

# Role of Water Soluble Carbohydrates in Improving Drought Stress Tolerance in Wheat: An Overview

Arpit Gaur<sup>1</sup>, Deepti Sharma<sup>2</sup>, Sonia Sheoran<sup>3\*</sup>, Sulekha Chahal<sup>2</sup>, Kaveri Chaudhary<sup>3</sup>, Gyanendra Singh<sup>3</sup> and Gyanendra Pratap Singh<sup>3</sup>

<sup>1</sup>Borlaug Institute for South Asia-CIMMYT, New Delhi

<sup>2</sup>Department of Biotechnology, Kurukshetra University, Kurukshetra

<sup>3</sup>ICAR-Indian Institute of Wheat & Barley Research, Karnal

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## \*Corresponding author:

E-mail: [Sonia.Sheoran@icar.gov.in](mailto:Sonia.Sheoran@icar.gov.in)

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## Abstract

Abiotic factors such as drought and heat stress impairs photosynthetic assimilates, shortening the carbon supply to the developing grains leads to yield loss. Under water stress, stem water-soluble carbohydrates (WSCs) mainly fructans, play an important role in buffering yield during the grain filling period in wheat. The stem WSCs may contribute up to 20% of the total dry weight of grain under irrigated conditions and upto 70% of grain dry matter under drought stress. Additionally, it maintains physiological balance under water-stressed conditions by acting as signalling molecules to various phytochemicals and hormones. Therefore, this drought adaptive trait can be a potential breeding target for sustainable wheat production, especially for water limiting conditions. Despite the proven contribution of stem WSCs to water-stress tolerance in wheat and compensating grain yield, a comprehensive review on this trait is still missing in the literature. With this review, efforts are made to compile the available information on the physiological, genetic and molecular aspects of accumulation and remobilisation of stem WSCs to bring more attention of plant scientists to this trait. Furthermore, effective molecular marker systems such as KASP to target stable loci identified using GWAS, QTL or meta-QTL studies may bring precision to the selection and accelerate the WSCs based wheat breeding program.

**Keywords:** Carbohydrate metabolism, Drought tolerance, Fructans, Wheat, WSC

## 1. Introduction

Climate change has significantly impacted the worlds' hydrological cycle, eventually affecting water availability in many parts of the world, including India (Gunathilaka *et al.*, 2018). This imbalance shows severe effects on agricultural production, especially on cereal crops that are widely cultivated under rainfed agriculture, such as wheat (*Triticum aestivum* L.). As a primary staple food for ca. 2.5 billion people, wheat is a sustainable source of global food security. The global production of wheat amounted over 765 million metric tons (Food Agriculture Organization

of the United Nations, 2021), however the rate of increase in annual wheat production has recently decreased from 3% (during 1970's and 1980's) to 0.9% in recent years is matter of concern (Gahlaut *et al.*, 2021). . Nearly 50% of the total wheat production from developing countries comes from regions with less than 600 mm annual rainfall, characterized by frequent drought and inadequate irrigation methods in cropping seasons (Gupta *et al.*, 2017). In wheat, water stress induces various morphological, physiological, and metabolic disruptions leading to an



inhibited rate of growth and development, loss of yield, and in extreme cases, loss of entire crop (Bharadwaj *et al.*, 2021). Depending upon the degree of stress and growth stage, wheat crops may face up to 90% yield loss (Senapati *et al.*, 2019, Own observations). To survive in such an unfavourable environment, the plant tries to readjust its metabolic and physiological activities. In wheat and its close relatives (barley and oat), the accumulation of water-soluble carbohydrates (WSCs) and subsequent remobilization into developing grains is one such adjustment (Drecker Shreds of evidence advocating the critical role of WSCs in plant complex systems of growth and development, 2014). In wheat, a developing grain harnesses fixed carbon from two primary sources: (1) current photosynthetic assimilates and (2) assimilates stored in vacuoles. Photosynthetic assimilates are directly provided to developing grains when the growth conditions are favourable. Conversely, in the absence of photosynthesis during the diurnal cycle or dwindling photosynthesis conditions that may arise due to ageing or an environmental factor, the stored sugars (WSCs) become a crucial carbon source (Ehdaie *et al.*, 2008; Schnyder, 1993). It indicates that WSCs accumulation and remobilization in wheat must be crucial for buffering grain yield under optimum and stressed conditions. WSCs are primarily made up of glucose (Glu), fructose (Fru), sucrose (Suc), and fructans; however fructans make most of the part of it. (Zhang *et al.*, 2015a) Fructans are sucrose-derived linear or branched polymers that range in length from trisaccharides (1-ketotriose, 6-ketotriose, and neoketotriose) to polysaccharides with hundreds of fructose units. Fructans, whether linear or branched, are formed by fructose molecules and often by terminal glucose. Wheat fructans of graminan-type are mixed levans that contain both (2-1)- and (2-6)-linked  $\beta$ -D-fructosyl units (Yáñez *et al.*, 2017).

The genetic mechanisms underlying the variation in WSC are still partially understood. Many previous studies have advocated the critical role of WSCs in plant complex systems of growth and development under optimum and hostile environments are available. For instance, sucrose signalling induces anthocyanin accumulation and activates pathogenesis-related (PR) genes in rice and arabidopsis (Gómez-Ariza *et al.*, 2007; Thibaud *et al.*, 2004). Important role of PR genes have been identified (Akbuldak *et al.*, 2020). For example, in *Arabidopsis Di19* (Drought-

induced) gene upregulates the PR genes in response to drought tolerance (Liu *et al.*, 2013). Increasing fructans concentration may help a wheat plant cope with salinity and/or drought stress by maintaining the membrane stability and reducing osmotic potential (Kerepesi and Galiba, 2000; Livingston *et al.*, 2009). Peshev *et al.* (2013) suggested the role of increased fructan in phloem mobile signalling and reactive oxygen species scavenging mechanism. Moreover, it is evident from previous studies that remobilization of WSCs to developing grains under optimum or water stress conditions may contribute up to 20% and 70%, respectively (Goggin and Setter, 2004; Ovenden *et al.*, 2017). Thus, the role of WSCs to grain growth could be very significant under water deficit conditions (Reynolds *et al.*, 2007).

Despite the availability of ample literature advocating the importance of WSCs in wheat, an updated and comprehensive review is still not available. Therefore, in this review, we aimed at the various aspects of WSCs to improve drought tolerance in wheat. Here, we discuss the physiological and molecular basis of accumulation, dynamic flux, and genetic variations of WSCs in wheat, and how the individual components contribute to drought tolerance. In addition we briefly describe the recent advancements and future thrust in context to breeding sustainable wheat using WSCs as a potential drought adaptive trait.

## 2. The accumulation

The freshly formed sucrose during photosynthesis is efficiently partitioned and transported to sinks either as sucrose by sucrose transporters or as glucose and fructose by hexose transporters after hydrolyzation by cell wall invertase. A partition of the sucrose is transported to vacuoles to form a short-term reservoir of water-soluble sugars., a part of sucrose remains unconverted, and another part converts to glucose, fructose and fructans. The glucose and fructose are formed in a reaction catalyzed by cell wall invertase whereas, fructans are formed in the reaction catalyzed by fructosyltransferase. In wheat, sucrose:sucrose-1-fructosyltransferase (*1-SST*), sucrose:fructose-6-fructosyltransferase (*6-SFT*) and fructan: fructan 1-fructosyltransferase (*1-FFT*) catalyzes the synthesis of 1-kestotriose, 6-kestotriose and 1,6-kestotetraose, and 1,1-kestotetraose forms of fructans,



respectively (Cortés-Romero *et al.*, 2012; Lasseur *et al.*, 2009; Xue *et al.*, 2008).

Genotypic potential, environmental conditions, edaphic factors and their interaction largely influence the accumulation and storage of stem WSCs (Ovenden *et al.*, 2017; del Pozo *et al.*, 2016). The WSC in wheat stem generally occurs between stem elongation and 15 days after anthesis (DAA); however, some studies suggests that the accumulation may continue up to 20DAA in optimum conditions (Kühbauch and Thome, 1989). Similarly Ehdaie *et al.*, 2006b observed that the maximum WSC level was reached 20 days after anthesis (DAA) in the penultimate internodes and peduncle of the well-watered plants, while it peaked at 10DAA in the lower internodes. In internodes, WSCs accumulation is likely to occur in acropetal order, *i.e.* lower internodes start accumulating the WSCs as soon as they complete their elongation phase while the upper internodes are still elongating (Bonnett and Incoll, 1993). WSC levels in the lower internodes were higher than those in the peduncles of both well-watered and drought-stressed plants at mid-grainfilling (Zhang *et al.*, 2014). On average, the WSC in the lower internodes mobilised the most stem WSC (51%) in drought and irrigated plants, followed by the penultimate internode and the peduncle (Ehdaie *et al.*, 2006b). Some of the previous studies in wheat revealed that WSC reserves continuously accumulate before anthesis and reach highest between 7DAA and 20DAA when photosynthetic tissue synthesize WSC at a greater rate than the requirement of the various sink (Gebbing, 2003; Li *et al.*, 2020). Nitrogen management in the field significantly affects the WSCs concentration in the wheat shoot; indeed, a per cent increase in nitrogen may reduce the WSCs level by 28% (Valluru *et al.*, 2011). The moisture content of the field shows an inverse relation with WSCs concentration in the wheat peduncle, *i.e.* with the increase in water stress, WSCs concentration also increases (Li *et al.*, 2020). Under severe drought conditions total WSCs in wheat peduncle may increase up to 25%, whereas, under rainfed conditions with no artificial irrigation, it may increase up to 17%. An increase in CO<sub>2</sub> level, rate of gaseous exchange, flag leaf chlorophyll and nitrogen content increases the rate and amount of WSCs accumulation in the wheat stem. Higher potential of WSCs accumulation in drought-tolerant genotypes in contrast to sensitive one has been suggested

in many previous studies (Macabuhay *et al.*, 2018; Zhang *et al.*, 2016).

Accumulation of WSCs occurs in every vegetative part of the wheat plant. The highest contribution to grain filling as a carbon source is provided by stem WSCs, specifically in water stress. The total WSC content in wheat stem may reach up to 60% of the dry weight and sometimes even more. This accumulation depends on space (internodes) and time (elongation phase). However, this spatio-temporal behaviour does not assure higher accumulation in lower internodes as the mean rate of accumulation is reported much higher in top internodes (Bonnett and Incoll, 1992; Schnyder, 1993). The peak amount of accumulation in different internodes of wheat stems depends upon the plant growth phase. In lower internodes, it peaks somewhere between stem elongation to 10DAA in penultimate its peak may be found between anthesis to 20DAA and in peduncle post-anthesis to 20DAA (Ehdaie *et al.*, 2006b; Schnyder, 1993; Bonnett and Incoll, 1992). Zhang *et al.* (2016) demonstrated a substantial contribution of root WSCs in grain filling. The WSC level in roots was up to 15% of dry weight; however, the storage pattern was similar to stems. Moreover, the stem morphology reinforces the potential impact on the accumulation process. In a recent study at ICAR-IIWBR, a certain degree of a linear relationship between peduncle length and WSC concentration at 15DAA was observed under water stress conditions. These results were in line with Pierre *et al.* (2010), who showed a close association with various stem morphological traits such as length of the main stem, internode length, solidness with WSCs concentration under water stress and irrigated conditions. Furthermore, 20% higher stem WSC had reported in reduced tillering genotypes in contrast to free tillering genotypes (van Herwaarden and Richards, 2002).

Rather than being an independent trait, WSC is a product of the sum of the concentrations of accumulated glucose, fructose, sucrose and fructans in vacuoles. Thus, WSC concentration shall depend on photosynthesis efficiency and carbohydrate metabolism. Hence, the molecules affecting photosynthesis and carbohydrate metabolism in a particular environment likely to affect the WSCs accumulation, also. Xue *et al.* (2008) presented the most transparent view on the molecular basis of WSCs accumulation in wheat under irrigated and water-stress



conditions. With Affymetrix GeneChip, an upstream analysis was performed using sixteen Seri/Babax RILs contrasting for total stem WSC concentration at anthesis. This study revealed a correlation between WSC concentration and mRNA transcript levels of at least 41 enzymes belonging to wheat carbohydrate metabolism. Total mRNA level of *1-SST* and *6-SFT* genes showed a significant positive correlation with WSC concentration; conversely, total mRNA level of soluble acid invertase, sucrose synthase, cellulose synthase, fructokinase and pyruvate dehydrogenase (E1 $\beta$  and E3) negatively correlated. Later, Xue *et al.* (2011) demonstrated a highly significant and positive correlation between mRNA levels of homologous series of *TaMYB* genes and fructosyltransferase (*1-SST* and *6-SFT*) genes eventually affected the stem WSC accumulation at anthesis in Seri/Babax RILs.

Recent genome-wide association studies (GWAS) have presented a more complex view on stem WSC accumulation in wheat at different growth stages and water regimes; however, the number of these studies are pretty less. The first-ever SNP based GWAS for stem WSC concentration was carried out by Dong *et al.* (2016). They identified nine putative genes for stem WSC content at 14DAA. However, only one gene (*1-SST*) was directly involved in WSC metabolic pathway, rest eight were involved in different activities such as glycerol metabolism, ABA response, immune response and mitogen-activated protein kinase. They also observed that the molecular mechanism of WSC accumulation in wheat stems varies with environmental conditions. The above evidence indicates that the underlying molecular mechanism of WSC accumulation is complex, and more number of studies are needed to dissect this complex trait.

### 3. The remobilization

Stored WSCs remobilize from source (vacuoles) to sink (developing grain) when the current assimilation rate declines due to the diurnal cycle, senescence and stress conditions. The declined rate of photosynthesis reduces available sugars that promote the remobilization of soluble sugars from reservoirs. Glucose, fructose, sucrose and fructans are components of stored WSCs. The first three sugars relocate to sink directly whereas, the fructans convert to hexose sugars before relocating to sink tissues. The pre- and post-anthesis rate of remobilization

significantly differ between water conditions as, with limiting conditions, it is relatively high compared to favourable conditions; furthermore, the drought-tolerant genotypes has more potential of remobilization in contrast to sensitive one (Liu *et al.*, 2020; Palta *et al.*, 1994). Liu *et al.* (2020) has demonstrated that pre-anthesis remobilization is higher in drought-stressed plants, whereas post-anthesis remobilization is higher in well-watered plants.

The study of the dynamic flux of WSCs is done based on individual segments (lower internodes, penultimate and peduncle) of the main stem. The remobilization rate is higher in lower internodes before anthesis and in penultimate and peduncle after anthesis. However, this pattern remains constant irrespective of water conditions, but the stress conditions and genotypic potential can affect the remobilization efficiency. For example, remobilization efficiency can increase by 65, 17, and 11% water deficit condition in the peduncle, penultimate and lower internodes, respectively (Ehdaie *et al.*, 2006a and 2006b). Conversely, Ma *et al.* (2014) demonstrated that the remobilization might increase by 110%, 137%, and 33% under severe drought stress in the whole stem, lower internodes, and upper internodes. Under terminal drought stress, stem WSC remobilization during the grain filling stage can contribute as much as 30-50% of grain yield (Piaskowski *et al.*, 2016) and in some elite cultivars up to 70% (Rebetzke *et al.*, 2008).

Genotypic potential and variation for WSCs remobilization to sink lay within the regulation of genes encoding fructans exohydrolases (FEHs) and cell wall/vacuolar invertase (cwINV). FEH and cwINV are highly similar proteins with different activities (Le Roy *et al.*, 2013). Fructans conversion to hexose that depends on the FEH activities is crucial for remobilization. Researchers have frequently reported different types of FEH in wheat. The two prominent FEHs are 1-FEH and 6-FEH that break inulin and levan fructans to fructose and sucrose (Van Riet *et al.*, 2008; Xue *et al.*, 2008). Two other exohydrolases are, 6-kestosexohydrolase (6-KEH) and 6,1-FEH hydrolyze 6-kestotriose and small graminian type fructans (Kawakami *et al.*, 2005; Van Den Ende *et al.*, 2005). Three isoforms of 1-FEH (*w1*, *w2* and *w3*) are known, but the isoform *w3* is speculated to be functionally more critical in remobilization (Zhang *et al.*, 2015; Zhang *et al.*, 2009; Van Riet *et al.*, 2008). However, studies suggest





that under drought stress, the mRNA level of *FEH* genes significantly increases in stem segments, but the peduncle and penultimate show a much higher transcript count, comparatively. Zhang *et al.* (2015) demonstrated early (15DAA) upregulation of 1-*FEH w3* under drought stress in contrast to irrigated conditions (>20DAA) which indicate that declined photosynthesis and senescence must have some regulatory control on this gene which needs further investigations.

Few early studies have advocated an inverse relationship between plant height and remobilization of soluble sugars to developing grain (Blum *et al.*, 1997; Shakiba *et al.*, 1996; Borrell *et al.*, 1993). Dwarf genotype with *Rht1* and *Rht2* alleles shows reduced accumulation but greater remobilization (Borrell *et al.*, 1993). To the best of our knowledge, the effect of stem morphology on remobilization is not widely studied yet and need to be investigated from various aspects.

#### 4. Role of WSCs in Water Stress Tolerance

The role of reserved WSCs' in water stress tolerance in wheat is much discussed for buffering grain yield by compensating the declined rate of current assimilation. Variations among wheat genotypes for accumulation and remobilization of WSC exist within the differential capacity of photosynthesis, respiration and carbon use efficiency under drought stress conditions (Tricker *et al.*, 2018). Therefore, drought-tolerant varieties presumably accumulate and remobilize more WSCs as a secondary source of carbon and maintain a better harmonious relationship between the source (CO<sub>2</sub> assimilation) and sink (developing grains) under water limiting conditions (Ruuska *et al.*, 2006;). A broad genetic variability in stem WSCs has been reported for wheat. Many studies have reported higher stem WSC content and remobilization in drought-tolerant genotypes than sensitive ones (Gupta *et al.*, 2011). The stem WSCs content positively correlates with final grain yield, especially in a water deficit environment (Ruuska *et al.*, 2006). Studies have shown relatively higher WSCs content in wheat stem under water-stressed than non-stressed conditions (Zhang *et al.*, 2016; Zhang *et al.*, 2014). In a similar study, Goggin and Setter (2004) reported an increase of 2.5 folds in the content of stem fructans of three high yielding Australian cultivars *viz.* Kauz, Westonia and Attila-A under rainfed conditions. Dreccer *et al.* (2009) evaluated a set of 194

Seri/Babax RILs under complete drought, rainfed and irrigated conditions and reported an increase in grain filling rate, grain weight and yield by 41%, 34% and 10%, respectively in high WSCs content RILs relative to lower ones. Contribution of 10-20% and 30-50% in kernel weight due to remobilization of WSCs under optimum and water stress conditions, respectively, has been advocated by Rebetzke *et al.* (2008) and Goggin and Setter (2004). Thus, remobilization of WSCs may contribute from 10% to 70% to the final grain weight and even more in some high potential genotypes.

As discussed earlier, reserved WSC is a composite trait of the accumulated amount of glucose, fructose, sucrose and fructans, which are essential sugars to maintain the integrity of plant life. Discussing the roles of the individual component during water stress would be beyond the objective of this article. Briefly, as: signalling molecules, ROS scavengers, and osmolytes, these sugars might be critical to help a wheat plant cope with drought stress conditions. Accumulation of soluble sugars under water stress may promote proline, a crucial osmolyte, accumulation that play a key role in ROS scavenging by stimulating antioxidant activity and stabilizing biomolecules (Hayat *et al.*, 2012; Sperdouli and Moustakas, 2012). Sugar accumulation also reduces photosynthesis and dehydration, maintaining water potential and turgidity in leaves (Xu *et al.*, 2007; F. Liu *et al.*, 2004). In addition, glucose induces stomatal closure to enhance adaptability to water stress (Osakabe *et al.*, 2014). Fructans reduce water leakage, protect membranes' structural integrity, and enhance recovery mechanisms (Valluru and Van Den Ende, 2008). Components of WSC may act as signalling molecules such as small fructans, and sucrose acts as phloem-mobile signalling under many stress conditions, including drought (Ruan, 2014; Van den Ende, 2013). Glucose also plays a vital role in the signalling and regulation of phytohormones related to water stress through sucrose non-fermenting 1-related protein kinase (SnRK1) and hexokinase (HXK1) energy sensors (Abhinandan *et al.*, 2018; Golldack *et al.*, 2014; Kim *et al.*, 2013). The reallocation of stored sugars may further enhance the water use efficiency in water deficit conditions (Zhang *et al.*, 2008).

Traces in this reference may find with the transgenic studies. Pilon-Smits *et al.* (1995) demonstrate the effect of



accumulation of bacterial fructans in transgenic tobacco. Lines with high WSC showed ~55% higher growth rate and ~59% higher dry weight under polyethylene glycol (PEG) simulated drought conditions. Li *et al.* (2007) demonstrate reduced electrolyte leakage rate and malondialdehyde concentration under cold stress in transgenic tobacco lines with *1-SST* gene from lettuce in contrast to wild type and anti-sense lines. Transformation of *1-FFT* from *Helianthus tuberosus* in tobacco leaves demonstrated the higher accumulation of fructans, which led to increased concentration of total WSCs and proline with subsequent reduction in malondialdehyde (MAD) under PEG simulated drought (Sun *et al.*, 2020). Higher accumulation of WSCs by stressed plants can invariably be seen in these studies. Therefore, presumably, besides compensating the grain weight, WSCs may also be playing a crucial role in maintaining physiological balance in a water-stressed wheat plant.

## 5. Breeding for stem WSCs

The facts presented earlier in this article advocate the potential contributions of stem WSCs to grain weight and water stress tolerance. With his comprehensive review, Blum (1998) probably first advocated the direct selection of stem WSCs as a potential trait for improving grain filling in wheat under water stress. Studies published on the recent genetic gains in modern wheat varieties of Australia, the United Kingdom and the southern Yellow and Hui Valley of China suggested inadvertent selection for increased WSCs (Gao *et al.*, 2017; Shearman *et al.*, 2005; van Herwaarden and Richards, 2002). This selection might have been assisted by selection for increased harvest index, erect canopies, greener areas, radiation interception, and other traits associated with enhanced photosynthetic capacity and better partitioning.

Rebutting the hypothesis that supports the requirement of consistent terminal drought for increased WSCs, Foulkes *et al.* (2007) and Shearman *et al.* (2005) advocated a positive correlation between progressive genetic gain in grain yield and increased WSCs under irrigated and terminal drought. The correlation studies between stem WSCs, grain yield, and associated traits take this dilemma to the next level. Some studies demonstrate a significant positive association between stem WSCs and grain yield (Gao *et al.*, 2017; Xue *et al.*, 2008), whereas others indicate variable, non-significant and even negative association

(Ovenden *et al.*, 2017; del Pozo *et al.*, 2016). However, the positive correlation of stem WSCs with grains per spike and thousand-grain weight is more stable and transparent, particularly under water-limited environments (Ruuska *et al.*, 2006; Fu *et al.*, 2020). Furthermore, Ovenden *et al.* (2017) suggested that the direct selection for stem WSC might not be a better strategy for improving yield under drought than direct selection for yield.

Genotypic variability and trait stability are two critical factors for the success of any breeding programme. Evidence suggesting the genotypic variations of accumulation and remobilization of stem WSCs at different growth phases and water conditions are available (Li *et al.*, 2020; Liu *et al.*, 2020; Hou *et al.*, 2018; Dong *et al.*, 2016; McIntyre *et al.*, 2012; Ruuska *et al.*, 2006). Various studies have identified low and high WSC genotypes with differential yield, stem biomass or yield tolerance index using recombinant inbred lines (RILs), cultivars, synthetic hexaploid derived lines, and double haploid population (Guerra *et al.*, 2021). These variations depend on numerous factors such as photosynthetic capacity, carbon use efficiency and partitioning, respiration, and several other physiological processes that affect the carbohydrate metabolisms in a vascular plant (Xue *et al.*, 2008). These factors are supposed to be highly sensitive to environmental conditions. Many studies have reported low to high genotype x environment interaction coupled with high residual variance for stem WSCs (Ovenden *et al.*, 2017; del Pozo *et al.*, 2016; Dong *et al.*, 2016). Despite the considerable influence of the environment, medium to high broad-sense heritability of 0.46-0.93 has been reported for stem WSCs, estimated at different growth stages and environments (Rebetzke *et al.*, 2008; Fu *et al.*, 2020; Li *et al.*, 2020). This suggests a cautious early selection while accounting genotype x environment interaction for this trait is possible (Ovenden *et al.*, 2017).

QTLs associated with accumulation and redistribution of stem WSCs may differentially express depending upon the stage and environment due to robust Environment X QTL (eQTLs) interactions (Ovenden *et al.*, 2017; Yang *et al.*, 2007). However, identification of stable loci (loci associated with BLUE/BLUPs, across multiple environments or studies) may solve the purpose of improving the selection abilities of a breeder. In the past two decades, efforts made to identify loci for stem WSC



Table 1. List of selected GWAS and bi-parental mapping studies for stem water soluble carbohydrates in wheat

| Trait   | Water regime | Population                 | Genotyping         | MTAs                 | QTLs                | Marker              | LG    | Position | R2   |
|---|--------------|----------------------------|--------------------|----------------------|---------------------|---------------------|-------|----------|------|
| <b>Guerra et al. (2021)</b>                                 |              |                            |                    |                      |                     |                     |       |          |      |
| water-soluble carbohydrate concentration at anthesis (WSCa) | WW and RF    | 225 spring wheat genotypes | 3243 SNP           | 96                   |                     | <i>iniaGBS56801</i> | 3A    | 4425     | 0.12 |
|   |              |                            |                    |                      | <i>iniaGBS72206</i> | 4B                  | 11169 | 0.1      |      |
|   |              |                            |                    |                      | <i>iniaGBS21574</i> | 5D                  | 1859  | 0.09     |      |
|   |              |                            |                    |                      | <i>iniaGBS13140</i> | 5B                  | 8732  | 0.09     |      |
|   |              |                            |                    |                      | <i>iniaGBS67502</i> | 1A                  | 8462  | 0.08     |      |
|   |              |                            |                    |                      | <i>iniaGBS86062</i> | 6B                  | 21361 | 0.08     |      |
|   |              |                            |                    |                      | <i>iniaGBS83719</i> | 6D                  | 5759  | 0.14     |      |
|   |              |                            |                    |                      | <i>iniaGBS52443</i> | 6B                  | 17021 | 0.12     |      |
|   |              |                            |                    |                      | <i>iniaGBS52444</i> | 6B                  | 17185 | 0.12     |      |
| <i>iniaGBS24966</i>   | 7B           | 33179                      | 0.09               |                      |                     |                     |       |          |      |
| <b>Fu et al. (2020)</b>                                     |              |                            |                    |                      |                     |                     |       |          |      |
| WSC10 (Stem WSC content at 10 days post-anthesis)           | WW           | 166 winter wheat genotypes | 660 K and 90 K SNP |                      |                     | <i>AX-109989656</i> | 1A    |          | 8.86 |
|   |              |                            |                    | <i>AX-109293426</i>  | 1A                  |                     | 12.98 |          |      |
|   |              |                            |                    | <i>AX-111648440</i>  | 1B                  |                     | 13.68 |          |      |
|   |              |                            |                    | <i>AX-94811887</i>   | 1D                  |                     | 10.38 |          |      |
|   |              |                            |                    | <i>BS00098423_51</i> | 2A                  |                     | ----- |          |      |
|   |              |                            |                    | <i>AX-110070963</i>  | 4A                  |                     | 10.16 |          |      |
|   |              |                            |                    | <i>AX-108959247</i>  | 6B                  |                     | 12.33 |          |      |
|   |              |                            |                    | <i>AX-110514480</i>  | 7D                  |                     | 15.43 |          |      |
|   |              |                            |                    | <i>AX-111668935</i>  | 1B                  |                     | 12.07 |          |      |
|   |              |                            |                    | <i>AX-111640220</i>  | 1D                  |                     | 9.85  |          |      |
|   |              |                            |                    | <i>AX-111552571</i>  | 2A                  |                     | 14.58 |          |      |
|   |              |                            |                    | <i>AX-108729610</i>  | 2B                  |                     | 11.24 |          |      |
| <i>AX-94829137</i>  | 3A           |                            | -----              |                      |                     |                     |       |          |      |
| <i>AX-111031397</i>   | 5A           |                            | 13.8               |                      |                     |                     |       |          |      |
| <i>AX-111274903</i>   | 6B           |                            | 8.17               |                      |                     |                     |       |          |      |
| <i>BobWhite_c39668_143</i>                                  | 1A           |                            | 11.77              |                      |                     |                     |       |          |      |
| <i>AX-110028549</i>   | 2A           |                            | 17.44              |                      |                     |                     |       |          |      |
| <i>AX-108784564</i>   | 7A           |                            | -----              |                      |                     |                     |       |          |      |
| <i>AX-108972618</i>   | 7A           |                            | 11.59              |                      |                     |                     |       |          |      |
| <b>Guerra et al. (2021)</b>                                 |              |                            |                    |                      |                     |                     |       |          |      |
| WSC20 (Stem WSC content at 20 days post-anthesis)           | WW           | 166 winter wheat genotypes | 660 K and 90 K SNP |                      |                     | <i>AX-109989656</i> | 1A    |          | 8.86 |
|   |              |                            |                    | <i>AX-109293426</i>  | 1A                  |                     | 12.98 |          |      |
| WSC30 (Stem WSC content at 30 days post-anthesis)           | WW           | 166 winter wheat genotypes | 660 K and 90 K SNP |                      |                     | <i>AX-109989656</i> | 1A    |          | 8.86 |
|   |              |                            |                    | <i>AX-109293426</i>  | 1A                  |                     | 12.98 |          |      |
|   |              |                            |                    | <i>AX-111648440</i>  | 1B                  |                     | 13.68 |          |      |
|   |              |                            |                    | <i>AX-94811887</i>   | 1D                  |                     | 10.38 |          |      |
|   |              |                            |                    | <i>BS00098423_51</i> | 2A                  |                     | ----- |          |      |
|   |              |                            |                    | <i>AX-110070963</i>  | 4A                  |                     | 10.16 |          |      |
|   |              |                            |                    | <i>AX-108959247</i>  | 6B                  |                     | 12.33 |          |      |
|   |              |                            |                    | <i>AX-110514480</i>  | 7D                  |                     | 15.43 |          |      |
|   |              |                            |                    | <i>AX-111668935</i>  | 1B                  |                     | 12.07 |          |      |
|   |              |                            |                    | <i>AX-111640220</i>  | 1D                  |                     | 9.85  |          |      |
|   |              |                            |                    | <i>AX-111552571</i>  | 2A                  |                     | 14.58 |          |      |
|   |              |                            |                    | <i>AX-108729610</i>  | 2B                  |                     | 11.24 |          |      |
| <i>AX-94829137</i>  | 3A           |                            | -----              |                      |                     |                     |       |          |      |
| <i>AX-111031397</i>   | 5A           |                            | 13.8               |                      |                     |                     |       |          |      |
| <i>AX-111274903</i>   | 6B           |                            | 8.17               |                      |                     |                     |       |          |      |
| <i>BobWhite_c39668_143</i>                                  | 1A           |                            | 11.77              |                      |                     |                     |       |          |      |
| <i>AX-110028549</i>   | 2A           |                            | 17.44              |                      |                     |                     |       |          |      |
| <i>AX-108784564</i>   | 7A           |                            | -----              |                      |                     |                     |       |          |      |
| <i>AX-108972618</i>   | 7A           |                            | 11.59              |                      |                     |                     |       |          |      |

**Li et al. (2020)**

|  |                        |                          |     |           |
|--|------------------------|--------------------------|-----|-----------|
| Stem water-soluble carbohydrates at the flowering stage (WSCf) | <i>Qesgf.acs-3B.1</i>  | <i>Xpsp3112-Xgwm72</i>   | 3B  | 6.96/8.09 |
|  | <i>Qesgf.acs-4A</i>    | <i>Xksm51-Xgwm637</i>    | 4A  | 9.14/9.58 |
| Water-soluble carbohydrates at the grain-filling stage (WSCg)  | <i>Qesgf.acs-7A.2</i>  | <i>Xbarc195-Xbarc121</i> | 7A  | 3.42/4.12 |
|  | <i>Qescg.acs-2D.1</i>  | <i>Xgwm261-Xiwmc112</i>  | 2D  | 3.92/4.62 |
|  | <i>Qescg.acs-4B.1</i>  | <i>Xgwm495-Xgwm251</i>   | 4B  | 4.91/3.08 |
|  | <i>Qescg.acs-5A.1</i>  | <i>Xmag694-Xgwm415</i>   | 5A  | 2.97/3.83 |
|  | <i>Qescm.acs-7A.2</i>  | <i>Xbarc195-Xbarc121</i> | 7A  | 3.48/8.94 |
| DS and WW  | 120 RILs               | 55K SNP                  | 460 |           |
| Pre-anthesis WSC remobilization rate. (WRRpr)                  | <i>Qerrpr.acs-6B.2</i> | <i>Xiwmc341-Xbarc198</i> | 6B  | 5.49/6.66 |
| Post-anthesis WSC remobilization rate. (WRRps)                 | <i>Qerrps.acs-4B.1</i> | <i>Xgwm495-Xgwm251</i>   | 4B  | 1.75/5.31 |
| Pre-anthesis WSC contribution rate. (WCRpr)                    | <i>Qerrps.acs-5A.4</i> | <i>Xgwm443-Xgfa2155</i>  | 5A  | 0.97/0.89 |
| Post-anthesis WSC contribution rate. (WCRps)                   | <i>Qerrpr.acs-6B.1</i> | <i>Xgfd13-Xiwmc737</i>   | 6B  | 4.92/5.76 |
|  | <i>Qerrps.acs-6B.1</i> | <i>Xiwmc341-Xbarc198</i> | 6B  | 5.81/5.32 |

**Nadia et al. (2017)**

|   |                 |     |    |           |
|---|-----------------|-----|----|-----------|
| Stem water-soluble carbohydrates at the grain-filling stage (SWSCG) | <i>Xiwmc112</i> | 2D  | 28 | 0.15-0.44 |
| Stem water-soluble carbohydrates at the maturity stage (SWSCM)      | <i>Xiwmc420</i> | 4AL | 7  | 0.15-0.44 |

**Dong et al. (2016)**

|                   |                               |     |     |      |
|-------------------|-------------------------------|-----|-----|------|
| WSC content 14DAA | <i>wsp_Ra_c26191_35761997</i> | 1AS | 54  | 8.2  |
|                   | <i>Tdurum_contig8382_300</i>  | 1AS | 58  | 7.6  |
|                   | <i>BobWhite_c4147_1429</i>    | 1BS | 63  | 6.8  |
|                   | <i>Excalibur_c12994_1060</i>  | 1BL | 82  | 7.7  |
|                   | <i>Kukri_c11000_1769</i>      | 1BL | 137 | 6.8  |
|                   | <i>BS00066305_51</i>          | 1BL | 159 | 8.6  |
|                   | <i>IAAV4884_8.1</i>           | 1BL | 159 | 8.1  |
|                   | <i>RFL_Contig3165_667</i>     | 1BL | 159 | 10.5 |
|                   | <i>BobWhite_c34125_183</i>    | 1BL |     | 7.6  |
|                   | <i>BS00063907_51</i>          | 1DL | 160 | 8.2  |
|                   | <i>Excalibur_c7963_1722</i>   | 2BS | 116 | 7.6  |
|                   | <i>GENE-0137_469</i>          | 2BS | 69  | 7.2  |
|                   | <i>GENE-1421_706</i>          | 2BS | 69  | 7.6  |





|                                    |     |      |      |
|------------------------------------|-----|------|------|
| <i>Kukri_c29640_92</i>             | 2BS | 6969 | 6.9  |
| <i>Kukri_rep_c106290_204</i>       | 2BS | 69   | 7.2  |
| <i>Ku_c34562_480</i>               | 2BS | 72   | 8.5  |
| <i>Excalibur_c40229_76</i>         | 2BS | 88   | 7.5  |
| <i>BS00022949_51</i>               | 2BS | 91   | 7.1  |
| <i>BS00065993_51</i>               | 2BS | 91   | 7.5  |
| <i>Excalibur_c11505_155</i>        | 3AS | 26   | 7.4  |
| <i>RAC875_c20134_535</i>           | 3AS | 26   | 7.2  |
| <i>Excalibur_c54388_193</i>        | 3B  | 66   | 7.5  |
| <i>Kukri_rep_c70097_286</i>        | 3B  | 66   | 8    |
| <i>wshp_CAP11_c558_382875</i>      | 3B  | 66   | 8    |
| <i>BS00003522_51</i>               | 3B  | 67   | 7.9  |
| <i>RAC875_c15109_510</i>           | 3B  | 81   | 7.9  |
| <i>TA002089-1495</i>               | 3B  | 81   | 7.3  |
| <i>RAC875_c35720_229</i>           | 3B  | 82   | 7.6  |
| <i>RAC875_c35720_456</i>           | 3B  | 82   | 8.4  |
| <i>wshp_Ex_rep_c68193_66971396</i> | 3B  | 83   | 8.5  |
| <i>BS00067163_51</i>               | 3DL | 130  | 14.5 |
| <i>D_GA8KES402JVTTY_74</i>         | 3DL | 130  | 14.6 |
| <i>GENE-1785_118</i>               | 3DL | 130  | 15.2 |
| <i>GENE-1785_626</i>               | 3DL | 130  | 12.4 |
| <i>Excalibur_c15280_1242</i>       | 4AL | 109  | 7.5  |
| <i>BS00062691_51</i>               | 4BS | 62   | 7    |
| <i>BS00074440_51</i>               | 4BS | 62   | 7.1  |
| <i>Tdurum_comtig57516_269</i>      | 4BS | 62   | 6.9  |
| <i>BS00074439_51</i>               | 4BS | 63   | 7    |
| <i>GENE-2129_76</i>                | 4BS | 63   | 7    |
| <i>RAC875_c45747_87</i>            | 4BS | 63   | 7    |
| <i>RAC875_c33933_350</i>           | 5AS | 35   | 8.4  |
| <i>RAC875_rep_c78046_324</i>       | 5DL | 50   | 7.2  |
| <i>Excalibur_c58260_332</i>        | 6BL | 65   | 9.2  |
| <i>RAC875_c5129_280</i>            | 6BL | 79   | 7.1  |



|                         |                          |     |       |       |
|-------------------------|--------------------------|-----|-------|-------|
|                         | <i>RAC875_c63889_486</i> | 7AS | 88    | 8.5   |
|                         | <i>wshp_bq170165A_</i>   | 7AL | 136   | 8     |
|                         | <i>Ta_1_1</i>            | 7AL | 148   | 7.5   |
|                         | <i>tp1b0045p11_893</i>   | 7AL | 150   | 6.9   |
|                         | <i>IACX2471</i>          | 7AL | 152   | 11.5  |
|                         | <i>wshp_Ku_</i>          | 7BS | 53    | 8     |
|                         | <i>c42539_50247426</i>   | 7DS | 20    | 13    |
|                         | <i>RAC875_c26328_75</i>  |     |       |       |
|                         | <i>TaSSF-D1</i>          |     |       |       |
| <b>Li et al. (2015)</b> |                          |     |       |       |
| WSCG-Low                | <i>Xgwm403</i>           | 1B  | 49.6  | 2.432 |
|                         | <i>Xbarc324</i>          | 3A  | 73.0  | 2.260 |
|                         | <i>Xgwm566</i>           | 3B  | 54.1  | 2.469 |
|                         | <i>Xbarc181</i>          | 1B  | 38.3  | 2.174 |
|                         | <i>Xbarc324</i>          | 3A  | 73.0  | 3.510 |
|                         | <i>Xgwm566</i>           | 3B  | 54.1  | 3.000 |
|                         | <i>Xgwm537</i>           | 7B  | 35.2  | 2.022 |
|                         | <i>Xwmc396</i>           | 7B  | 67.3  | 2.131 |
|                         | <i>Xgwm358</i>           | 5D  | 26.2  | 2.620 |
|                         | <i>Xwmc182</i>           | 6B  | 43.8  | 3.073 |
|                         | <i>Xbarc175</i>          | 6D  | 79.1  | 2.222 |
|                         | <i>Xgwm131</i>           | 7B  | 7.6   | 2.292 |
|                         | <i>Xbarc187</i>          | 1B  | 31.5  | 3.764 |
|                         | <i>Xgwm458</i>           | 1D  | 55.3  | 2.276 |
|                         | <i>Xgwm148</i>           | 2B  | 46.5  | 3.369 |
|                         | <i>Xbarc175</i>          | 6D  | 79.1  | 3.628 |
|                         | <i>Xgwm46</i>            | 7B  | 53.5  | 2.409 |
|                         | <i>Xgwm413</i>           | 1B  | 25.9  | 2.585 |
|                         | <i>Xwmc181</i>           | 1B  | 38.3  | 2.114 |
|                         | <i>Xgwm259</i>           | 1B  | 106.8 | 2.229 |
|                         | <i>Xgwm261</i>           | 2D  | 23.2  | 2.041 |
|                         | <i>Xbarc314</i>          | 3A  | 110.1 | 2.268 |
|                         | <i>Xgfd23</i>            | 4D  | 32.9  | 2.143 |
|                         | <i>Xgwm361</i>           | 6B  | 37.7  | 2.602 |
|                         | <i>Xgwm413</i>           | 1B  | 25.9  | 2.921 |
|                         | <i>Xgwm429</i>           | 2B  | 40.4  | 2.027 |
|                         | <i>Xgwm374</i>           | 2B  | 60.7  | 3.439 |
| WSCG-Low                |                          |     |       |       |
| WSCF-Low                |                          |     |       |       |
| WSCF-Low                |                          |     |       |       |
| WSCF-Site               |                          |     |       |       |
| WSCG-Low                |                          |     |       |       |
| WSCG-Site               |                          |     |       |       |





accumulation and remobilization in wheat under varying environments using bi-parental QTL mapping and GWAS (Table 1). The identified potential SNPs and putative candidate genes related to WSC provide opportunities for breeding higher WSC wheat cultivars. Few of these identified loci collocate with QTLs for different agronomic traits. For instance, Rebetzke *et al.* (2008) collocated the QTLs of WSCC, WSC total amount per square meter, and WSC per tiller with *Ppd-D1*, *Rht-B1*, and *Rht-D1*. Fu *et al.* (2020) observed that loci for stem WSCs at 10, 20 and 30DAA were in the vicinity of previously identified QTLs for the number of spikes per plant/unit areas, TKW and grain yield. These studies have advocated that pyramiding favourable alleles support the increment in stem WSCs content under abiotic stress in wheat (Zhang *et al.*, 2014; Li *et al.*, 2015). Therefore, deployment of allelic variations of genes favoring drought adaptability is a key approach in wheat molecular breeding. Khalid *et al.*, 2019 developed two KASP (Kompetitive allele-specific PCR) markers for water-soluble carbohydrate genes (*TaSST-D1* and *TaSST-A1*) associated with plant height and thousand grain weight (TGW) in the diversity panel. Recently, Fu *et al.* (2020) also developed high-throughput KASP markers for five pleiotropic loci for stem WSC content (SWSCC) and thousand kernel weight (TKW) and validated in different environments. These KASP markers would be valuable tools for MAS targeting simultaneous improvement in SWSCC and TKW. Such studies further strengthen the hypothesis that somehow, stem WSCs, and grain yield and contributing traits have a close association.

## 6. Conclusion

Stem WSCs maintains the grain yield and physiological balance by compensating the fixed carbon shortage during the diurnal cycle, senescence and stress conditions. Thus it can be a potential target for wheat breeders. As a prerequisite for a breeding program, ample genetic variation may be found to accumulate and remobilise stem WSCs across various wheat germplasms. Since these variations lay within the differential capacity of photosynthesis, carbohydrates metabolism and respiration that are influenced by environment and genotype x environment interactions, stability of this trait may slow down the selection process. However, medium to high heritability for this trait, reported under various experimental conditions, shows careful early generation

selection possibilities. Furthermore, efficient molecular marker systems may bring precision to the selection and accelerate the WSCs based wheat breeding program.

## Conflict of Interest

The authors declare that they have no conflict of interest.

## Ethical Compliance Statement

NA

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