



E-ISSN: 2278-4136

P-ISSN: 2349-8234

[www.phytojournal.com](http://www.phytojournal.com)

JPP 2021; 10(1): 2558-2565

Received: 24-10-2020

Accepted: 22-11-2020

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## Low productivity of wheat in Bastar region with special Enphasis on effect of temperature on phenology, growth and yield of wheat: A review

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**Abstract**

The changing climate is one of the biggest threats to agriculture during the years ahead. According to estimates, on an average 50% yield losses in agricultural crops are due to different abiotic factors. The expected changes in the climate could strongly affect the wheat production worldwide. Among various factors affecting wheat productivity, the increase in atmospheric temperature has the most significant effect. The temperature above optimum shortens the vegetative and reproductive phases. Generally, the growing degree days (GDD) or heat unit requirement to produce a mature winter wheat crop is approximately 2200, using 4° Celsius as the base temperature. Exposure to heat stress accelerates the development stages in wheat crop which in turn leads to reduced grain yield as well as quality. The high temperature during vegetative stage reduces the number of effective tillers per unit area and during reproductive stages leads to reduced grain number as well as grain weight. This review highlighted the outcome of high temperature on growth, yield and its attributing characters of wheat and need for further research studies.

**Keywords:** high temperature, wheat, CO<sub>2</sub>, climate change

**Introduction**

Wheat (*Triticum aestivum* L.) represents 25% of the world's cereal production and constitutes one of the main food sources of carbohydrates, proteins, fibers, amino acids, and vitamins, providing 20% of the calories and 25% of proteins consumed worldwide on a daily basis (FAO 2019) [28]. Although being produced worldwide under diverse environmental conditions, the required optimum temperature for wheat anthesis and grain filling is from 12 to 22 °C (Tewolde et. al, 2006) [97]. The average maximum decadal temperature of wheat production in India is always a gamble against temperature. The decadal mean month wise data of Jagdalpur shows that in the decade 1980-1989 November, December, January, February and March the maximum temperature was 28.6, 27.5, 28.3, 31.7 and 35.0 respectively, while in decade 2010-2019 monthly mean data of November, December, January, February and March was 28.4, 26.9, 27.5, 31.5 and 33.0 respectively. The average maximum temperature during wheat growing season diminishes in the decade 2010-2019 with 0.7 °C in contrast with decade 1980-1989. Increasing of each degree of temperature reduces wheat yield by 4.1% to 6.4% (Liu et. al, 2016) [48]. Several yield parameters are affected by high temperatures as vegetative weight, grain number and weight, as reviewed by Akter et al, (2017) [5]. Grain number is strongly affected by high temperatures, especially between spike initiation and anthesis (Farooq et. al, 2011) [30]. Grain mass is reduced with high temperature after anthesis, particularly when the treatment is imposed in early stages (Castro et. al, 2007) [20]. Heat stress also shortens grain filling duration, as reviewed by Altenbach, (2012) [9] affecting starch and storage protein deposition. On the other hand, during grain filling, high temperature has been reported to increase protein grain content, as kernel size is smaller, and this augment seems to be higher when high temperatures are imposed in early stages of grain filling (Corbellini et. al, 1998 and Daniel et al, 2001) [24].

About 21% of the world's food depends on the wheat (*Triticum aestivum*) crop, which grows on more than 200 million hectares of farmland worldwide (<https://wheat.org/>). Although wheat is traded internationally and developing countries are major importers (43% of food imports), the reality is that 81% of wheat consumed in the developing world is produced and utilized within the same country, if not the same community (CIMMYT, 2018). It is important to know how climatic change will affect growth, development, water use and productivity of the wheat crop in India, which is one of the important staple food crops of India, accounting for about 35% of the food grain production of the country. The wheat production has increased tremendously from 12.3 Mt in 1965 to 107.59 Mt in 2019-20, which is 11.60 Mt more than the

average wheat production in India. This has been possible due to the increase in area under wheat from 13.4 to 29.6 mha (Department of Agriculture and Co-operation, 2019). Mall and Singh (2000) <sup>[52]</sup> observed that small changes in the growing season temperature over the years appeared to be the key aspect of weather affecting yearly wheat yield fluctuations. Pathak *et al.*, (2003) <sup>[63]</sup> concluded that the negative trends in solar radiation and increase in minimum temperature, resulting in declining trends of potential yields of wheat in the Indo-Gangetic plains of India.

Temperature is one of the major environment factors affecting the growth, development and yields of crops especially the rate of development. On one hand, crops have basic requirement for temperature to complete a specific phenophase or the whole life cycle. On the other hand, extremely high and low temperatures can have detrimental effects on crop growth, development and yield particularly at critical phenophases such as anthesis. The nutritional value of wheat is extremely important as it takes an important place among the few crop species being extensively grown as staple food sources. The importance of wheat is mainly due to the fact that its seed can be ground into flour, semolina, etc., which form the basic ingredients of bread and other bakery products, as well as pastas, and thus it presents the main source of nutrients to the most of the world population. A huge increase in demand for cereals is predicted if the food needs for the estimated world population growth are to be met. But there is another potentially great benefit to these communities and that is the possibility to ensure such staple crops are nutritionally-balanced and help remove the millions of cases of nutritionally-related deficiency disease that afflict them. It should be emphasised that in the past there has not been a single instance where plants have been bred to improve their nutritional content. If this has occurred it is purely by accident not design (Lindsay 2002; Welch and Graham 2002) <sup>[47, 100]</sup>. Over three billion people are currently micronutrient (i.e. micronutrient elements and vitamins) malnourished. This global crisis in nutritional health is the result of dysfunctional food systems that do not consistently supply enough of these essential nutrients to meet the nutritional requirements of high-risk groups (Welch 2005) <sup>[99]</sup>. One sustainable agricultural approach to reducing micronutrient malnutrition among people at highest risk (i.e. resourcepoor women, infants and children) globally is to enrich major staple food crops with micronutrients through plant-breeding strategies. Available research has demonstrated that micronutrient-enrichment traits are available within the genome of wheat (as well as other food crops) that could allow for substantial increases in the levels of minerals, vitamins and other nutrients and health-promoting factors without negatively impacting crop yield. Importantly, micronutrient bioavailability issues must be addressed when using a plant breeding approach to eliminate micronutrient malnutrition. Enhancing substances (e.g. ascorbic acid, S-containing amino acids, etc) that promote micronutrient bioavailability or decreasing antinutrient substances (e.g. phytate, polyphenolics, etc) that inhibit micronutrient bioavailability, are both options that could be pursued in breeding programs (Welch 2002; Welch and Graham 2004; Welch 2005) <sup>[47, 101, 99]</sup>.

### Effect of Temperature on Wheat Phenology

#### High temperature and food production

Brocklehurst (1977) <sup>[19]</sup> and Nicolas *et al.*, (1984) <sup>[58, 59]</sup> observed that the rate of grain development stimulates and the

grain filling duration was shortened under increased temperatures. Chang (1982) <sup>[21]</sup> also reported that the grain growth is mainly influenced by the duration and the rate of grain filling. Shpiler and Blum (1986) <sup>[88]</sup> reported that decrease in grain yield was almost entirely determined by a shorter duration of grain filling while the temperature effect was observed on grain growth rate or grain number per ear. Shukla *et al.* (1988) <sup>[89]</sup> observed that maximum damage to grain weight was due to high temperature during third and fourth weeks after anthesis. Boese (1987) <sup>[18]</sup>, reported that the grain filling phase was by far the most sensitive to high temperature, in wheat among the growth stages following the ear emergence. Hoogendoorn and Gale, (1988) <sup>[39]</sup> found that the shortest genotypes were more sensitive than tall or semi dwarf genotypes to heat stress during grain filling and concluded that the short duration varieties may not be suited to environments where heat commonly shortens the grain filling period. Grain filling rate was found to be more temperature sensitive than day to anthesis and duration of grain filling (Zhong Hu and Rajaram, 1994) <sup>[103]</sup>. Increased temperature significantly reduced the days to anthesis, maturity duration and flag leaf area. Likewise higher post anthesis temperature i.e. 26.6 °C 30.6 °C contributed to decline in productive ears, biological yield, 1000-grain weight and grain under late sowing compared with normal sowing (Singh and Ziauddin Ahmad, 1997) <sup>[93]</sup>. Late sown crop gets expose to mean maximum temperature of about 35 °C during grain growth and causes yield reduction of 270 kg ha<sup>-1</sup> / degree rise in temperature (Rane *et al.*, 2000) <sup>[72]</sup>.

### Physiological and biochemical changes under high temperature.

#### Photosynthesis

Singh *et al.* (1982) <sup>[91]</sup> reported that photosynthetic rate and stomatal conductance were significantly correlated with the yield at all stages of crop development, but the relationship was found stronger during grain filling which might be due to premature loss of chlorophyll associated with heat sensitivity. Physiological studies have shown that the rate of photosynthesis depends greatly on the temperature under which the plants are grown. Further, increased temperature results in premature plant senescence and reduced photosynthetic activity in a similar way as the other biochemical processes following a parabolic relationship (Ludwig *et al.*, 1965; Alkhatib and Paulsen, 1984) <sup>[50, 6]</sup>. Differences in photosynthesis among genotypes under high temperature conditions have been shown to be associated with a loss of chlorophyll and change in the chlorophyll a: b ratio due to premature leaf senescence (Al-Khatib and Paulsen, 1984; Harding *et al.*, 1990) <sup>[6, 37]</sup>. Extreme condition of temperature lead to denaturation of enzymes and unfolding of nucleic acids. It is suggested that special lipids occurs in membranes their proteins have some special structure and their DNA is protected by special histon like protein (Salsbury and Ross, 1992) <sup>[81]</sup>. It is concluded that, root temperature is involved in shoot senescence, which in turn may regulate photosynthate partitioning and grain development. Grain filling in wheat depends on two major sources of carbon i.e. current photosynthesis in leaves and ears, and the mobilization of stored carbohydrates from the stem into the developing grains. When the current photosynthetic source is inhibited by any environmental stress, the grain filling becomes more depended on stem reserves (Blum *et al.*, 1994 and Gupta, 2002) <sup>[17, 35]</sup>. Ferris *et al.* (1998) <sup>[31]</sup> worked on high temperature stress found that

the grain fertilization and grain set were most sensitive to high temperature conditions. High temperature causes modification in membrane function mainly by alteration of membrane fluidity. Alkhati and Paulsen (1999) [7] exposed different species to 22, 32 and 42 °C temperature regimes and found that the photosynthetic rates of protoplasts and chloroplasts from all species decreased with increasing temperature. Photo system II (PSII) activity declined steadily in protoplasts, chloroplasts, and thylakoids of millet and rice from 22 to 42 °C but decreased abruptly in organelles of wheat from 32 to 42 °C. The results suggest that differences in photosynthetic responses to high temperature are associated with light reactions and extreme sensitivity of wheat may be attributable to injury to PSII. A higher or lower degree of membrane lipid saturation is beneficial for high temperature tolerance (Klueva *et al.*, 2001) [43]. Gupta and Gupta (2005) [36] reported that the high temperature adversely affects the photosynthetic functioning and the thylakoid membrane particularly the PS II complexes located on the membrane, which are most heat sensitive part of the PS mechanism. In addition, rubisco and other enzymes of carbon metabolism are also adversely influenced by high temperature.

#### Water status

Sairam *et al.* (2000) [80] reviewed that extent of oxidative injury and activity of antioxidant enzymes in relation to heat stress induced by manipulating dates of sowing and increases in temperature by late sowing significantly decreased leaf relative water content, ascorbic acid content and increased H<sub>2</sub>O<sub>2</sub> content at 8<sup>th</sup> and 23<sup>rd</sup> days after anthesis. The activities of superoxide dismutase (SOD) and catalase were also highest in heat tolerant varieties. Paulsen and Machado (2001) [64] worked on hypothesis and observed that high temperature interacts with drought to affect water relations and the effect was greater in heat sensitive wheat (*Triticum aestivum*) than in sorghum. The combined stresses reduced soil water content and relative water content and unevenly raised leaf turgor potential over time. The results further demonstrated that crops maintained nearly stable water relation regardless of temperature when moisture was ample, but high temperature strongly affects water relation when water was limiting. The enhancement of the thermo tolerance of wheat might improve its potential to acclimate for high temperature and drought.

High temperature seems to cause dehydration in plant tissue and subsequently restricts growth and development of plants. During flowering, a temperature of 31 °C is generally considered as an upper limit of maintaining water status of a crop (Atkinson and Urwin, 2012) [11]. With a concomitant increase in leaf temperature, wheat plants exposed to heat stress substantially decrease the water potential and the relative water content in leaves, and eventually reduce photosynthetic productivity (Farooq *et al.* 2009) [29]. Simultaneously, the rate of transpiration and plant growth are severely affected. Almeselmani *et al.* (2009) [8] observed that high temperature imposed after tillering showed a significant reduction of water potential in wheat, and the reduction was higher in genotypes susceptible to heat stress. In general, different antioxidants are associated with dehydration tolerance and are stimulated under heat stress. This is because of increased transpiration in stressed leaf and dropping of osmotic potential (Ahmad *et al.* 2010) [4]. Heat stress also increases hydraulic conductivity of cell membrane as well as plant tissues primarily for increased aquaporin activity (Martinez-Ballesta *et al.* 2009) [53] and to a greater extent for reduced water viscosity (Cochard *et al.* 2007) [22].

#### Influence of environmental factors on wheat phasic development

Ouabbou *et al.* (2000) [60] studied on response of crops to high temperatures under controlled conditions and in the field and observed photosynthesis stomatal conductance yield component and harvest index during maturation from anthesis to maturity and conclude low stomatal conductance showed that senescence was accelerated by high temperature. Altering planting dates which exposed plants to different temperature regimes during maturation affected the variability among cultivars and elucidated triads related to yield under stress. Heat stress ranging from 28 to 30 °C may alter the plant growth duration by reducing seed germination and maturity periods (Yamamoto *et al.* 2008) [102]. Warm environment produces lower biomass compared to plants grown under optimum or low temperature. Day and night temperature around 30 and 25 °C, respectively, may have severe effects on leaf development and productive tiller formation in wheat (Rahman *et al.* 2009) [67]. However, the prevalence of reproductive stage heat stress has been found to be more detrimental in wheat production (Nawaz *et al.* 2013) [57]. One degree rise in average temperature during reproductive phase can cause severe yield loss in wheat (Bennett *et al.* 2012) [14].

#### Sowing to emergence

Unlike the responses to other environmental variables, wheat starts to respond to temperature as soon as the seed is imbibed (Roberts, 1988) [75] and continues to respond upto maturity (Angus *et al.*, 1981). The cardinal temperatures for wheat germination are minimum between 3.5 to 5.5 °C, optimum between 20 °C to 25 °C and maximum around 35 °C (Savin and Slafer, 1991) [84]. The genetic variability for harvest index, number of spikelets per spike, 1000 grain weight and spike length were significant. The seed stock produced from plant grown under abiotic stress conditions significantly decreased the amount of the energy in 1 g of dry matter, which decreased the rate of germination and affected the plant growth. The growing season for wheat is limited by high temperatures at sowing and maturation. As wheat is grown over a wide range of latitudes in India, it is frequently exposed to temperatures above the threshold for heat stress. For example, high maximum and minimum temperatures in September (about 34 °C/20 °C) adversely affect seedling establishment, accelerate early vegetative development, and reduce canopy cover, tillering, spike size and yield. High temperatures at the end of February (25 °C/10 °C) and during March (30 °C/13 °C) and April (30 °C/20 °C) reduce the number of viable florets and the duration of grain filling. The situation is similar for sorghum and pearl millet, which are exposed to extreme high temperatures in Rajasthan (Abrol *et al.*, 1991; Abrol and Ingram, 1996) [2, 1].

Ambient temperature around 35-37 °C severely affects embryonic cell in wheat which reduces crop stands through impairing seed germination and emergence (Essemine *et al.* 2010) [27]. Heat stress mostly affects the plant meristems and reduces plant growth by promoting leaf senescence and abscission, and by reducing photosynthesis (Kosova *et al.* 2011) [45].

Sharma *et al.* (2002) [87] reported that within increase of 0.5 °C in mean temperature in Punjab, Haryana and Uttar Pradesh and another is reduction in productivity of wheat crop by 10 per cent climate projections indicate a continual decrease in wheat yield. The growing season for wheat is limited by high temperatures at sowing and maturation. As wheat is grown



over a wide range of latitudes in India, it is frequently exposed to temperatures above the threshold for heat stress.

#### **Vegetative, spikeletes initiation and stem elongation phase**

Reduction in total number of leaves and spike bearing tillers is also an effect of high temperature during this phase (Midmore *et al.*, 1984)<sup>[55]</sup>. Owen (1971)<sup>[61]</sup> and Saini and Aspinal (1982)<sup>[71]</sup> reported that temperatures above 30 °C during floret formation cause complete sterility, ultimately reduced grains spike<sup>-1</sup>. The spikeletes initiation phase is distinguished by a pronounced elongation of the apex and initiation of primordial at a constant rate which may be thrice the rate of leaf primordial initiation. Saini *et al.* (1986)<sup>[77]</sup> found the greatest sensitivity to temperature and the greatest variation between genotypes in the stem elongation phase while working with wheat aestivum and durum. Vegetative phase of growth is characterized by initiation of leaf primordial by the shoot apex. The rate of leaf initiation increases under high temperature and light intensity. This leaf appearance rate is a major component of crop leaf development, which finally determines the interception of radiation and potential crop growth (Loomis and Connor, 1992, Slafer and Rawson, 1994)<sup>[49, 95]</sup>. It is suggested that the final leaf number is not constant and can be modified by environmental conditions prevailing during this phase. Thus, leaf number is reduced by vernalization and long day conditions (Rahman, 1980)<sup>[69]</sup>. Decreasing in light intensity also decreased the leaf number (Rawson and Zajac, 1993; Slafer and Rawson, 1994)<sup>[74, 95]</sup>. Slafer and Rawson (1994)<sup>[95]</sup> screened 25 wheat varieties concluded that all genotypes and all phases were sensitive to temperature although they may differ in the sensitivity of their response to temperature. Slafer and Rawson (1994)<sup>[95]</sup> compared the relative sensitivity of the phase and concluded that the general response to temperature was much stronger in the vegetative than in the spikelet initiation phase and much stronger in the stem elongation phase than in the spikele phase.

Heat stress reduces the number of grains leading to lower harvest index in wheat (Lukac *et al.* 2011)<sup>[51]</sup>. However, the influence of heat stress on both the number and size of grains varies with the growth stages encountering heat stress. For instance, temperatures above 20 °C between spike initiation and anthesis speed up the development of the spike but reduce the number of spikelets and grains per spike (Semenov 2009)<sup>[85]</sup>. Heat stress adversely affects pollen cell and microspore resulting into male sterility (Anjum *et al.* 2008)<sup>[10]</sup>. Even high temperature of above 30 °C during floret development may cause complete sterility in wheat depending on genotypes (Kaur and Behl 2010)<sup>[42]</sup>. In wheat, the anther produced under 3 days heat stress during anthesis was found to be structurally abnormal and nonfunctional florets (Hedhly *et al.* 2009)<sup>[38]</sup>. Day/ night high temperature of 31/20 °C may also cause shrinking of grains resulting from changing structures of the aleurone layer and cell endosperm (Dias *et al.* 2008)<sup>[25]</sup>.

#### **Anthesis, grain growth and maturity**

Sinha and Swaminathan, (1991)<sup>[94]</sup> reported the 0.5° C increase in winter temperature would reduce wheat crop duration by seven days and reduce yield by 0.45 ton ha<sup>-1</sup>. The optimum temperature for wheat anthesis and grain filling ranges from 12 to 22 °C (Shewry 2009)<sup>[86]</sup>. Plants exposed to temperatures above 24 °C during reproductive stage significantly reduced grain yield and yield reduction

continued with increasing duration of exposure to high temperature (Prasad and Djanaguiraman 2014)<sup>[66]</sup>.

The developmental events occurring during this phase are pollination, fertilization, grain set and grain filling. Since the development during this phase directly determines the grain growth it is the most intensively researched phase in wheat development.

Nicolas *et al.* (1984)<sup>[58, 59]</sup> showed that high temperature during early or late period of cell division accelerated grain development. Dry matter accumulation and cell division proceeded at higher rate but had shorter duration in high temperature treatment due to which here was a reduction in yield. Bhullar and Jenner (1983, 1986)<sup>[15, 16]</sup> also reported that brief warming of wheat ears reduced the total grain weight mainly due to reduction in individual grain weight and also a small reduction (2.6 to 12.8%) in grain number. Shukla *et al.* (1988a)<sup>[89]</sup> observed that an increase in 1000-grain weight over control in I week of anthesis and then a decrease in subsequent weeks. The difference were significant during I, III and IV weeks. Gupta *et al.* (2002)<sup>[35]</sup> reported that grain weight rather than grain number were more affected under post anthesis high temperature conditions. High temperature imposed from 10 days after anthesis reduced yield of wheat through effects on individual kernel mass and the responsiveness to temperature generally declined with time so that early heat exposure reduced individual kernel mass more than later heat treatment (Randall and Moss, 1990)<sup>[70]</sup>. Stone and Nicolas (1995)<sup>[96]</sup> tried to determine the most heat sensitive stages of grain development and concluded that mature individual kernel mass was most sensitive to heat stress. They also concluded that reduction in mature kernel mass resulted primarily from reductions in duration rather than rate of grain filling. Rahaman *et al.* (1997)<sup>[68]</sup> worked on different wheat genotypes under late sowing conditions and found that high temperature at anthesis stage caused sterility resulting in lower yield. Further, all the high yielding genotypes had significant lower canopy temperatures and medium chlorophyll content. The grain yield was found positively associated with biomass, harvest index, 1000- grain weight whereas chlorophyll content are negatively correlated with canopy temperature and days to anthesis. Rane *et al.* (2000)<sup>[72]</sup> observed that the late sown crop gets exposed to mean maximum temperature of above 35 °C during grain growth period and caused yield reduction of 270 kg ha<sup>-1</sup> degree<sup>-1</sup> rise in temperature. Sikdar *et al.* (2001)<sup>[90]</sup> found that the grain number, 1000-grains weight and main shoot weight were higher in heat tolerant cultivars as compared to sensitive cultivars. They suggested that relative grain number per ear and 1000-grains weights and main shoot weight be used to determine heat tolerance of wheat under late sowing condition. Saini *et al.*, (2002)<sup>[79]</sup> showed that in wheat all the yield determining traits were reduced under late sowing with the exception of harvest index, which registered an increase.

#### **Effect of Temperature on Wheat Growth, Yield and Yield Components**

(Mukherjee *et al.*, 2019)<sup>[56]</sup> reported that the analysis results indicate that the wheat yield loss corresponds to the increase in the number of days with a temperature above 35° C during the maturity stage (March). Direct impacts of temperature on wheat yield can be depicted by GDD and the frequency of extreme temperatures above 35° C during the growing season. They also reported that normalized GDD time series indicates a general high-GDD period during 2002–2010. A high-GDD environment can either shorten wheat maturity or directly

harm crop growth when the temperature exceeds the critical threshold. Additionally, a high GDD leads to early maturity which affects growth and yield. High temperature conditions also contribute to an overall negative effect on grain filling and physiological maturity. Wheat crop exposed to temperatures above 34° C after the anthesis stage has a significantly low yield due to accelerated senescence, decreased rate and duration of grain filling and reduction in grain weight. By quantifying the number of days with temperatures above 35 °C in March, which are critical for the grain filling and maturity, they found that the frequency of extreme stress (above 35 °C) conditions during crown root initiation, flowering, and grain filling stages can cause significant yield reduction and may lead to total crop damage. Additionally, continuous days with high temperatures can shorten wheat maturity.

Sinha and Swaminathan, (1991) <sup>[94]</sup> reported that the integrated impact of a rise in temperature and CO<sub>2</sub> concentration on yield of crops may be negative. An increase in winter temperature of 0.5° C would thereby reduce 10 per cent of wheat production in the high yield states of Northern India.

In northern India, a 1° C rise in mean temperature had no significant effect on potential yields but irrigated and rainfed yields increased in most places. An increase of 2° C in temperature reduced potential wheat yields at most places. A 2-3° C increase in temperature will reduce yields in the majority of the wheat growing areas (Aggarwal and Sinha, 1993) <sup>[3]</sup>, and this yield reduction will be greater in non-irrigated (and thus water stressed) crops due to rainfall variability. Therefore, the warmer regions will suffer crop losses. A minor increase of only 0.5° C during the winter is expected to decrease wheat yield by 0.45 t ha<sup>-1</sup>.

Hundal and Kaur, (1996) <sup>[40]</sup> examined the climate change impact on productivity of wheat crop in Punjab using CERES-wheat. They concluded that, if all other climate variables were to remain constant, temperature increase of 1,

2 and 3° C from present day condition, would reduce the grain yield of wheat by 8.1, 18.7 and 25.7%.

Attri and Rathore (2003) <sup>[12]</sup> reported that the yield enhancements of the order of 29 to 37% and 16 to 28% are obtained for different genotypes, under rainfed and irrigated conditions respectively, for a temperature rise coupled with elevated CO<sub>2</sub> levels (T max + 1.0° C, T min + 1.5° C and 460 ppmv CO<sub>2</sub>) compared with in the current climate. A further increase of temperature (T max + 2.0° C, T min + 2.5° C and 460 ppmv CO<sub>2</sub>) resulted in a yield reduction, but it was still higher than under the current climate. An increase of temperature in the order of 3° C or more cancels out the beneficial effects of elevated CO<sub>2</sub> in all the cultivars under study. Yields of normally sown cultivars (HD2329 and WH542) were higher under delayed sowing by 10 days and lower under advanced sowing by 10 days strategies, whereas the reverse trend was observed for late-sown cultivars (HD2285, Sonalika, Raj3765). A latitudes in India, it is frequently exposed to temperatures above the threshold for heat stress. For example, high maximum and minimum temperatures in September (about 34/20 °C) adversely affect seedling establishment, accelerate early vegetative development, reduce canopy cover, tillering, spike size and yield. Reduction in anthesis, maturity and evapotranspiration under A1 and an enhancement under A2 strategies were observed in normally sown cultivars, whereas the reverse trend was seen in late-sown cultivars.

Heat stress affects various plant processes leading to morpho-physiological alterations in wheat plants, hindering the development processes and eventually resulting into great yield loss (McClung and Davis 2010; Grant *et al.* 2011) <sup>[54, 33]</sup>. Plant responses to heat stress differ significantly with the extent and duration of temperature, and the growth stages encountering the stress (Ruelland and Zachowski 2010) <sup>[76]</sup>. Some common effects of heat stress on growth and productivity, grain development, and yield of wheat are presented in Table 1.

**Table 1:** Effects of heat stress at different stages of growth and development of wheat

Heat Stress	Growth stages	Major effects	Reference
45 °C	7 days after germination	Reduced length and dry mass of shoot and root; decreased chlorophyll and membrane stability index	Gupta <i>et al.</i> (2013) <sup>[34]</sup>
42 °C	Seedling stage	Inhibited roots and first leaves development; increased reactive oxygen species (ROS) and lipid peroxidation (LP) products in the coleoptile and developing organ	Savicka and Skute (2010) <sup>[83]</sup>
37/28 °C day/night	From 10 to 20 days post anthesis until maturity	Shortened grain filling period and maturity; drastically reduced fresh weight, dry weight, protein, and starch content in grain; reduced grain size and yield	Hurkman <i>et al.</i> (2009) <sup>[41]</sup>
34/26 °C (day/night)	At the grain-filling stage	Increased leaf temperature; decreased leaf chlorophyll and maximum quantum yield of photosystem-II; decreased in individual grain weight and grain yield	Pradhan and Prasad (2015) <sup>[65]</sup>

Temperature has a complex relationship with spikelet formation, maturity and grain yield since there is usually an optimum value for different processes. The adverse effects of high temperature were found during the grain development phase (Shukla *et al.*, 1988) <sup>[89]</sup>. Grain weight per ear has been found negatively correlated with grain number and therefore, selection for superior grain weight per ear at high density might be desirable (Rawson and Bagga, 1979) <sup>[73]</sup>. Savin and Slafer (1991) <sup>[84]</sup> reported that wheat is a sink limited crop where the capacity of the grain to accept assimilates was more important in determining the grain weight than the capacity of green tissues transport assimilates. Pande *et al.* (1992) <sup>[62]</sup> reported that by increasing sink size and weight, the grain density was decreased and hence wheat may not be a sink limited crop during grain growth. Gibson *et al.* (1999) <sup>[32]</sup>

found that the grain yield was reduced by 78%, kernel number was reduced 63% and kernel weigh was reduced by 29 per cent at 35 °C/20 °C compared with 20 °C/20 °C from 10 days after anthesis until ripeness. High temperature imposed from 20 days after anthesis decreased kernel weight by 18%. Elena *et al.* (2002) <sup>[26]</sup> concluded that the significance of the heat stress response and expression of HSPs in thermo tolerance of cereal yield and quality is major avenue for increasing thermo tolerance in cereals via conventional breeding or genetic modification. Gupta *et al.* (2002) <sup>[35]</sup> studied the effect of normal and late sown condition on grain growth and yield determining parameters in contrasting wheat genotypes and suggested that tolerance for both grain number and grain weight are important under late sowing but grain number is more important for sustaining the growth under these

conditions. Sarkar *et al.* (2002) <sup>[82]</sup> showed that path analysis confirmed the results of correlation and revealed the importance of the three traits on grain yield, suggesting their direct use for genetic improvement of wheat suited for any environment. Rane *et al.* (2003) <sup>[71]</sup> indicated that the stem reserves play a significant role in determining grain yield under late sown environment.

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