JOURNAL OF CURRENT RESEARCH IN FOOD SCIENCE

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Review on effect of increased temperature on respiratory costs: Focus on crops

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Abstract
Temperature has an effect on physiological, biochemical, morphological, anatomical and agronomic systems of the plant at different levels. The increased temperature which fastens photosynthesis and respiration of plants and microbes, especially in temperate latitudes. Plant growth and development highly affected by temperature. Production and productivity of plants influenced due to extreme temperature. The phenological stages of the plant like flowering or blooming are very sensitive to extreme temperature for all species and also during developmental stage. Extreme temperature would also affect the crop calendar in tropical regions. The effects of temperature are associated with water deficits and excess soil water demonstrating. To develop more effective adaptation strategies to counterbalance the influences of better temperature extreme events connected with a changing climate the interaction of temperature and water has a vital role. As many studies showed that studying the characteristics of crops and following breeding of plant for adaptation extreme environmental events especially increased temperature are important to grow crops in different agro-ecological zones. The main objective of this seminar is to review the effect of increased temperature on respiratory costs by giving emphasis on crops. This seminar was done to assess the effects and impacts of increased temperature on growth, development and yield, and its attributing characters of crops, and respiratory costs of crops from different sources to provide relevant knowledge to the producers and readers.

Keywords: Temperature, respiratory cost, crops

1. Introduction
Human activities are substantially increasing the concentrations of atmospheric greenhouse gases, particularly carbon dioxide, methane, chlorofluorocarbons and nitrous oxides. Increased concentrations of greenhouse gases will increase average world temperature as Global circulation models predict. Global mean temperatures will rise 0.3°C per decade during the next century with an uncertainty of 0.2 to 0.5%, under the business scenario of the Intergovernmental Panel on Climate Change (IPCC), Thus, global mean temperatures should be 1°C above the present values by 2025 and 3°C above the present value by 2100 (Houghton *et al.,* 1990) [21].

Increased temperature especially in temperate latitude increase the photosynthesis and respiration of plants and microbes. Photosynthesis is less response to increase temperature as compared to respiration. Increase the flux of carbon dioxide to the atmosphere is one of the causes of global warming. Temperature effects at different levels of organization, biochemical, physiological, morphological, agronomic and systems are considered. Identifying researches for germplasm improvement and crop management that may mitigate the adverse effects of higher day and night temperatures. The plasmalemma and membranes of cell organelles play a vital role in the functioning of cells. Disruption of cellular activity or death are caused by any adverse effect of temperature stress on the membranes. Heat injury to the plasmalemma may be measured by ion leakage (Chaisompongpan *et al.,* 1990; Hall, 1993) [17]. Denaturation of the membrane proteins or melting of membrane lipids are caused to injury membranes from a sudden heat stress event which leads to membrane rupture and loss of cellular contents from either (Ahrens and Ingram, 1988) [2]. Heat stress may be an oxidative stress (Lee *et al.,* 1983) [24]. At high temperatures, peroxidation of membrane lipids has been observed (Mishra and Singhal, 1992; Upadhyaya *et al.,* 1990) [31, 37], which is a symptom of cellular injury. Increase cell tolerance to heat may be the result of enhanced synthesis of an anti-oxidant by plant tissues (Upadhyaya *et al.,* 1990, 1991) [37, 38] but no such anti-oxidant has been positively identified.

Objective
To review the effect of increased temperature on respiratory costs.

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2. Review of literature

2.1 Temperature in the plant environment

From all the planets, the thermal environment on earth is particularly fit to give rise to and sustain life. This is because life functions in an aqueous medium and the range of temperatures encountered over most of the earth's surface generally ensures that sufficient water is maintained in the liquid state. The temperature at which biological processes can occur is generally limited by the freezing point of water on the low side and the irreversible denaturation of proteins on the high side. Between these two extremes, a plot of growth versus temperature for individual organisms assumes the shape of an asymmetric bell curve, similar to that for individual enzyme reactions or multiple enzyme-catalyzed metabolic sequences.

2.1.1 Temperature influences plant distribution

Temperature is thought to be one of the most important factors limiting the worldwide distribution of plants. Distribution limits often reflect temperature characteristics of major metabolic processes, especially photosynthesis. The temperature range compatible with growth of higher plants lies generally between 0◦C and 45◦C, although there are some plants that exceed either of these limits and within those limits' temperature compatibility is very much species dependent. For a number of different species typical of grain and fruit production specific temperature is summarized by (Hatfield *et al*., 2008, 2011) [8, 11].

As a general rule, temperatures that are optimum for growth reflect the geographical region in which the species originated. Thus, plants native to warm regions either require or perform better at higher temperatures those that originated in cooler areas of the world. The optimum for maize (*Zea mays*), a plant of tropical origin, is in the range 30℃ to 35℃ and it will not grow below 12℃ to 15℃. Garden-cress (*Lepidium sativum*), a temperate herb, will grow at temperatures as low as 2℃ but its maximum temperature for growth is 28℃. Biogeography is the effects of temperature on physiology and metabolism in turn influence plant distribution. At times, temperature-related metabolic effects not only limit distribution, but have significant economic implications as well. Cotton (*Gossypium*), for example, is a southern crop in part because cool night temperatures in northern latitudes adversely affect fiber cell wall thickening, and the northern limits for maize production are very much limited by its inability to grow at lower temperatures. Responses to temperature differ among crop species throughout their life cycle and are primarily the phenological responses, i.e., stages of plant development. For most plant species; vegetative development usually has a higher optimum temperature than for reproductive development. Cardinal temperature values for selected annual (non-perennial) crops are given in for different species (Hatfield *et al*., 2008, 2011) [8, 11].

2.1.2 Extreme temperature effects on crops

There are two major forms of extreme temperature stress on crops - heat and cold. An increase in global temperatures may have either or both of these two acute effects: more frequent high temperature stress and less frequent cold temperature stress. Increase in temperature will lengthen the effective growing season in areas where agricultural potential is currently limited by cold temperature stress. Thus, increased temperature will cause a pole ward shift of the thermal limits to agriculture. Global warming impact will be greater in the northern than southern hemisphere because there is more high-latitude area cultivated in the northern hemisphere. In tropical regions the crop calendar may be affected by increased temperature. In the tropics, however, global warming, though predicted to be of only small magnitude, is likely to reduce the length of the effective growing season, particularly where more than one crop per year is grown. Acute effects of high temperature are most striking when heat stress occurs during anthesis. In rice, heat stress at anthesis prevents anther dehiscence and pollen shed, to reduce pollination and grain numbers (Mackill *et al.,* 1982; Zheng and Mackill, 1982) [27].

2.1.3 Long-term effects of high temperatures on crops

Acute effects of extreme temperature stress are more important than the chronic effects of continuously warmer temperatures on crop growth and development. Chronic effects of high temperature include effects on grain growth discussed above. Record crop yields clearly reflect the importance of season-long effects on crop yields: crops generally yield the foremost where temperatures are cool during growth of the harvested component. Crop growth simulations show that rice yields decrease 9% for each 1°C increase in seasonal average temperature. This chronic effect of high temperature differs significantly from the acute effect of short-term temperature events, because seasonal temperature effects are mostly a result of effects on crop development. There is much greater genotypic variation in thermal requirements for vegetative than for reproductive development in most grain crops. As long-term temperatures increase, grain-filling periods decrease, and there appears to be little scope to manipulate this effect through existing genetic variation within species (Kropff *et al.,* 1993) [24].

2.2 Crop growth and development

Plant development is customarily divided into vegetative and reproductive phases, with either ear emergence or anthesis as the event that separates the two phases. In the past 30 to 40 years, the sequence of pre-anthesis phenological events has been critically assessed with respect to grain yield potential and sensitivity to weather variables, particularly prevailing temperature and day length. Several systems are used to classify the sequence of phenological events. We identify five developmental stages of Wheat:

a. Germination - seeding to seedling emergence
b. Canopy development - appearance to first spikelet initiation, the double ridge stage
c. Spikelet production - first spikelet initiation to terminal spikelet formation
d. Spikelet development - terminal spikelet formation to anthesis
e. Grain development - anthesis to maturity

These stages are generally based on early recognized features of the apical meristem. They mark significant changes in morphology or physiology of different crop organs. Numbers of leaf and tiller primordial are determined before spikelet initiation, but temperature is controlled their subsequent growth and development, and day length during the differentiation of spikes into spikelets. Similarly, floret number within each spikelet is established by anthesis, at which time the potential grain number per spike is

established. At high temperatures, productivity of wheat and other crop species falls decidedly. During some stages of development of wheat in India is consistently exposed to extreme temperatures (Abrol *et al.,* 1991) [1].

2.2.1 Vegetative phase

Numerous experiments have observed the effects of temperature on the duration from sowing or emergence to heading under field conditions and controlled environment. However, few experiments have been conducted with enough cultivars to assess the genetic variability in this trait. The major conclusions from these studies are:

1. At one stage or another, all genotypes are sensitive to temperature. Temperature sensitivity, however, varies greatly with genotype.
2. Phenological stages differ in sensitivity to temperature.
3. The duration of phase from sowing to first spikelet initiation is less sensitive to change in temperature than are other phases, although genotypes do differ in thermo-tolerance during this phase.
4. The stages during which environment has the greatest impact on yield are from first spikelet initiation or terminal spikelet formation until anthesis. Both dominant yields contributing attributes that are spikelet number and floral number (potential grain number) are established during these phases. On the other hand, Grain weight appears to be much less sensitive to heat stress than is grain number.

2.2.2 Grain development phase

According to Asana and Williams (1965) [6] reported that the experiments under controlled conditions from 25 to 35°C, the average grain weight decreased 16% for each 5°C increase in temperature. In pot experiments, grain yield decreased by 17% for each 5°C rise (Wattal, 1965) [1, 41]. For every 1°C rise in temperature, there is a depression in grain yield by 8 to 10%, mediated through 5 to 6% fewer grains and 3 to 4% smaller grain weight. To elucidate the causal factor for reduced grain filling in wheat because of higher temperatures, Wardlaw (1974) [39] studied the three main components of the plant system. The three components are: (a) source - flag leaf blade; (b) sink - ear; and (c) transport pathway - peduncle. It depicted that the optimum temperature of photosynthesis range from 20 to 30°C with photosynthesis decreasing rapidly at temperatures over 30°C. The rate of 14C assimilate movement through the stem was independent of temperature from 1 to 50°C; the rate of 14C assimilate movement out of the flag leaf, phloem loading, was optimum around 30°C. Thus, in wheat, temperature effects on translocation result indirectly from direct temperature effects on source and sink activities. As Wardlaw *et al. (*1980) [40] showed that in a subsequent experiment with source-sink relationships changed through grain excision, defoliation and shading treatments, heat stress still reduced grain weight. This result supports the earlier findings that temperature effects on grain weight are direct effects rather than assimilate availability (Bremner and Rawson, 1978; Ford *et al.,* 1978; Spiertz, 1974) [11]. Furthermore, respiration effects do not appear to be the direct cause of decreased grain size in heat-stressed wheat (Wardlaw, 1974) [39].

Reduction of grain weight by heat stress could even be explained mostly by effects of temperature on rate and duration of grain growth. As temperature increased from 15/10°C to 21/16°C, duration of grain filling was reduced from 60 to 36 days and grain growth rate increased from 0.73 to 1.49 mg/grain/day with a result of minimal influence on grain weight at maturity. Further increase in temperature from 21/16°C to 30/25°C resulted in decline in grain filling during 36 to 22 days with a minimal increase in grain growth rate from 1.49 to 1.51 mg/grain/day. Thus, mature grain weight was significantly reduced at the absolute best temperature. Under long-term exposure to heat stress, increased grain nitrogen concentration is almost entirely as a result of decreased starch content rather than a change in total grain quality (Bhullar and Jenner, 1985) [9].

The conversion of sucrose to starch within the endosperm is decreased by elevated temperatures. Furthermore, heat stress effects on final grain weight were associated with reduced levels of soluble starch synthetase activity. In summary, heat reduction of grain yield results from: (a) reduced numbers of grains formed; (b) shorter grain growth duration; and (c) inhibition of sucrose assimilation in grains (Hawker and Jenner, 1993) [20].

2.3 Photosynthesis and high temperature stress

Variability in leaf photosynthetic rates within or between species is typically unrelated to differences in productivity. Similarly, high photosynthetic rates at high temperatures do not necessarily support high rates of crop dry matter accumulation. The temperature optimum for photosynthesis is broad, presumably because crop plants have adapted to a relatively wide range of thermal environments. A 1 to 2°C increase in average temperature is not likely to possess a substantial impact on leaf photosynthetic rates. Further, there is a chance that photosynthesis of crop plants can adapt to a slow increase in global mean temperatures. Thus, global warming is not likely to affect photosynthetic rates per unit leaf area gradually or on a closed canopy basis over the next century. While photosynthetic rates were found to be temperature-sensitive in other crops, wheat and rice appear to vary. In wheat, no measurable differences were found in photosynthetic rates per unit flag leaf area or on a whole-plant basis in the temperature range from 15 to 35°C (Bagga and Rawson, 1977) [7]. In rice, there is little temperature effect on leaf CO_2 assimilation from 20 to 40°C (Egeh *et al.,* 1994) [16].

Recent research has shown significant variation among wheat cultivars with reference to reduction in photosynthesis at very heat. Photosynthesis of germplasm adapted to higher temperature environments was less sensitive to heat than was germplasm from cooler environments (Al-Khatib and Paulsen, 1990) [3].

2.3.1 Mechanisms for heat tolerance

Crop plants are immobile. They necessity adapt to prevalent soil and weather conditions. Apart from transpiration cooling, plants are unable to manage their tissue temperatures to any significant extent. On the other hand, plants have evolved several mechanisms that enable them to tolerate higher temperatures. These adaptive thermo tolerant mechanisms reflect the environment in which a species has evolved and they largely dictate the environment where a crop could also be grown. Four major aspects of thermo tolerance are studied: (1) thermal dependence at the biochemical and metabolic levels; (2) thermal tolerance in reference to membrane stability; (3) Induced thermo tolerance through gradual temperature increase is

production of warmth shock proteins; and (4) photosynthesis and productivity during heat stress.

2.3.1.1 Thermal stability of cell membranes
The plasmalemma and membranes of cell organelles play a crucial role in the functioning of cells. Any adverse effect of temperature stress on the membranes leads to disruption of cellular activity or death. Heat injury to the plasmalemma could even be measured by ion leakage (Chaisompongpan *et al.,* 1990; Hall, 1993) [17]. Injury to membranes from a sudden heat stress event may result from either denaturation of the membrane proteins or from melting of membrane lipids which ends up in membrane rupture and loss of cellular contents (Ahrens and Ingram, 1988) [2]. Heat stress could even be an oxidative stress (Lee *et al.,* 1983) [24]. Peroxidation of membrane lipids has been observed at high temperatures (Mishra and Singhal, 1992; Upadhyaya *et al.,* 1990) [31, 37], which is a symptom of cellular injury. Enhanced synthesis of an anti-oxidant by plant tissues may increase cell tolerance to heat (Upadhyaya *et al.,* 1990, 1991) [37, 38] but no such anti-oxidant has been positively identified.

A relationship between lipid composition and incubation temperature has been shown for algae, fungi and higher plants. In *Arabiodopsis,* exposed to high temperatures, total lipid content decreases to about one-half and the ratio of unsaturated to saturated fatty acids decreases to one-third of the levels at temperatures within the TKW (Somerville and Browse, 1991). Increase in saturated fatty acids of membranes increases their melting temperature and thus confers heat tolerance. An *Arabiodopsis* mutant, deficient in activity of chloroplast fatty acid W-9 desaturase, accumulates large amounts of 16:0 fatty acids, resulting in greater saturation of chloroplast lipids. This increases the optimum growth temperature (Kuns *et al.,* 1989; Raison, 1986) [25, 34].

In cotton, however, heat tolerance does not correlate with degree of lipid saturation (Rikin *et al.,* 1993) [35] and similar differences in genotypic differences in heat tolerance have been unrelated to membrane lipid saturation in other species (Kee and Nobel, 1985) [23].

2.3.1.2 Biochemical processes
Temperature effects on the rates of biochemical reactions could also be modelled as the product of two functions, an exponentially increasing rate of the forward reaction and an exponential decay resulting from enzyme denaturation as temperatures increase. The greatest concern is whether it is possible to increase the upper limit of enzyme stability to prevent denaturation. Failure of only one critical enzyme system can cause death of an organism. This fact may explain why most crop species survive sustained high temperatures up to a relatively narrow range, 40 to 45°C. The relationship between the thermal environment for an organism and the thermal dependence of enzymes has been well established (Senioniti *et al.,* 1986) [36]. The shape of this function also describes temperature effects on most biological functions, including plant growth and development. The function can be categorized by the three cardinal temperatures - minimum, optimum and maximum. Modellers frequently simplify the relationship into a stepwise linear function. The stepwise linear function has a plateau rather than an optimum temperature (Hatfield *et al.*, 2008, 2011) [8, 11].

The thermal dependence of the apparent reaction rate for selected enzymes may indicate the optimal thermal range for a plant. The range over which the apparent Michaelis-Menten constant for CO_2 (K_m) is minimal and stable is termed the thermal kinetic window (Mahan *et al.,* 1987) [28]. For crop plants, the thermal kinetic window (TKW) is generally established as a result of thermally induced lipid phase changes, rubisco activity and the starch synthesis pathway in leaves and reproductive organs (Burke, 1990) [12]. In cotton and wheat, the time during which foliage temperature remained within the TKW was related to dry matter accumulation. The cumulative time that rainfed crop foliage is outside the TKW provides an index of the degree of extreme temperature stress of the environment. Irrigation is one management option to reduce crop exposure to heat stress (Burke *et al.,* 1988) [13].

Temperatures that inhibit cellular metabolism and growth for a cool season C_3 species such as wheat may not inhibit warm-season C_3 species such as rice (*Oryza sativa* L.) and C_4 species such as sorghum, maize (*Zea mays* L.) and sugar cane (*Saccharum spontaneum* spp.). The identification of TKWs for different species can aid in the interpretation of the differential temperature stress responses for crop growth and development among species (Burke, 1990) [12].

2.3.1.3 Physiological and molecular indicators of tolerance to increased temperature
Plants have evolved various mechanisms to ensure survival under elevated temperatures. These strategies are classified into long-term phenological and morphological evolutionary adaptations such as changing leaf orientation, transpirational cooling or alterations in the membrane lipid composition, or short-term stress avoidance and acclimation mechanisms. Among general stress tolerance mechanisms, stress proteins, osmo-protectants, free-radical scavengers, ion transporters and factors involved in signaling cascades and transcriptional control are essential to counteract stress effects (Wang *et al.*, 2004) [42].

2.4 Effects of temperature on total respiration
Plant respiration rates are affected by numerous abiotic factors, and temperature is one of particular significance. There is a direct relationship between respiratory rate and temperature in the short term because the kinetics of most metabolic reactions is highly temperature dependent (Raison, 1980). In addition to short-term responses, plants grown at low temperatures often show higher rates of respiration than plants grown at higher temperatures when both are measured at the same temperature (Amthor, 1989; Collier and Cummins, 1990) [4, 15]. This stimulation of respiration by growth at low temperatures has been reported to be an adaptive feature of plants grown in cold and arctic climates compared with related species or ecotypes from warmer climates (Billings, 1974; McNulty and Cummins, 1987) [10, 29]. It has also been suggested that the increased rate of respiration at low temperatures involves a greater participation by the alternative pathway (McNulty *et al.*, 1988; Purvis and Shewfelt, 1993) [30, 33].

For example; Total respiratory activity of Mung bean hypocotyls was over 2-fold higher in low-temperature-grown versus high-temperature-grown plants whether measured at the higher (28°C) or the lower (19°C) growth temperature. However, total respiration was the same for hypocotyls from plants grown at 19°C as for plants grown at

28°C when measured at their respective growth temperature, indicating a marked acclimation response of respiration to growth temperature in hypocotyls.

2.4.1 Efficiency of respiratory ATP production
ATP production efficiencies from sucrose and reducing equivalents were estimated according to Amthor (1994) [5]. It assumed that oxidation of 1 mol of sucrose via pyruvate produces 58 mol of ATP, and that all sucrose is degraded by invertase. The number of ATP produced via mitochondrial oxidation of reducing equivalents (P_{ATP}; mol ATP) was estimated as where [$H^+_{III, IV}$] and [$H^+_{I, III, IV}$] are the numbers of protons pumped into the inter-membrane space when a pair of electrons flows through Complex III/IV and Complex I/III/IV, respectively. We adopted 6 for [$H^+_{III, IV}$] and 10 for [$H^+_{I, III, IV}$]. [$NADH_{cyt}$], [$NADPH_{cyt}$], [$FADH_2$] and [$NADH_{mit}$] are the concentrations of the corresponding reductants, and the subscripts 'cyt' and 'mit' indicate the cytosol and mitochondrial matrix, respectively, and indicate the compartments where these reductants are produced. In the respiratory oxidation of sucrose via pyruvate, [$NADH_{cyt}$], [$NADPH_{cyt}$], [$FADH_2$] and [$NADH_{mit}$] are given the values 4, 0, 4 and 16, respectively. [H^+_{ATP}] is the number of protons moving through H+-ATPase per ADP that undergoes phosphorylation; a value of 3 was used for the calculation (Amthor, 2000).

2.4.2 Heat shock proteins
Synthesis and accumulation of proteins were ascertained during a rapid heat stress. These were designated as 'Heat Shock Proteins' (HSPs). Subsequently it was shown that increased production of these proteins also occurs when plants experience a gradual increase in temperature more typical of that experienced in a natural environment. Correlation between synthesis and accumulation of heat shock proteins and heat tolerance suggests, but does not prove, that the two are causally related. Further evidence for a causal relationship is that some cultivar differences in heat shock protein expression correlate with differences in thermo-tolerance. In genetic experiments, heat shock protein expression co-segregates with heat tolerance. Another evidence for the protective role of heat shock protein is that mutants unable to synthesize heat shock proteins and cells in which HSP70 synthesis is blocked or inactivated, are more susceptible to heat injury. The mechanism by which heat shock proteins contribute to heat tolerance is still not certain. One hypothesis is that HSP70 participates in ATP-dependent protein unfolding or assembly/disassembly reactions and they prevent protein denaturation during stress. If this mechanism is true, then heat shock proteins may provide a significant basis for increasing heat tolerance of crop plants in a global warming situation (Pelham, 1986). HSPs provide a significant opportunity to increase heat tolerance of crops. To elucidate their mechanisms of action and to exploit their potential contribution to increasing heat tolerance, four lines of investigations are suggested:
1. Establish the biochemical activities of individual HSPs as a preliminary step
2. Characterize the genetic variability of specific heat shock proteins across a wide range of germplasm. For production of low and high levels of HSP synthesis develop iso-population and near isogenic lines are selected
3. Analyze the molecular details of HSPs processes and establish all participating protein substrates appear to participate in maintaining the conformation or assembly of other protein structures
4. Identify specific HSP mutants or create transgenic mutant plants to complement molecular and biochemical understanding with genetic approaches

Conflict of interest
I declare no conflict of interest.

3. Summary and Conclusion
Temperature may be a primary factor affecting the speed of plant development. Warmer temperatures expected with climate change and the potential form or extreme temperature events will impact plant productivity. Temperature extremes across all species affect the phenological stages of the crop among them pollination is the most sensitive and through this developmental stage it would greatly affect production. Few adaptation strategies are available to deal with temperature extremes at this developmental stage aside from to pick for plants which shed pollen during the cooler periods of the day or are in determinate so flowering occurs over an extended period of the season. In controlled environment studies, warm temperatures increased the speed of phenological development; However, there was no effect on leaf area or vegetative biomass compared to normal temperatures. The major impact of warmer temperatures was during the reproductive stage of development and altogether cases grain yield could loss up to 80% 90% from abnormal temperature regime. Temperature effects are increased by water deficits and excess soil water demonstrating that understanding the interaction of temperature and water are going to be needed to develop simpler adaptation strategies to offset the impacts of greater temperature extreme events related to a changing climate.

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