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Effect of temperature on stem reserve mobilization for grain development in wheat

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Abstract

Wheat (*Triticum aestivum*) is the first important and strategic cereal crop for the majority of world's populations. In 100 grams, wheat provides 327 calories and is an excellent source of multiple essential nutrients, such as protein, dietary fiber, manganese, phosphorus and niacin. Several B vitamins and other dietary minerals are in significant content. High temperature (>30°C) at the time of grain filling is one of the major constraints in increasing productivity of wheat in tropical countries like India (Zhao 2007). This survey/review may likewise help in interdisciplinary study regards to influence of temperature stress on stem reserve mobilization when wheat plants suffer from arrested photosynthesis during stress condition

Keywords: Wheat, temperature stress, stem reserve mobilization, grain development

Introduction

Wheat (*Triticum* spp.) is a cereal grain, originated from South West Asia but now cultivated worldwide. It belongs to family Gramineae. Wheat (*Triticum aestivum*) is the first important and strategic cereal crop for the majority of world's populations. It is the most important staple food of about two billion people (36% of the world population). Yield loss of 29% is expected by 2080 due to global warming, in wheat. Annual yield loss in wheat due to global warming is expected to be 7.7 billion dollars, and by 2025, this would be around 18 billion dollars. To meet the requirement, there will be need to produce just double from the present production level, to feed near about 950 million people by 2050 if, the population growth continues with the present growth rate.

Reserve accumulation in the stem and the size of the storage strongly depend on the growing conditions before anthesis. Total stem nonstructural carbohydrate (TNS) at anthesis was shown to vary from 50 to 350 g kg-1 dry mass in different experiments (Kiniry, 1993) [22]. Under optimal growing conditions with regard to temperature, water regime (Davidson and Chevalier, 1992) [9] and mineral nutrition (Papakosta and Gagianas, 1991) [28], carbon assimilation rates are high and a proportion of the assimilation during stem elongation is reduced by stress, storage in stems is reduced.

High temperature (>30°C) at the time of grain filling is one of the major constraints in increasing productivity of wheat in tropical countries like India (Zhao 2007) [46]. It has been reported that single grain mass falls by 3% - 5% for every 1°C rise in temperature above 18°C (McDonald 1983) [26]. The supply of assimilates to the developing grain originates both from direct transport of current assimilation to kernels, and from the remobilization of temporarily stored assimilates in vegetative plant parts (Gebbing *et al.*, 1999) [15]. The reserves deposited in vegetative plant parts before anthesis may buffer grain yield when conditions become adverse to photosynthesis and mineral uptake during grain filling (Tahir and Nakata 2005) [40].

Stem reserve carbohydrates are commonly considered as total-nonstructural carbohydrates (TNC) or water soluble carbohydrates (WSC) and distinguished from the structural carbohydrates present in cell walls (Ruska *et al.*, 2006) [33]. Stem reserve carbohydrates principally consist of fructan, sucrose, glucose, fructose and starch, although fructan is the main reserve (Wardlaw and Willenbrink, 1994) [44]. Carbohydrate storage ability in stem and remobilization efficiency of reserves for grain development are effective components contributing to grain yield (Ehdaie *et al.*, 2006a, b) [12]. Ability of carbohydrate storage in stem is determined by stem specific weight and stem length (Blum 1998) [13]. The amount of accumulated WSC in stem depends upon environmental conditions in pre- and post-anthesis until linear growth stage of grain (Blum 1998, Takahashi *et al.*, 2001) [13, 41].

Though, heat stress affects the metabolic pathways at every stage of life of wheat finally leading to yield reduction, the effect of high temperature is particularly severe during grain filling; these losses may be up to 40 % under severe stress (Hays *et al.*, 2007). Other effects of high temperatures are decreased grain weight, early senescence, shriveled grains, reduced starch accumulation, altered starch-lipid composition in grains, lower seed germination and loss of vigour (Balla *et al*., 2012) [2]. In late sown wheat, terminal heat stress is the main cause of yield reduction which is responsible for shortening of grain growth period and improper grain filling (Reynolds *et al*., 2001; Rane *et al*,. 2007). Every 1°C rise in temperature above 28°C during grain filling, results in yield reduction by 3–4% (Reynolds *et al*., 1994, 1998; Wardlaw *et al*. 1989) [].

Parameters used for heat stress tolerance

1. Reserve accumulation

Reserve accumulation and storage capacity in the stem strongly depend on the growing conditions before anthesis. Total TNC at anthesis was shown to vary from 50-350 g/kg dry mass in different experiments (Kiniry, 1993) [22]. Under optimal growing conditions with regard to temperature, water regime (Devidson and Chevaliar, 1992) [9] and mineral nutrition (Papakosta and Gagianas, 1991) [28], carbon assilmilation rates are high and a proportion of the assimilates is allocated to storage. When carbon assimilation during stem elongation is reduced by stress, storage in stem is reduced. When the ambient CO2 concentration is raised to increase assimilation, more carbon get stored in stems (Winzeler *et al*., 1989). Potential stem storage as a sink is determined by stem length and stem weight density. Stem weight density is equal to stem dry weight per unit stem length. Storage and remobilization may vary along the stem. In winter barley, the basal internodes were found to contribute the most to grain filling (Bonnett and Incoll, 1992a) [5]. In wheat, the peduncle and the penultimate internode contribute contained the most storage (Wardlaw and Willenbrink, 1994) [43], with variations in storage and remobilization under different experimental conditions being larger in the penultimate than in the fourth stem internode. (Bonnett and Incoll, 1992a) [5].

Stem length is important in affecting stem reserve storage. The Rht1 and Rht2 dwarfing genes of wheat were found to reduce reserve storage by 35% and 39% respectively, as a consequence of a 21% reduction in stem length (Borrell *et al*., 1993) [6].

Ehdaie *et al*., (2005) [11] evaluated the hypothesis that internode length, weight, and specific weight of genotypes affect accumulation and mobilization of stem reserves. Balanced partitioning of stem length into upper and lower internodes and internode maximum specific weight are important in genotypic accumulation and mobilization of stem reserves in wheat.

The development and growth of grains depend mainly on current assimilates that are directly translocated to the grains, but carbohydrate assimilated after anthesis are temporarily stored in the stem, before being mobilized to the grains and play important role. The third source of carbohydrates to grains are very important for grain filling under stress is the carbohydrates synthesized before anthesis accumulated mainly in the stem and mobilized to developing kernel (Ehdaie *et al*., 2006) [12].

2. Reserve utilization

Stem reserve mobilization, or percentage of stem reserves in total grain mass, is affected by sink size, by the environment and by cultivar. The demand by grain sink is a primary factor in determining stem reserve mobilization. When sink size is get reduced by degraining, more reserves get stored in the stem, compared with intact ears (Kuhbauch and Thome, 1989) [15]. The interaction between ear size and demand for stem storage appears to depend on the environment, before or during grain filling (Bonnett and Incoll, 1992a) [5].

Fokar *et al*., (1998) [13] established the role of stem reserves in sustained wheat grain filling under heat stress and observed significant variation among cultivars in the reduction in grain weight per ear (RGW), kernel number and single kernel weight. Differences in RGW a mong cultivars were found responsible for variation in the reduction in both kernel weight and kernel number whereas, variation in the potential capacity for using mobilized stem reserves among cultivars was attributed to variations in both kernel weight and kernel number under ear shading and defoliation

Nayyar *et al.,* (2012) [27] evaluated 21 Pakistani genotypes for stem reserve utilization and concluded that, tested genotypes vary considerably in stem reserve utilization when subjected to post anthesis chemical desiccation inhibiting the photosynthesis.

Sanghera and Thind (2014) [35] studied the impact of heat stress during grain filling period of wheat negatively effects the dry matter production of wheat genotypes. Delay in sowing date significantly reduces the dry matter accumulation of wheat genotypes at anthesis as well as maturity. This reduction in dry matter accumulation in grain may be attributed to high temperature stress faced by late sown genotypes during their grain filling period.

Zamani *et al*., (2014) [45] evaluated the ability of different wheat genotypes for accumulation and remobilization of stem water soluble carbohydrates (WSC) under heat stress and concluded that WSC remobilization increased under heat stress and there is strong association between maximum WSC concentration in main stem and WSC remobilization was found.

3. Proline content

Heat stress imposed at anthesis and milky growth stages significantly increases proline concentration in leaves of wheat, also it increases soluble protein content. High temperature decreased the membrane stability index at both at anthesis and milky growth stages (Khan *et al*. 2015) [31].

Under high temperature, free proline is involved in osmotic adjustment to protect pollen and plant enzymes from heat injury and also provides a source of nitrogen and other metabolites (Verslues and Sharma 2010) [42]. Certain heat shock genes are triggered, resulting in the synthesis of heat shock proteins, whereas other soluble and insoluble proteins have also been shown to exhibit changes in abundance under high temperature stress (Simmonds 1995, He *et al*., 2005) [38, 18].

Khan *et al*., (2013) evaluated twenty wheat genotypes including advance lines and cultivated varieties for terminal heat stress under glass house conditions in pot culture using completely randomized design with three replications. Plants were exposed to 35-40 °C temperature 3 hours daily for five consecutive days. Control plants were kept under normal temperature conditions. The stress tolerance indicators such as Superoxide dismutase (SOD), Peroxidase (POD), Photosynthates stem reserves (PSR), Membrane stability index (MSI) and grain yield revealed significant ($p<0.05$) effect of high temperature on growth and physiological attributes of wheat at anthesis growth stage.

Asthir *et al*., (2012) [1] studied effect of high temperature in relation to carbon partitioning and grain sink activity in ten genotypes of wheat under normal (November, 25.6°C during grain filling) and late planting conditions (December, 29.4°C). Significant reduction in total free sugars and sucrose content was observed during grain development. Results suggested that decline in sugar content in spite of high sucrolytic enzymes may be correlated to more utilization of assimilates over production/translocation for grain sink activity under high temperature influences.

Gabal and Tabl (2014) [14] evaluated heat tolerance of wheat through physiological approaches. The relative value proline content higher amount was found in HT cultivar compared to that in HS cultivar expected cultivar Giza168 which was observed as HS cultivar but showed high relative value proline content. The seedling proline content at 35° C and membrane injury (%) maintained a significant negative correlation (r = - 0.818**) across the six Egyptian wheat cultivars, indicating that wheat cultivars with high proline level at 35° C tended to show greater thermotolerance.

Hussain *et al.,* (2015) reported that sowing dates severely influenced protein and carbohydrate contents in subsequent grains of wheat crop. Wheat crop sown from the seeds obtained from the crop previously sown at November 10 and 25 showed better grain protein and carbohydrate content as compared to December 10 and 25.

4. Canopy Temperature Depression

The heat tolerant cultivars showed higher canopy temperature depression than the heat sensitive cultivars in both the growing conditions indicating the higher ability of heat tolerant cultivars to maintain cooler canopy environment than the heat sensitive ones.

Renolds *et al*., (1994) [31] reported the existence of varietal difference for canopy temperature depression among wheat germplasm tested under heat stress condition.

Renolds *et al*., (1998) [32] concluded that potential to keep canopy cool is one of the important traits of high temperature tolerant wheat genotypes.

Sikder and Paul (2010) [37] tested four heat tolerant (Gourab, Sourav, Kanchan and Shatabdi) and two heat sensitive (Sonora and Kalyansona) wheat cultivars under normal and late growing post-anthesis heat stress conditions revealed higher pre-anthesis stem reserves mobilization to the final grain weight and floret sterility in heat sensitive cultivars compared to heat tolerant cultivars.

5. Membrane Stability Index

High temperature causes modifications in membrane functions mainly because of the alteration of membrane fluidity. In plant cells, membrane–based processes such as photosynthesis and respiration are especially important. Three commonly used assays of heat tolerance in plants (Blum 1988) are related to the plasmalemma (cell membrane stability), the photosynthetic membranes and the mitochondrial membranes. The indirect/ slower heat injuries include inactivation of enzymes in chloroplast and mitochondria and increased fluidity of membrane lipids. Different physiological traits such as membrane thermostability (Sadalla *et al*. 1990; Shanahan *et al.,* 1990; Renolds *et al*., 1994) [31, 36] and proline content (Hasan *et al*., 2007) have been associated with performance of irrigated wheat under high temperature level which could also be used as selection criteria to identify heat tolerant cultivar. Membrane thermostability has been widely accepted as a suitable technique for estimating the cellular thermotolerance to plants. MTS has a positive correlation with yield performance. It is a quick tool of screening against heat stress (Shanahan *et al*., 1990) [34].

Efeoglu and Terziglu (2007) [10] reported that high temperatures at seedling growth decreased MTS in wheat.

Khan *et al.,* (2015) [21] examined the effect of high temperature stress on 6 wheat cultivars and reported that high temperature significantly affected total proline, soluble protein content, membrane stability index (MSI), yield and various yield components.

6. Stomatal conductance

Heat stress led to increased stomatal opening. In general, highly variable leaf temperatures and stomatal opening within the relatively short intervals illustrates the high stomatal sensitivity to change. At the interface between atmosphere and plant, leaf stomata provide the entryway for CO2 for photosynthetic carbon fixation, while preventing excessive water loss. Through their role in transpiration, stomata also help control leaf temperature. Net stomatal conductance depends on both plant-specific traits, such as stomatal density, leaf age and size, sub-stomatal CO2 concentration, guard cell and epidermal cell turgor (Jones, 1992) [19], and on signals received from the environment. It was also demonstrated that plantsincrease stomatal conductance under high temperatures. Reynolds *et al*., (1994) evaluated that there is significant correlation between yield and flag leaf photosynthesis. Leaf conductance can be measure on individual plants and can be used in selecting plants (Reynlds *et al*., 2001).

Globally, stomata are responsible for the flow of CO2 fixed and water lost by plants. Further characterizing stomatal responses to stress will have many applications from modelling energy fluxes to determining ecosystem responses or individual plant survival in a future climate.

7. Heat Shock Proteins

Production of high levels of heat shock proteins can also be triggered by exposure to different kinds of environmental stress conditions, such as infection, inflammation, exercise, exposure of the cell to toxins (ethanol, arsenic, trace metals, and ultraviolet light, among many others), starvation, hypoxia (oxygen deprivation), nitrogen deficiency (in plants), or water deprivation. Several heat shock proteins function as intra-cellular chaperones for other proteins. They play an important role in protein–protein interactions such as folding and assisting in the establishment of proper protein conformation (shape) and prevention of unwanted protein aggregation. By helping to stabilize partially unfolded proteins, HSPs aid in transporting proteins across membranes within the cell. HSPs are synthesized during heat stress in plants and protect plants during stress. HSPs are not expressed at 25°C was observed and expression doubled when temperature raised to 37°C.

Ciaffi *et al*., (1996) [8] reported polymeric fraction of gluten during grain filling period above 35°C temperature.

Skylas *et al*., (2002) [39] suggested that seven different types of proteins were expressed when plants are exposed to stress.

8. Stay green

“STAY-GREEN” is one of the most significant traits, which allows plants to keep their leaves in the active photosynthetic state under high temperature to maintain assimilation process and increase crop yield (Kumar *et al.* 2013) [24]. Thus, exploiting “STAY-GREEN” trait in combination with other valuable traits may provide a solution for crop improvement against increasing threat of global warming. Plant genotypes exhibiting “STAY-GREEN” traits show delayed leaf senescence under stress and increased yields (Peleg *et al.* 2011; Gregersen *et al.* 2013; Reguera *et al.* 2013) [29, 16, 30].

The association between “STAY-GREEN” and useful agronomic traits, such as tolerance to biotic and abiotic stresses, as well as improved yield production, has been widely reported (Kassahun *et al*. 2010; Luche *et al*. 2015) [20, 25].

Conclusion

In the recent past, we have witnessed the serious threat posed by the sudden climatic changes, in the form of heat stress which toll heavily on the productivity of wheat crop depending upon the extent and magnitude of growth and yield reduction. It is therefore, required to develop tools not only to increase the crop productivity but also sustain a stable level of productivity under climate change scenario. Information regarding heat tolerance is still inadequate. For improving heat stress tolerance in wheat, either stable photosynthesis or high remobilization of stem reserves be eveluated. The traits like stay green/delayed senescence

canopy temperature depression (CTD), stomatal conductance and membrane thermo -stability etc. appear to be a potentially powerful indirect selection criterion to determine heat stress tolerance capability of plant and may be used in breeding to develop heat stress tolerant lines varieties.

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