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Assimilate limitation compensating factors under environmental stresses in wheat

Vidisha Thakur[1] and Jagadish Rane[2]

[1]*BanasthaliVidyapeeth, Jaipur, Rajasthan- 304022*
[2]*ICAR-National Institute of Abiotic Stress Management, Malegaon, Baramati, Pune- 413115*

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***Corresponding author**
Email: vidisha.thakur30@gmail.com

Abstract

In recent years, considerable efforts have been made to understand the factors controlling grain weight in wheat. In addition to sink capacity, the supply of assimilates for developing grain determines its weight. The current photosynthesis of the flag leaf is the most important source of assimilation, and the onset and rate of senescence are important factors for determining grain yield. Hence stress induced leaf senescence can reduce the supply of assimilates for grains. Under such conditions, assimilate contributions of stored non structural carbohydrates in stem and photosynthesis of non foliar parts of the plant such as spike are crucial for grain development. Non structural carbohydrates in wheat stem have been estimated and efforts have been made to reveal the mechanisms of assimilate partitioning. The hormone levels and activities of enzymes involved in assimilate partitioning and carbohydrate metabolism in wheat stem and grains have been significantly correlated with grain filling in wheat. Remobilization efficiency of stem reserves is increased under heat or drought stress along with increase in the proteins associated with senescence and Reactive Oxygen Species handling in the tolerant cultivars. The heat and drought tolerant wheat cultivars have a higher Water Soluble Carbohydrates content in stem, higher mobilization efficiency, longer duration of grain filling and stronger sink activity. However, some of the key issues such as intra-spike assimilation distribution have not been sufficiently addressed. This review has been compiled for information related to assimilate supply to the developing wheat grain under stress conditions and also enlists opportunities to translate this knowledge into traits for improvement of climate resilience in wheat.

Keywords: Grain weight, assimilate, photosynthesis, stem reserves, intra-spike assimilation

1. Introduction

Productivity of wheat cultivar is the function of grain weight and grain numbers per unit area irrespective of growth environments. While grain number is determined at early phases of plant growth, the grain weight is largely determined by ambient and edaphic conditions that prevail during grain development. The individual grain weight is an important trait for increasing the yield potential of wheat (Xie *et al.,* 2015) and is generally reduced when plant experiences stress during grain filling (Fig. 1).The time period of grain filling and its rate has significant effect on final yield (Motzo *et al.* 2004; Sadras and Egli, 2008). Grain filling duration is between 362 to 400 growing degree days (GDD) and the rate of grain filling ranges from 0.12 to 0.22 mg GDD^{-1} depending upon the environment and genotype (Xiaoli *et al.,* 2018). Miralles and slafer (1995) stated that rate of grain filling varies at different positions in the spike resulting in differences in grain weight. Carpel weight is directly related to final grain weight in case of central spikelets (Hasan *et al.,* 2011).Wheat breeding has created substantial reduction in nitrogen and phosphorus levels in grain as a result of biomass dilution (Ortiz-Monasterio *et al.,* 1997). Genetic variation has been observed for micronutrient concentration in grains (Calderini and Ortiz-Monasterio, 2003). Grain nutrient concentration tends to get diluted at the cost of improvement in weight. However grain position in the spike has been correlated to nitrogen concentration (Simmons and Moss, 1978). Within the spikelets, the distal lighter grains had low N content than the heavier proximal grains on central and basal spikelets (Herzog and Stamp, 1983). This suggests that nutrient content of the grains is affected by grain position in spike. Therefore, nutrient partitioning within spike and dilution effect both need to be considered in subsequent breeding programs for yield improvement. Previous efforts have focused on higher grain number per square meter than enhancement in grain size. The distal grain setting in spikelets has contributed to increase in the grain number (Calderini and Slafer, 1999). However, the selection for additional grains in spikelets is compromising the nutritional quality of grains (Calderini and Ortiz-Monasterio, 2003).

Wheat crop often gets exposed to drought and high temperature during grain growth particularly in subtropical conditions (Rane *et al.,* 2007). Under drought stress wheat yield is mostly decreased by 50% or less of the irrigated control (Yu *et al.,* 2014). A mild terminal drought stress (60% relative soil moisture content) has been found to decrease the grain yield by more reduction in the kernel weight than the grain number (Rasheed *et al.,* 2014, Zhang *et al.,* 2014). Hence, any efforts to improve grain yield of wheat under these stresses should consider insights into the mechanisms of grain development and also the supply of assimilates for developing grains particularly when plants experience stress. As depicted in Fig 1, the major causes of decrease in grain weight can be damage to the leaves which serve as main source of assimilate, impaired metabolism and anatomical defects in assimilate supplying parts of the plant. The conceptual illustration in the figure emphasizes that a series of events that occur mainly contributes to reduction in overall grain weight as well as intra-spike discrimination in distribution of assimilates while the sink size and its variation within the spike is largely governed by genetic make of the genotypes. Both the sink capacity and the sources capacity thus determine the grain weight while any of the events in assimilate supply to grain can be an opportunity point for improving the resilience of grain development process to stresses like drought and high temperature. The following sections explore such opportunities for improvement of grain weight of wheat under abiotic stress conditions caused by drought and high ambient temperature. Del Pozo et. al. (2016) found that drought stress decreased the grain yield per spike by 16.2% in the tolerant cultivar and by 27.9% in sensitive cultivar. But under combined heat and drought stress, the same cultivar did not show high tolerance. High temperature significantly reduced the grain weight and number of grains in wheat (Su *et al.* 2011). It has been reported that during grain filling with every 1°C rise in temperature above 18°C, there is 3% - 5% reduction in single grain weight (Hu *et al* 2016). Several other studies have reported that postanthesis rise in ambient temperature resulted in 9 to 15% reduction in individual grain weight. The cumulative effects of high temperature expressed as heat sum °C×h, the reduction in grain weight equated to 0.03% to 0.06% per °C h (>32°C) (Ling *et al.,* 2013). Studies have demonstrated that short periods of high temperature (near 40°C) during grain filling result in progressive reduction in sensitivity. The stress applied at 15, 30 and 40 DAA caused average reduction in individual grain weight by 15, 9, and 1% , respectively (Chang *et al.*, 2015; Wang *et al.,* 2012). A day of high temperature (40/21°C day/night) during grain filling decreased the individual grain weight by 10–30% compared with a control (21/16°C day/night) (Campbell *et al.* 1999; Groos *et al.* 2003). Mahrookashani *et al.* (2017) observed that the individual grain weight was decreased by 13%–27% under drought stress and by 43%–83% under combined heat and drought stress. Heat stress significantly decreased grain number by 14%–28%, grain yield by 16%–25% and straw yield by 15%–25%. Also, the response of cultivars were similar for heat but different for drought and combined heat and drought treatments.

2. Contribution of leaves to grain filling in wheat

Flag leaf photosynthesis in wheat contributes about 30–50% of the assimilates for grain filling (Sylvester-Bradley, 1990) and initiation of grain filling coincides with the onset of senescence. There are characteristic changes in the anatomy of a leaf under stress conditions which can be considered as a significant manifestation of the regulation of photosynthesis at the morphological

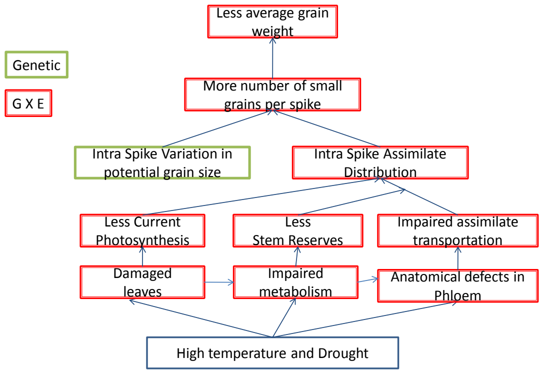

Fig. 1 Genotype (G) x environment (E) interaction and genetic factors responsible for reduction in grain weight

level. It follows that moderate water limitation during vegetative phase will decrease growth of leaf thus decreasing photosynthesis. As drought intensifies and leaf water potential reach -1.5 MPa, closing of stomata occurs and further decreases photosynthesis (Acevedo *et al.* 1991; Kobata *et al.,* 1992; Palta *et al.,* 1994). As CO_2 in the leaf decreases, electron transport is inhibited. Photoinhibition causes damage to the photosynthetic system of leaf (Long *et al.,* 1994). Maintenance of the plant's water status and open stomata is therefore important not only for cooling but also for maintaining a high conductance for CO_2, which keeps photo-synthetic dark reactions going and electron transport functioning (Loomis and Amthor, 1996). Enhanced chlorophyll fluorescence is observed when light harvesting exceeds the capacity of the dark reactions; consequently, fluorescence measurements are now used widely for detection of stress effects on crops (Seaton and Walker, 1990).

Maximum loss of grain yield occurs when the wheat plants are exposed to water scarcity at flowering and grain filling stages as a consequence of substantial decline in the rate of photosynthesis and hence assimilate supply for grains. This is the outcome of constrained metabolic performance (eg. degradation of chloroplasts and closure of stomata (Pinheiro *et al.* 2000). Plant leaf gas exchange has been studied and a decrease of 64% in net photosynthesis has been reported under severe stress (relative soil water content, RSWC<40%), whereas under mild stress (40 %< RSWC<55%) the decrease is only 28% (Yan *et al.* 2016).

Heat stress breaks down chlorophyll, impedes photosynthesis rate and induces leaf senescence thereby affecting grain weight and quality. High temperature during grain filling has been reported to reveal significant increase in level of proteins involved in photosynthesis in tolerant genotypes implying their critical role in tolerance (Wang *et al.,* 2015). Heat-shock proteins were reported to be induced in the leaves by drought (Wang *et al.,* 2003), cold (Sabehat *et al.,* 1998) and heat (Lee *et al.,* 2007) repairing degraded proteins. The proteins related to photosynthesis significantly increased by heat stress, presumably to protect the photosynthetic machinery from heat (Law and Crafts-Bradner, 2001). The proteins related to reactive oxygen species scavenging counteract the damage due to heat stress. The defense processes require energy which is produced by increased level of energy metabolism related proteins (Yan *et al.,* 2006).

The relationship between grain yield and rate of photosynthesis is not straightforward for a number of reasons. Firstly, yield differences in wheat are more often associated with harvest index than with differences in radiation-use efficiency (Calderini *et al.,* 1995). Where yields are primarily limited by assimilate supply, an association between photosynthetic capacity and performance cannot necessarily be expected. The possibility for genetic variation in the photosynthetic metabolism to environment should not be ruled out. Wheat like other crops fixes carbon through photosynthesis and releases the assimilated carbon through respiration, primarily night respiration, which determines the crop carbon balance. Once gross carbon fixation rate has been simulated, net carbon fixation can be calculated by estimating the cost of growth, maintenance, and photorespiration (Loomis and Amthor, 1996).

3. Contribution of spike photosynthesis to grain filling in wheat

Spike morphological traits are often unused as selection criteria in wheat breeding (Wang *et al.,* 2016). However, the physiology of spikes is yet to be explored for improvement of genetic gain in productivity of wheat. Spike photosynthesis has a direct effect on grain yield (Tambussi *et al.,* 2007; Xiao *et al.,* 2011). Depending on genotype and treatment, the spike can contribute 10%–59% of total grain weight (Li *et al.,* 2017; Araus *et al.,* 1993). The grain photosynthesis is able to account for 33-42% of this photosynthesis (Evans and Rawson, 1970). In another study, shading the ear decreased grain weight by 59% and genetic variation was observed for this parameter (Araus *et al.,* 1993). A C4 photosynthetic pathway is present in the developing wheat grain that is absent in the leaves. The concept of the photosynthetic area above the flag leaf node in wheat as an important determinant of grain yield has existed for many years (Simpson *et al.* ,1968; Hsu and Walton, 1971); however, the role of spike photosynthesis has been omitted from analyses of the areas of specific photosynthetic modules with respect to their influence on grain yield. A correlation between spike weight and other morphological traits of spike have been reported (Maydup *et al.,* 2007). Earlier it was proposed that the use of gigas spike types can boost potential grain number (Gaju *et al.,* 2009) which can be a trait for increasing assimilation capacity of canopy of spikes. Parry *et al.,* (2011) stated that the spike canopy photosynthesis proportion may be used as a trait in wheat breeding programs.

4. Contribution of stem reserves to grain filling

An increase in assimilate availability around anthesis is able to improve the distal grain weight [Roder *et al.,* 2008]. Under harsh environments such as heat stress and water deficit, stem reserves as water soluble carbohydrates support grain development and hence productivity of wheat (Ehdaie *et al.*, 2008; Gupta *et al.,* 2011; Yang *et al.* 2000). Translocation of stem reserves contribute 20 to 40% weight of the grain in favourable condition (Saint Pierre *et al.,* 2010) and this can be up to 70% under stressed conditions during grain filling (Plaut *et al.,* 2004; Rebetzke *et al.,* 2008). Van Herwaarden *et al. (*1998) showed that under dry conditions in the field, the apparent contribution of stored assimilates could be more than 75% of grain yield as compared with 37–39% under high rainfall conditions. Ehdaie and Waines (1996) have reported that in wheat exposed to drought, almost 50 % of the grain yield was estimated to derivate from re-translocated assimilates stored prior to anthesis. According to some studies stem reserves accounted for 64% and 81% of total grain C and N, respectively under stress (Dreccer *et al.,* 2009, Plaut *et al.,* 2004, Van Riet *et al.,* 2008).

A reduction in plant water status and photosynthesis caused by drought stress induces the conversion of stored reserves into soluble (transportable) sugars and mobilization of sugars into grains (Blum *et al.*, 1994; Palta and Fillery 1995;Yang *et al.,* 2001a, Plaut *et al.,* 2004). This dehydration tolerance strategy is sustained even under severe chemical dessication of the plant (Blum *et al.,* 1983; Hossain *et al.,* 1990). The phloem translocation was unaffected until late in the stress period, whereas other processes, such as photosynthesisetc, were strongly inhibited (Farre *et al.*, 2016). The temperature range of 1 to 50°C had no effect on the movement within the stem (Gebbing and Schnyder 1999). Because of this relative insensitivity, there is continuing translocation of assimilates, which could be a key ability for stress tolerance. Defoliation experiment and stem water soluble carbohydrate content of three high yielding local cultivars revealed that under water stress a significantly higher grain weight was retained by one cultivar (Lok1) due to higher stem reserve remobilization as compared to other two cultivars (Kumar *et al.,* 2017).The genetic variability with respect to intra-spike variation in grain size can be one of the opportunity to improve grain weight per spike and hence to improve the productivity of wheat.

Wardlaw (1974) observed that the assimilate loading from leaves was maximum at 20-30°C; however there was an abrupt decline above 30°C. The conclusion was that the effect of high temperature on biomass partitioning in wheat was indirectly related to the abnormal behavior of source and sink along with the reduced photosynthesis rate. In a recent study by Ram K *et al.*, (2018) genotypes with faster reserve mobilization showed maximum grain yield per meter square under unfavorable conditions and stipulated that stem reserve mobilization is best physiological strategy for selection of tolerant and high yielding genotypes for drought and high temperature conditions. Further, anatomical features which determine the ease of translocation of assimilates through phloem can offer additional opportunities for identification of relevant traits for improving performance of wheat under drought and high temperatures.

4.1. Traits related to stem reserve mobilization under stress conditions

Different traits have been associated with improved stem reserve remobilization (Fig. 2). Sufficient carbohydrate storage before grain filling is a major condition for stem reserves for grain filling. This may be associated to the traits that promote high yield potential, before anthesis. The stem reserve carbohydrates are termed as non-structural carbohydrates (NSCs) or water soluble carbohydrates (WSCs). NSCs include glucose, fructose, sucrose and fructan. Fructans are main components of NSCs in wheat stems (Rouska *et al.,* 2006; Joudi *et al.*, 2012) and constitute up to 85% of total NSCs at the maximum accumulation stage (Goggin *et al.* 2004), while sucrose accounts for only 10% (Cruz-Aguado *et al.* 2000). In a study by (Dreccer *et al.* 2009) the individual grain weight, from the average pool and the contribution of WSC to yield was significantly greater in the high vs. low WSC lines. Therefore, a higher proportion of final average individual grain weight in high WSC crops was dependent on the pool of stored stem carbohydrates, 11.5% vs. 8.2% in low WSC lines.The drought tolerant cultivars have higher stem NSC than sensitive cultivars under both control and stress condition (Gupta *et al.* 2011). High WSC lines had a lower grain number per gram of spike weight or spike N at anthesis. This can be attributed to compensatory mechanisms between the grain number and grain weight. Nevertheless, it is worth investigating as to whether this could explain the differences in the spike structure, such as larger rachis, for larger or faster delivery of sugars to the grains.

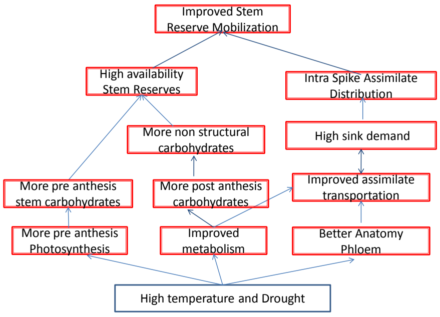

Fig. 2. Scope for improved stem reserve remobilization under high temperature and drought.

The accumulation of NSCs in stem begins at internode elongation from jointing to grain filling stage, but the total quantity depends on genotype and environment (Del pozo *et al.,* 2016; Dreccer *et al.,* 2009). NSC accumulation and remobilization varies in different internodes (Wardlaw *et al.* 1994; Shakiba *et al.* 1996). About 45% of the maximum mass of the stem is present in peduncle and penultimate internode and 55% is present in the lower internodes (Borrell *et al.,* 1993). The maximum accumulation of NSCs occurs between the peduncle and penultimate internode (Dreccer *et al.,* 2009; Zhang *et al.,* 2015) but (Li *et al.,* 2015) found that the lower internodes had higher water-soluble carbohydrate than those in peduncles. The WSC content in the lower internodes had highly significant correlations with thousand grain weight (TGW) at anthesis stage under non-stressed conditions and at the middle of grain filling period under water deficit. Thus, the length of lower internodes should be sufficient to store enough stem NSC to provide assimilates during the grain filling (Ehdaie *et al.,* 2006a). At 21 DAA (days after anthesis), mobilization of photosynthate starts from the upper part of stem (such as peduncle and penultimate internode), but it starts earlier at 10 DAA from the lower part of stem in wheat (Ehdaie *et al.*, 2008). Borrel *et al.*, (1993)concluded that under irrigated conditions, plant height and mobilization of stem reserves are positively correlated. In a study by Saint Peirre *et. al.* (Gupta *et al.,* 2011), stem solidness of different genotypes had a positive correlation with NSC per stem and grain yield. Blum (1998) stated that the ability to store carbohydrate in stem is determined by stem specific weight and stem length. Ehdaie *et al.,* (2006) also reported that dry matter mobilized under well-watered and drought conditions correlated significantly and positively with maximum weight of internodes but there was no correlation between stem length and stem reserve mobilization in their study (Ehdaie *et al* .,2008). Earlier, Shakiba (1996) observed a negative correlation between specific weight of peduncle and penultimate internode and WSC content at anthesis under control and drought stress. According to Wang *et al.,* (2012) under heat stress, the mobilization efficiency increases, partially compensating for reduced stem carbohydrates content. Zamani *et al.,* (2014) observed that WSC remobilization increased by 60% on average under heat stress and different genotypes showed variation for WSC remobilization. The cultivars differ not only in the amount of mobilized assimilates but also in efficiency of mobilization in different internodes of the main stem (Ehdaie *et al.,* 2006b).

4.2. Techniques to estimate stem reserve contribution

Different methods have been applied to determine the apparent contribution of stem reserves in grain yield.There is a strong positive correlation between stem dry matter and stem NSC content, therefore post-anthesis changes in stem dry weight in wheat is used as an effective indirect method to estimate the stem reserve remobilization to grain (Ehdaie *et al.,* 2008).To reveal genotypic differences in the absence of photosynthesis Nicolas and Turner (1993) used a leaf spray of KI on wheat under post-anthesis stress. Other methods such as, inhibiting current photosynthesis during grain filling by defoliation (Fokar *et al.,* 1998), labeling methods (Schnyder, 1992) or applying darkness (Yang *et al.*, 2002) have also been used.

4.3. Association of stem reserves with other processes

Tahir *et al.,* (2005) observed that heat stress significantly reduced the nitrogen remobilization efficiency of genotypes, however WSC remobilization efficiency increased and significant differences were observed among genotypes. Nitrogen remobilization efficiency under all conditions significantly correlated with grain yield, grain weight and grain filling duration. Palta *et al.,* (1994) found that the remobilization of nitrogen was increased under water deficit; therefore, the grain N accumulation was not affected despite the reduction in N uptake post-anthesis. However, nitrogen mobilization depends on genotype and environmental conditions (Barraclough *et al.,* 2010) They also observed that the NSC remobilization efficiency was positively correlated with grain weight and harvest index.

The rate of chlorophyll loss from flag leaf under heat stress positively correlated with nitrogen and NSC remobilization efficiencies suggesting a link between remobilization efficiency and senescence. Initiation of whole-plant senescence is a requirement for remobilization of stem water-soluble carbohydrates to grain in wheat as demonstrated by extensive studies (Yang *et al.,* 2006). Early senescence induced by controlled soil drying could increase the rate of grain filling and improve kernel weight by improving remobilization of assimilates to grains. High temperature decreases the chlorophyll content in the leaves and accelerates senescence (Fokar *et al.,* 1998). The link between accelerated leaf senescence and loss of chlorophyll from the leaves and the promotion of NSC remobilization from the stem is not clear. An increase in proteins related to stem senescence and reserve remobilization lead to higher stem reserve remobilization efficiency. Rapid leaf senescence may be an indication of reserve mobilization to the grain under stress (Assaf *et al.* 2014). Carbohydrate and nitrogen metabolism is involved in balancing stem reserve mobilization and non-senescence, but the exact mechanisms are unknown. In addition, the predominance of proteins associated with ROS handling has been observed in order to sustain stem reserve remobilization under drought condition (Bazargani *et al.* 2011). Tillers contribute to final grain yield under high temperature conditions but the utilization of stem reserves in tillers as compared to the main stem is not known. Srivastava *et al.*, (2017) observed that defoliation treatment hindered the capacity of the plants to remobilize their entire stem reserves to developing grains suggesting that grain filling might be source limited.

4.4. Enzymes associated with stem reserve mobilization

The enzymes involved in the stem reserve accumulation and mobilization are given in the table 1. Fructan is synthesized by four fructosyltransferase (FT) enzymes (Lammens *et al.,* 2012; Cimini *et al.*, 2015). The mobilization of stored reserves requires fructan hydrolysis, which is catalyzed by fructanexohydrolase (FEH) enzymes (Xue *et al.*, 2008). Three enzymes take part in sucrose metabolism in the wheat stem:--Sucrose phosphate synthase, sucrose synthase (SS) and soluble acid invertase .Wardlaw and Willenbrink (2000) observed that under water stress, an early fall in fructancontent is coincident with a rise in fructanexohydrolase and acid invertase in the internodes. In case of rice and wheat, ADP-glucose pyrophosphorylase (AGPP) and SS activity in superior grains was higher than that of inferior grains (Yang *et al.,* 2001a, Jiang *et al.,* 2003). The enhanced SS activity in the grains of drought stressed plants of tolerant cultivar as compared to those of sensitive one increased the sink strength and attributed towards faster remobilization of assimilates to the grains. Sucrose synthase activity is therefore regarded as biological marker of sink strength (Xu *et al.,* 2019).

4.5. Role of plant hormones in assimilate translocation

The hormone levels in grains have been significantly correlated with grain filling of wheat. Abscisic acid (ABA) and cytokinins are involved in regulation of seed development (Davies *et al.,* 1987). ABA has been assumed to be important in regulation of the transport of reserves to the developing seeds or fruits (Tietz *et al.* 1981; Eewens *et al.,* 1975). Many studies have reported a correlation between the ABA content and the growth rate of fruits or seeds (Schussler *et al.,* 1991; Wang *et al.,* 1987; Ross *et al.,* 1990; Kato *et al.,* 1993; Yang *et al.,* 1999). Plant senescence is delayed by a high level of cytokinins (Buchanan-Wollaston, 1997; Nooden *et al.,* 1997), whereas a high ABA concentration accelerates senescence and therefore control the time available for nutrient

Table 1. Enzymes involved in the stem carbohydrate reserve metabolism.

SNo	Enzyme	Function
1	1-SST (sucrose:sucrose 1-fructosyltransferase)	Fructan biosynthesis: catalyzes the production of 1-ketose from sucrose
2	1-FFT (fructan:fructan 1-fructosyltransferase)	Fructan biosynthesis: sucrose alpha-glucosidase activity, transferase activity
3	6-SFT (sucrose:fructan 6-fructosyltransferase)	Fructan biosynthesis: sucrose 1F-fructosyltransferase activity
4	6G-FFT (fructan:fructan 6G-fructosyltransferase)	Fructan biosynthesis: sucrose alpha-glucosidase activity, transferase activity
5	1-fructan exohydrolase (1-FEH)	Fructan hydrolysis: catalyze the reaction of depolymerisation of fructan, with (2,1) [Xue et al. 2008]
6	6-fructan exohydrolase (6-FEH)	Fructan hydrolysis: catalyze the reaction of depolymerisation of fructan, with (2,6) linkages[De Coninck et al. 2005; Van den Ende et al. 2004; Van den Ende et al. 2006]
7	6&1-FEH	Fructan hydrolysis: catalyze the reaction of depolymerisation of fructan, with (2,6) and (2,1) linkages [Davies et al. 1987]
8	Sucrose phosphate synthase	Catalyzes sucrose synthesis and influences the movement of assimilates from the source to the developing grains [Pinheiro et al 2005].
9	Sucrose synthase (SS)	Catalyzes a reversible conversion of sucrose into fructose and uridine diphosphate glucose [Gonzalez et al. 1998] attributed towards faster remobilization of assimilates to the grains [37]
10	Soluble acid invertase	Hydrolyzes sucrose into glucose and fructose [Thitisaksakul et al. 2012]

mobilization (Nooden, 1998; Madhu *et al.,* 1999; Tadas *et al.,* 1999). However, there are contradictory reports about the involvement of ABA in regulating both senescence and assimilate mobilization (Brown *et al.* 1991; Schussler *et al.* 1991; De Brujn and Vreugdenhil 1992; Sharp *et al.* 2002). Yang *et al.* (2003) observed that under water stress ABA was positively and significantly correlated with stem reserve remobilization and grain filling rate but zeatin (Z) + zeatin riboside (ZR) concentrations in the stems and leaves was reduced. Exogenous ABA increased the chlorophyll loss, enhanced the remobilization of prestored carbon from the stem to the endosperm, and increased grain weight (Yang *et al.* 2001b). An increase in ABA and reduction in cytokinin levels induces early senescence under drought in wheat and rice which leads to higher and faster stem NSC remobilization to grains and increases grain filling rate, but shortens the grain filling period (Yang *et al.* 2003; Yang *et al.* 2001). Exogenous kinetin reduced remobilization of carbohydrate reserves (Yang *et al.* 2003). The hormone gibberellin is likely to be involved in induction of reserve mobilization under stress (Yang *et al.* 2001b). Superior grains have a higher level of ethylene (ETH) than inferior grains of wheat (Yang *et al.* 2006a). A study found that plastic covered ridge and furrow planting significantly affected the Z +ZR and ETH levels in grains, and that promoted the grain filling of inferior grain of wheat (Liu *et al.* 2013a). Liang *et. al.* (2017) observed that high pre-anthesis NSC reserves led to an increase in Z + ZR content and decrease in ETH evolution rate in the inferior grain, which enhanced the sink strength and grain filling rate of the inferior grain of wheat.

4.6. Genetic improvement of stem reserve mobilization

Plaut *et. al.* (2004) found that under water deficit condition, rate of grain filling is more in the tolerant than in sensitive wheat cultivar. The favorable WSC alleles haveincreased from 1.13 in the pre-1960 to 4.41 in the post-2000 in wheat. This suggests that stem reserves contribution to grain yield has been indirectly taken into consideration. QTL studies showed that many genes control WSC accumulation and are important for grain size and stability (Rebetzke *et al.,* 2008). Li *et. al.,* (2015) identified 22 favourable alleles for stem water-soluble carbohydrates, out of which five loci individually contributed to significantly higher TGW. The gene expression analysis indicated that 1-FEH w3 was likely the main gene involved in the total 1-FEH enzyme activity. High rate of fructan degradation was positively correlated to 1-FEH w3 gene, therefore, to a higher stem WSC remobilization (Zang *et al*. 2015). The 1-FEH w3 Westonia allele contributes to high grain weight in drought stress during grain filling. A marker generated in the promoter region of 1-FEH w3 is associated with high stem fructan remobilization capacity (Nicolas *et al*. 1993). Among the five sucrose transporter genes (SUTs) reported in wheat (Aoki *et al*. 2004; Deol *et al*. 2013; Mukherjee *et al*. 2015; Ahmed *et al*. 2018), the high gene expression of TaSUT1 in grain and the correlation with the grain filling demonstrated the crucial role for TaSUT1 in sucrose reloading to grain and high yield. Significant differences in TaSUT1 gene expression between treatments and varieties indicate the genotypic variations towards two different soil moisture levels.

5. Conclusion

Improving photosynthesis is an approach which targets increasing yield potential, but it will also be necessary to reduce the yield gap between favourable and unfavourable. environments in order to provide resilience to abiotic stresses such as drought and high temperatures. While stem reserve mobilization has been extensively studied, spike photosynthetic contribution under stress conditions needs to be explored. It is evident that the stem reserve mobilization is an alternative strategy adopted by plants to compensate for the reduced capacity of leaf photosynthesis during stress. It is important to note that genetic variation exist for this trait which needs to be explored for wheat improvement. Components of stem reserve supply for grain development can offer opportunity to identify relevant traits to ensure grain yield stability across the target environments. In addition, it is essential to focus on genetic variation in contribution of current spike contribution to developing grains specifically with focus on intraspike assimilate distribution which needs attention.

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