask confounding interactions between organ temperatures (Ayeneh *et al*., 2002), CT has been used as a selection criterion to improve wheat's adaptation to drought and heat.

Shefazadeh *et al*. (2012) reported that grain yield was negatively correlated with CT in both timely and late-sown wheat crops, indicating that CT always influences grain yield. However, a higher correlation coefficient under late sowing conditions showed that CT influences grain yield more strongly in the presence of heat stress. In this research, CT explained 71 and 54.2% of grain yield variation in more and less heated environments, respectively. Strong correlation was found between yield and canopy temperature under different drought levels ($P < 0.05$ and $P < 0.01$ under dryland and supplemental irrigation conditions, respectively) and heat stress ($P < 0.01$) (Mohammadi, unpublished).

There is much evidence that root traits are important adaptive attributes for drought tolerance (Manschadi *et al*., 2006, 2008; Reynolds *et al*., 2007: Christopher *et al*., 2008). However, since root traits are difficult to measure in realistic field situations, cooler canopy temperature has been suggested as a surrogate that indicates a genotype's ability to maintain transpiration because their roots can access water deep in the soil profile (Lopes and Reynolds, 2010). The latest bread wheat cultivar released for warm dryland regions (Karim) showed optimum CT in comparison with other breeding lines (Shefazadeh *et al.,* 2012; Mohammadi, unpublished). This may be attributed to root traits. On the other hand, high correlations between grain-filling period and yield components with canopy temperature, particularly in terminal growth stages, were observed in Gachsaran, Iran (Table 3).

Table 3. Correlation coefficients between canopy temperature, grain-filling period and yield components under warm dryland (heat and drought) and heat (full irrigation) conditions (Mohammadi, unpublished).

Traits	Heat and drought (dryland)	Heat (full irrigation)
Grain-filling period	-0.752**	0.099^{ns}
Grain yield	-0. 720**	-0.871***
Thousand-kernel weight	-0.504*	-0.671**
Number of kernels per spike	-0.556*	-0.134^{ns}

***, ** and *** Significant at the 0.05, 0.01 and 0.001 probability levels, respectively.**

The use of such traits as indirect selection criteria for yield improvement in a breeding program will thus depend on their relative importance (genetic correlation with yield), ease and cost of measurement, extent of genetic variation, heritability, genotype × environment interaction and whether they are associated with adverse pleiotropic effects or genetic linkages (Richards *et al*., 2002). In conclusion, canopy temperature is a good trait to use as an indirect selection criterion because measurement is quick (10 seconds), easy (aim the instrument and pull the trigger) and inexpensive.

Source/sink limitation

Heat stress affects wheat yield and grain quality through constraints on sink strength and source capacity. Grain yield depends on the number of grains per unit area (sink) and the availability of assimilates (source) to fill those grains (Zhang *et al*., 2010). When some spikelets are removed before grain-filling, there are differential responses in final grain mass. Differences resulted from sink limitations (in the case of non-responsive cultivars) or source limitations (in the case of responsive cultivars). The grain growth rate of responsive cultivars increased and resulted in higher final mass of individual grains (Slafer and Savin, 1994).

In a study of 20 wheat genotypes under normal and heat stress conditions in Khouzestan, Iran, Radmehr *et al.* (2004) calculated source and sink restrictions based on the mean dry weight of remaining grains in treated spike and control (without removal of flag leaf and spikelets). All 20 genotypes had no sink restrictions, and the contribution of flag leaf to grain dry weight was 12%. However, some genotypes showed source limitations estimated at 0-34% (average 12.6%) and 5.7-41.2% (average 17.2%) under favorable and unfavorable conditions, respectively. Thus source limitation due to exposure to terminal heat stress was greater by 6%. Likewise, results indicated that source limitation was greater in genotypes with larger grain size.

Mohammadi (2012) conducted a study to determine whether yield is limited by sink size or by the assimilates available for grain-filling in commercial wheat cultivars and breeding lines in warm dryland areas of Iran. In this study, the weight and growth rate of individual grains of responsive cultivars were source-limited, and source and sink strengths of these cultivars were not balanced. The effect on grain growth of changes in the source-sink relationship seems to imply that assimilate availability in control plants in this study was insufficient to fully meet grain growth requirements. This may be due to the fact that during post-anthesis, wheat yield is either source-limited or co-limited by both source and sink. Enhancing assimilate availability and differential grain responses by spikelet removal indicated that grain growth of responsive cultivars was initially source-limited and later sink-limited, once maximum grain growth was reached.

Mohammadi (2012) also reported that the reduction in thousand-grain weight was 11.3% per degree centigrade of increase in mean temperature from anthesis to physiological maturity under heat stress when compared with cooler conditions. Increased grain growth rate could not compensate for this reduction. As the mean daily temperature rises, the productivity of wheat decreases, partly due to an accelerated crop development rate, which reduces crop duration. Grain weight under high temperature stress is a better criterion for heat screening than physiological attributes such as membrane thermal stability, antioxidant activity, phenolic content or paraquat tolerance. Tolerant genotypes could not be identified based on these attributes, and the data were not consistent enough to be used as screening criteria. Grain weight is still preferred for breeding purposes, as it has the advantage of combining the effects of many different factors, even though the relative importance or the physiological basis of each factor is not known (Mohammadi *et al.,* 2007). Nevertheless, Radmehr *et al.* (2004) reported that grain weight had no significant effect in determining final yield. Thus the cause of grain yield reduction must be sought in other yield components, such as number of grains per spike and number of spikes per unit area.

Mohammadi (2012) showed that grain-filling duration in two different environments, created in April and May, decreased by about 15 days in the warmer environment. Selecting wheat cultivars with high grain weight that yield reasonably well in diverse environments led to the release of two wheat cultivars, Dehdasht (durum wheat) and Karim (bread wheat), for warm dryland areas by Iran's Dryland Agricultural Research Institute. These two wheat cultivars have significantly higher thousand-grain weight than older cultivars (Table 1). Modhej (2008) believes that earliness can reduce the effect of source limitation, and that early genotypes, because they flower and develop grain before the onset of high temperatures, produce heavier grains. This implies that the sooner spike emergence occurs, the longer grain growth will last (Radmehr *et al.*, 2005). High temperatures reduced grain weight by decreasing grain growth duration, but not grain growth rate; therefore, grain weight was low due to reduced grain-filling duration (Asseng *et al.,* 2011; Lobell *et al.,* 2012). On the other hand, higher temperatures decrease grain size due to high respiration rate, which in turn reduces grain weight because of forced grain maturity (Gribson and Paulsen, 1999; Stone and Nicolas, 1984; Tashiro and Wardlaw, 1989). Consequently, maintaining optimum grain weight under heat stress conditions (which indicates optimum source capacity and assimilate availability) is a measure of heat tolerance. Similar findings have been reported by many other authors (Tyagi *et al*., 2003; Singh *et al*., 2006).

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