

Effect of water-deficit on stem reserve mobilization for grain filling in wheat (*Triticum aestivum* L.)

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Abstract

The grain filling and development is considered as a key step for wheat yield and is most sensitive to water-deficit. In order to understand the effect of water-soluble carbohydrates (WSC) accumulation and mobilization of water-deficit tolerance, wheat lines viz., check PBW725, parent DS5U^(5A) and introgression lines (ILs) (5U-24, 5U-26, 5U-27 and 5U-31) were used in this experiment. We examined the pattern of accumulation and mobilization water-soluble carbohydrates in peduncle (Ped), upper internodes (U_{int}), middle internodes (M_{int}) and basal internodes (B_{int}) under water-deficit. B_{int} showed highest mobilization of WSC reserves for grain filling indicating that the lower portions of the stem may exhibit higher remobilization efficiency under water-deficit conditions. Among the ILs, IL 5U-26 showed highest mobilization of WSC in all the internodes. Correlation analysis depicted that increase in mobilization of WSC from U_{int}, M_{int}, B_{int} and Ped enhanced TGW significantly. Highest significant correlation of percent increase in TGW was found with percent change of WSC in Ped (0.97, significant at p<0.01). Also, defoliation studies were carried out under both irrigated and rain-fed conditions to study the mobilization of stem reserves that can provide essential carbon resources for grain-filling to compensate grain weight under defoliated conditions. TGW was reduced after defoliation with significant minimum reduction in IL 5U-26 under irrigated conditions while with non-significant reduction in IL 5U-26 under rain-fed conditions. Also, IL 5U-26 exhibited maximum increase in stem reserve mobilization (SRM) under rain-fed conditions. This indicated that water-deficit considerably increased the remobilization of stem reserves, which enhanced grain filling and contributed significantly to grain weight in 5U-26. Thus, 5U-26 with improved mobilization efficiency can be used in future breeding programmes to enhance grain filling and ultimately yield in wheat.

Keywords: Wheat, Stem reserve mobilization, Grain filling, Water-deficit

1. Introduction

Optimum moisture levels are essential for healthy plant growth and completion of its life cycle. (Hatfield and Prueger, 2015). The situation of inadequate moisture caused by sub-optimum rains and poor irrigation practices,

leads to water deficit stress in rain fed areas (Bharucha *et al.*, 2014) which substantially hinders crop growth and plant productivity. Also, water-deficit is one of the major abiotic factors affecting global agricultural productivity



including wheat. More than 35% of the global population depends on wheat (*Triticum aestivum* L.), one of the agricultural crops, as their staple food. Both environmental water resource limitations and global climate change have an impact on its production (Shrief and Mohsen, 2015). Understanding the natural genetic diversity in traits associated to drought resistance is important since wheat frequently grows in water-limited environments during its life cycle.

In India, the observed general trend in precipitation indicates fewer wet days and an increment in the hot days is estimated to have adverse effects on India's food security. Water stress affect wheat production as it influences various morphological and physiological characteristics viz., leaf size, stomatal conductance, photosynthetic rate and also affects the anatomical features of a plant (Bhusal *et al.*, 2020). The most sensitive phase to water availability is post-anthesis phase i.e. grain filling period. Water stress at the grain filling stage affects reserve mobilization and is regarded as one of the major factors influencing the final grain yield (Salem *et al.*, 2008). The final productivity in cereal crops in terms of grain yield is a complex biochemical and physiological process that is primarily linked with the accumulation and remobilization of assimilates in plants (Biswal and Kohli, 2013). For wheat grain filling, two different types of carbon sources are: storage assimilates (either pre- or post-anthesis), which are translocated from stem reservoirs (primarily in leaf sheaths and culms) and current photosynthetic assimilates in green parts of the plant (mainly in flag leaves), which are translocated directly to the developing grain (Liu *et al.*, 2020). The genotype and water supply have an impact on the implication of the above two processes (Haberle *et al.*, 2008). Grain is primarily filled with current photo assimilates supplied by green organs when there is an optimum water supply. While under water-deficit, grain is primarily filled by remobilized components as water stress leads to early leaf senescence (Arous *et al.*, 2020). The contribution of the organs involved in the above processes constitute essentially their proximity to the developing grain, their photosynthetic efficiency, their survival periods and the hydraulic resistance of the conductive tissues to ensure the optimum flow of sap (Bijan-zadeh and Emam, 2012).

The organs that are located above the upper node viz., awns, the spike's neck, grain envelopes and flag leaf

are mostly responsible for the current photosynthesis (Sanchez-Bragado *et al.*, 2014). Among these organs, the flag leaf has a significant role in formation and transfer of the photo-assimilates to the developing cereal grains, thus, affecting final grain productivity (Khaliq *et al.*, 2008). According to Kong *et al.* (2016), the maturing grains are the major sinks while the upper two leaves are considered the primary source. Under optimal conditions, defoliation of the flag leaf blade in wheat has resulted in an increased supply of assimilates from the stem and chaff to the developing grains (Biswal and Kohli, 2013). According to Saint Pierre *et al.* (2010), stem reserves (water-soluble carbohydrates) are readily available for mobilization to other parts of plant. The role of translocation of stem WSC reserves to grain filling becomes more significant when current photosynthesis is lowered by partial defoliation (Borrás *et al.*, 2004). The drought tolerant cultivars have greater ability to store assimilates and more efficiently remobilize these reserves to developing grains under water deficit environments (Ahmadi *et al.*, 2016). Lines with the improved capability to mobilize the stored stem reserves under water-deficit conditions are considered to be tolerant and are likely to yield better (Pierre *et al.*, 2010). Variation in grain weight of different wheat genotypes can be evaluated with flag leaf defoliation (Lv *et al.*, 2020). Therefore, one of methods for selecting the water-deficit tolerant wheat cultivars could be investigating the translocation of stem reserves in such genotypes. Given the foregoing, the current study was conducted to evaluate the genetic variations among wheat lines for capacity of stem reserve mobilization under water-deficit environments.

2. Materials and Methods

2.1. Experimental Sites, Year, Treatments and Plant material

The present research was carried out during the rabi season 2021-22 at the laboratories of Department of Botany and the experimental field area of Punjab Agricultural University (PAU), Ludhiana. The daily maximum temperature during May ranges from 40-45 °C and minimum daily temperature ranges from 0-4 °C during January. The soil of field area was alluvial sandy loam soil. The experimental sites were managed with 2-yr rotations of wheat and rice.



The crop for this study was laid out in alpha lattice design in three replications under control (timely irrigated) and rain-fed conditions (by withholding irrigation and letting the crop grow under rain-fed conditions). Sowing of lines was done using dibbling method. The sowing was done on 15th November, 2021. The dimensions of each plot were 1×0.8 square metres with four rows spaced 0.20 m apart. 8 grams of seed was used for planting the crop in each plot.

The plant material used for the experiment was a disomic substitution DS5U^(5A) and four introgression lines (ILs) derived from three-way cross of Pavon *ph1b*, WL711 and DS5U^(5A). Wheat variety PBW725 was used as check. The DS5U^(5A) line was developed in the background of cultivar WL711 where chromosome 5A was substituted by chromosome 5U from tetraploid wheat wild non-progenitor species. Pavon *ph1b* mutant has 70MB deletion in *Ph1b* locus on chromosome 5B, thus, suppressing this locus and inducing homeologous chromosome pairing in wheat. The ILs used in the study were developed by crossing DS5U^(5A) line twice with Pavon *ph1b* mutant and thereafter the selected BC₁F₁ with *ph1b* locus in homozygous condition and chromosome 5U and 5A in heterozygous conditions were selected and crossed with WL711 to develop BC₁F₁ ILs named as 5U-24, 5U-26, 5U-27 and 5U-31. Each IL has genomic fragments from chromosome 5U of *Aegilops triuncialis* accession pau 3549 (2n=4x=28, U^UC^CC^C) in background of wheat genome.

2.2. Sampling and Data Recording

On the first day of anthesis, the tillers were tagged for sampling. Tillers were sampled at anthesis, 15 days after anthesis (15DAA) and at maturity for all the lines in irrigated and rain-fed conditions from all the three replications.

2.3. Estimation of stem water soluble carbohydrates (WSC)

The tillers were divided into peduncle, upper internodes, middle internodes and basal internodes and accumulation of WSC in each internode was estimated through Yemm & Willis (1954) method. Mobilized WSC were calculated as maximum WSC accumulated at post anthesis – residual non-mobilized WSC at maturity.

Also, to validate the results defoliation studies were carried out to test stem reserve mobilization (SRM) under rain-fed conditions which were as follows:

2.4. Defoliation treatment and grain weight estimation

Before the commencement of anthesis, five tagged tillers from different plants with similar spike length were defoliated by removing the upper two leaves (flag leaf and penultimate leaf). Five other tillers served as the experiment's control; they were tagged but not defoliated. When mature, all the tagged tillers were harvested separately, the respective spikes were individually threshed and the grain weight was noted. Based on the percentage decrease in thousand grain weight (TGW) for every line, stem reserves were calculated. For each tested line, the mean kernel weight under defoliation was compared to the mean kernel weight in the controls to determine the percentage reduction in kernel weight (Blum, 1998).

2.5. Statistical analysis

The data obtained was analysed using three-way factorial randomized complete design (CRD) with three replications in Statistix 10 software. Lines and irrigation were the two factors used in analysis of data. Means, analysis of variance (ANOVA), standard deviation and coefficient of variance were obtained to determine the effect of treatment (irrigation), lines and their subsequent interaction for all measured traits. Correlation heatmap was constructed using software R-studio version 3.2.

3. Results

3.1. Accumulation of WSC in stem internodes

Water-deficit significantly affected the accumulation of WSC in all the stem internodes [Peduncle (Ped), Upper internodes (U_{int}), middle internodes (M_{int}) and basal internodes (B_{int})] as compared to irrigated conditions (Table 1) (Supplementary table 1). At all the three stages (anthesis, 15DAA and maturity), water-deficit significantly increased WSC accumulation in all the stem internodes of parent, check and most ILs. However, IL 5U-31 showed a decrease in accumulation of WSC under rain-fed conditions by 2.66%, 2.73%, 6.08% and 12.28% in B_{int}, M_{int}, U_{int} and Ped, respectively (Fig. 1). Maximum percent increase in accumulation of WSC under rain-fed conditions was exhibited by IL 5U-26 in all the internodes and it increased by 36.03%, 39.85%, 19.90% and 37.04% in B_{int}, M_{int}, U_{int} and Ped, respectively. Parent DS5U^(5A) exhibited an increase in WSC by 1.23%, 0.080%, 14.35% and 14.56% in B_{int}, M_{int}, U_{int} and Ped, respectively.



Table 1: Analysis of variance across wheat lines, treatments (irrigation) and their interactions for mean WSC accumulated in B_{int} , M_{int} , U_{int} and Ped, mobilized WSC in B_{int} , M_{int} , U_{int} and Ped and stem reserve mobilization.

S. No.	Source of variation	Mean accumulated WSC at three stages (0DAA, 15DAA and maturity) in:				Mobilized WSC in:				
		(B_{int})	(M_{int})	(U_{int})	Ped	(B_{int})	(M_{int})	(U_{int})	Ped	SRM
1	Lines	1735.72***	1706.52***	2231.4***	3801.12***	2901.3***	4223.1***	2187.3***	6898.6***	29.090***
2	Irrigation	3271.84***	3369.8***	3422.25***	8281***	35532.3***	17822.2***	21462.2***	18906.2***	12.308***
3	Genotypes* Irrigation	1053.27***	1281.51***	583.39***	1649.11***	580.5***	419.9**	164 ^{ns}	445.5**	10.079***
4	Error	42.92	68.33	65.67	88.5	89.2	74	84.8	104.8	0.113

***significant at $p \leq 0.001$, **significant at $p \leq 0.01$, *significant at $p \leq 0.05$, ns- non-significant

Table 2: Analysis of variance across wheat lines, treatments (irrigation), sub-treatments (defoliation) and their interactions for thousand grain weight (TGW).

S. No.	Source of variation	TGW
1	Lines	286.634
2	Treatment	3.48
3	Sub-treatment	49.684
4	Lines*Treatment	59.675
5	Lines* Sub-treatment	1.343
6	Treatment*stage	1.219
7	Lines*Treatment* Sub-treatment	0.271
8	Error	0.069

3.2. Mobilization of WSC in stem internodes

Significant variation in mobilization of WSC was observed among the ILs and irrigation regimes (Table 1) (Supplementary table 2) and water-deficit significantly enhanced the mobilization of WSC in all the internodes of studied lines. IL 5U-26 outperformed parent DS5U^(5A), check PBW725 and all other ILs by exhibiting highest percent increase in mobilization of WSC in all the internodes viz., Ped (28.34%), U_{int} (25.60%), M_{int} (28.29%) and B_{int} (31.32%). Contrastingly,

5U-31 exhibited lowest percent increase in mobilization of WSC in all the internodes [B_{int} (10.95%), U_{int} (13.44%), M_{int} (12.44%) and B_{int} (13.79%)] followed by check PBW 725 [B_{int} (11.68%), U_{int} (15.24%), M_{int} (12.23%) and B_{int} (14.93%)] (Fig.2) under rain-fed conditions as compared to control. Among the internodes, B_{int} exhibited higher percent increase (14.93%, 22.56%, 26.05%, 31.32%, 24.74% and 13.79% in PBW725, DS5U^(5A), 5U-24, 5U-26, 5U-27 and 5U-31, respectively) in mobilization of WSC under rain-fed conditions.

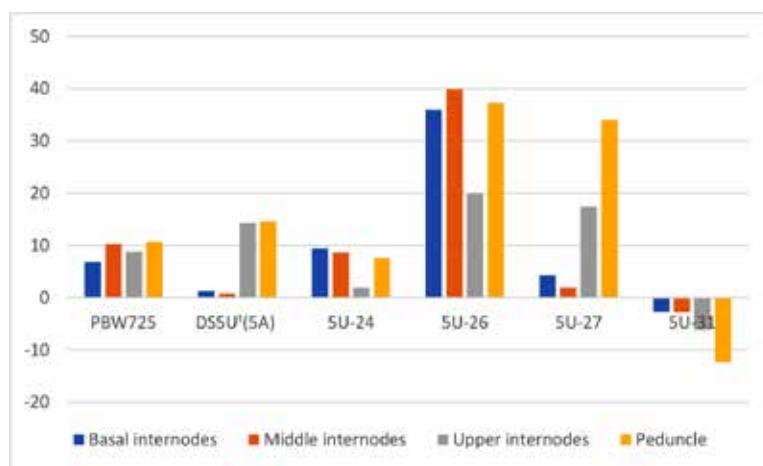


Fig. 1: Percent change in accumulation of WSC under rain-fed conditions



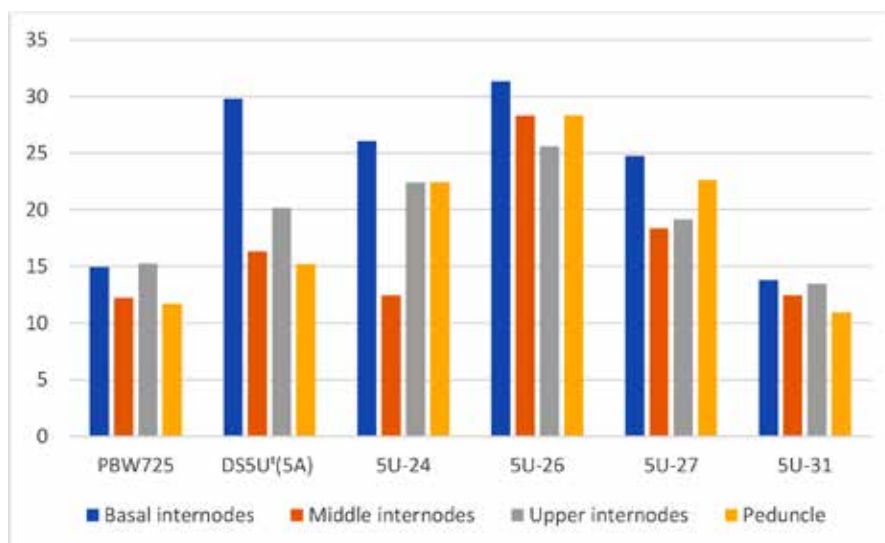


Fig. 2: Percent increase in mobilization of WSC under rain-fed conditions

3.3. Correlation analysis

Fig. 3 shows correlations amongst percent change in accumulated WSC under rain-fed conditions in basal internodes (B_accum), percent change in accumulated WSC under rain-fed conditions in middle internodes (M_accum), percent change in accumulated WSC under rain-fed conditions in upper internodes (U_accum), percent change in accumulated WSC under rain-fed conditions in peduncle (P_accum), percent change in mobilized WSC under rain-fed conditions in basal internodes (B_mobilized), percent change in mobilized WSC under rain-fed conditions in middle internodes (M_mobilized), percent change in mobilized WSC under rain-fed conditions in upper internodes (U_mobilized), percent change in mobilized WSC under rain-fed conditions in peduncle (P_mobilized). Correlation

analysis results depicted that increase in mobilization of WSC from U_{int}, M_{int}, B_{int} and Ped significantly enhanced TGW. Highest significant correlation of percent change in TGW was found with percent change of WSC in peduncle (0.97, significant at $p < 0.01$) followed by percent change of WSC in upper internodes (0.90, significant at $p < 0.05$), percent change of WSC in basal internode (0.84, significant at $p < 0.05$) and percent change of WSC in middle internodes (0.81, significant at $p < 0.05$). Therefore, increase in mobilization of WSC in all the internodes significantly enhanced the TGW with peduncle contributing the most towards enhancement of TGW. It further shows that increase in accumulation of WSC under rain-fed conditions did not significantly affect the TGW while its mobilization does affect TGW under rain-fed conditions.

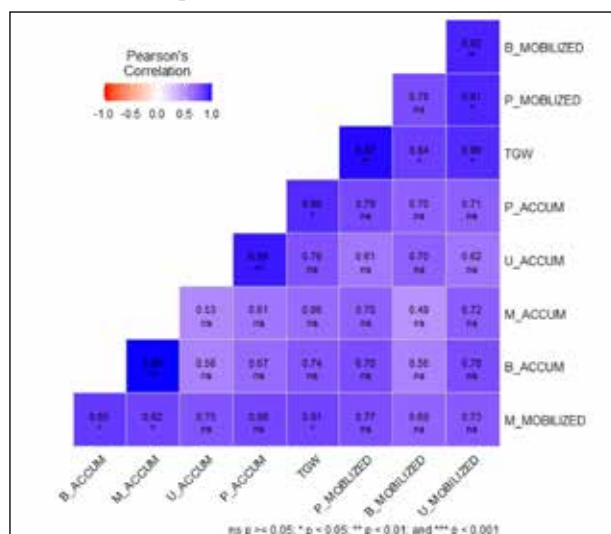


Fig. 3: Correlation heatmap of the percent change in WSC accumulated, mobilized and TGW under rain-fed conditions. *, ** and *** indicate significant at $p < 0.05$, $p < 0.01$ and $p < 0.001$. (B_accum- percent change in accumulated WSC under rain-fed conditions in basal internodes, M_accum- percent change in accumulated WSC under rain-fed conditions in middle internodes, U_accum- percent change in accumulated WSC under rain-fed conditions in upper internodes, P_accum- percent change in accumulated WSC under rain-fed conditions in peduncle, B_mobilized- percent change in mobilized WSC under rain-fed conditions in basal internodes, M_mobilized- percent change in mobilized WSC under rain-fed conditions in middle internodes, U_mobilized- percent change in mobilized WSC under rain-fed conditions in upper internodes, P_mobilized- percent change in mobilized WSC under rain-fed conditions in peduncle).



3.4. Effect of defoliation on TGW and SRM

Effect on TGW

TGW under control and defoliation treatment varied significantly among the lines, irrigation regimes, defoliation treatments and their interactions (Table 2). It showed a significant decrease in defoliation treatment under both irrigated and rain-fed conditions except for 5U-26 in which TGW did not decrease significantly in defoliation treatment under rain-fed conditions (Table 3).

Table 3: Thousand grain weight (TGW) (grams) in control and defoliated conditions under irrigated and rain-fed conditions

Lines	Treatment	Sub-trt	TGW	Lines	Treatment	Sub-trt	TGW
PBW725	Irrigated	TGW	41.10 ^a	PBW725	Rain-fed	TGW	35.61 ^{fg}
		TGWD	38.41 ^b			TGWD	33.57 ⁱ
DS5Uⁱ(5A)	Irrigated	TGW	39.46 ^{cd}	DS5Uⁱ(5A)	Rain-fed	TGW	37.71 ^{bc}
		TGWD	37.23 ^{gh}			TGWD	36.64 ^{de}
5U-24	Irrigated	TGW	32.71 ^j	5U-24	Rain-fed	TGW	34.57 ^h
		TGWD	30.11 ^{mn}			TGWD	32.71 ^j
5U-26	Irrigated	TGW	30.92 ^{lm}	5U-26	Rain-fed	TGW	36.53 ^e
		TGWD	29.84 ⁿ			TGWD	36.14 ^{ef}
5U-27	Irrigated	TGW	28.87 ^o	5U-27	Rain-fed	TGW	32.01 ^{jk}
		TGWD	27.63 ^p			TGWD	31.28 ^{kl}
5U-31	Irrigated	TGW	27.13 ^p	5U-31	Rain-fed	TGW	22.83 ^r
		TGWD	25.46 ^q			TGWD	20.54 ^s

Means with the different letter are significantly different.

SRM

Significant variation in SRM was observed among the ILs, parent DS5Uⁱ(5A) and check PBW725 under both irrigated and rain-fed conditions (Table 1) (Supplementary table 3). Under irrigated conditions, IL 5U-26 exhibited maximum SRM (96.50%) whereas 5U-24 exhibited minimum SRM (92.03%). Similarly, under rain-fed conditions, IL 5U-26 recorded maximum SRM (98.92%) whereas 5U-31 showed minimum value (89.96%). Overall mean showed that SRM was higher under rain-fed conditions than under irrigated conditions. Maximum percent increase in SRM was exhibited by parent DS5Uⁱ(5A) (2.98%) followed by 5U-24 (2.78%) and 5U-26 (2.50%) while minimum percent increase in SRM was observed in PBW725 (0.86%) under rain-fed conditions. However, 5U-31 showed a decrease in SRM by 04.41% rain-fed conditions (Fig. 4).

Under irrigated conditions, maximum percent decrease in TGW after defoliation was observed in PBW725 (6.56%) and 5U-31 (6.16%) while minimum percent decrease in TGW after defoliation was observed in IL 5U-26 (3.50%) (Table 3). Similarly, under rain-fed conditions, maximum percent decrease in TGW after defoliation was recorded in 5U-31 (10.04%), followed by PBW 725 (05.75%) while minimum (non-significant) decrease (01.08%) was exhibited by 5U-26.

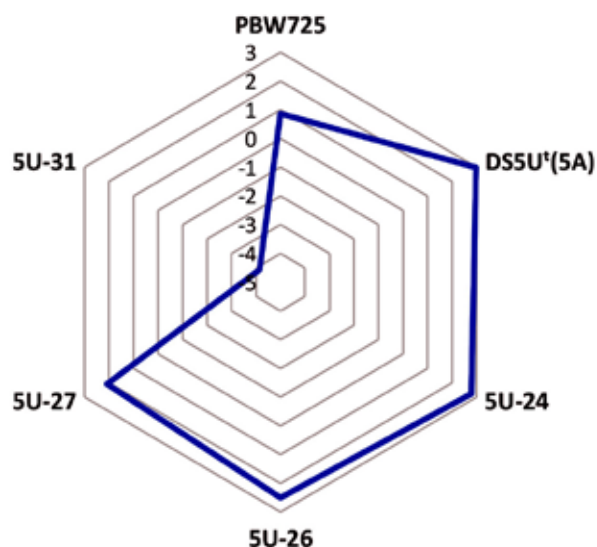


Fig. 4. Percent change in SRM under rain-fed conditions



4. Discussion:

Water scarcity is one of the significant environmental constraints to global plant productivity (Michiels *et al.*, 2004). Accumulation and mobilization of WSC plays a great role in grain filling under the stress environments. In wheat stem, WSC accumulate from the duration of stem elongation to the primary stages of grain filling. WSC act as temporary carbohydrate reservoir (Gebbing, 2003). When plant experience water-deficit, translocation of WSC during grain filling period has a significant role in grain weight and ultimately in final grain productivity (Wardlaw and Willenbrink 2000). Several other experiments have also reported that the accumulation of WSC in stem was affected by the level of drought stress and its interaction with genotypes that affected the balance between sources and sinks of assimilates (Ovenden *et al.*, 2017). In a recent experiment conducted by Liu *et al* (2020), drought stress increased accumulation of WSC in stem internodes in the primary phase of grain filling, but in the later phase, it substantially enhanced its degradation and remobilization in all the internodes. In the present study also, we found higher levels of WSC accumulation and mobilization in all the internodes under rain-fed conditions with maximum mobilization in IL 5U-26 (greater water-deficit tolerance) indicating higher mobilization would benefit line specific stress resistance; higher rate of grain filling and thus compensating the grain weight loss under stress. Similar outcomes were obtained in another study by Liu *et al* (2020) where drought stress increased the rates of stem water-soluble carbohydrate remobilization and contribution rates. It has been suggested by a study (Li *et al.*, 2015) that higher WSC content in the stem can act as a basis for wheat breeding under water-deficit; accumulation of stem WSC varied among internodes and each internode responded differently to water-deficit. In our research, B_{int} internodes had greater mobilization efficiency than Ped , U_{int} and M_{int} . Li *et al* (2015) reported similar results where lower internodes had higher WSC content than in peduncle and stem. Earlier, it was suggested in a study (Ehdaie *et al.*, 2006) that lower internodes should be long enough to store required stem WSC and become a primary source during the period of grain filling. Consequently, it should be feasible to produce lines with considerable length of lower internodes and greater stem WSC, which would have higher water-deficit tolerance. Correlation analysis

depicted that TGW was significantly enhanced with increased mobilization of WSC in all the internodes with peduncle contributing the most towards enhancement of TGW. Also, thousand grain weight was significantly and positively correlated with WSC content in lower internodes.

Under well-watered conditions, the primary source of grain filling comes from the organs above the top node, such as flag leaf, grain envelopes, spike's neck and awns (Sanchez-Bragado *et al.*, 2014). Among them, the flag leaf is majorly responsible for production and transferring of photosynthetic assimilates to the cereal grains, thereby influencing final grain yield (Khaliq *et al.*, 2014). However, in locations with poor water availability, where wheat crops are subject to severe water-deficit situations, wheat plants typically exhibit drought-induced early senescence. This basically hinders carbon fixation (Guoth *et al.*, 2009), assimilates remobilization (Gregersen *et al.*, 2008) and promotes the degradation of leaf chlorophyll. Under such circumstances, grain filling relies primarily on stem reserves that have already been stored rather than on current photosynthesis (Ehdaie *et al.*, 2006). Therefore, in the present study, to evaluate the role of SRM in grain filling, defoliation of leaves was carried out under both irrigated and water-deficit conditions. We observed that the TGW was reduced after defoliation with minimum reduction in IL 5U-26 under rain-fed (non-significant) and irrigated conditions. Also, the parent DS5U^(5A) and ILs (5U-24, 5U-26 and 5U-27) exhibited higher SRM and thus, had higher utilization of stem reserves under rain-fed conditions and were thought to be relatively stress tolerant in relation to those with lower percent SRM (check PBW725 and IL 5U-31) which were considered as stress susceptible. Out of tolerant ILs, 5U-26 exhibited maximum stem reserve mobilization under both irrigated and rain-fed conditions. This indicates that flag leaf defoliation considerably increased the remobilization of stem reserves, which enhanced grain filling and ultimately prevented the loss in grain weight. The variation in TGW of different wheat cultivars were assessed in a study by Rivera-Amado *et al* (2020) when only the flag leaf was removed where stored stem reserves played a significant role in grain filling. The accumulation and translocation of stem reserves can therefore provide essential carbon resources during the grain development phase to enhance grain yield performance (Rathey *et al.*, 2009). Higher capacity of stem reserve accumulation and remobilization



has been regarded as a water-deficit stress adaptive trait in crops including wheat. In various studies conducted under optimum and water-deficit conditions, flag leaf defoliation enhanced the translocation of stored stem assimilates to developing grain in wheat (Ali *et al.*, 2010), rice (Saitoh *et al.*, 2002) and barley (Jebbouj and Yousfi, 2009).

Thus, in IL 5U-26 improved mobilization of WSC and enhanced stem reserve mobilization contributed significantly towards TGW under rain-fed conditions. Therefore, IL 5U-26 can be used in future breeding programmes to enhance grain filling and ultimately the grain weight in wheat. Also, the results of present study inferred that the basal internodes of the stem had the highest rate of water-soluble carbohydrate remobilization, indicating that the lower portions of the stem may provide more useful indicators of remobilization efficiency.

Authors contributions

AS and NG conceived and designed the research. KK and NG conducted the experiments and collected the data. SS, SK and KK did the statistical analysis. KK wrote the primary draft of the manuscript. NG, AS and SK reviewed and improved the manuscript.

Declarations

Ethical Approval Not applicable

Consent to participate Not applicable

Consent to publish Not applicable

Competing interests The authors declare no conflict of interest.

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Supplementary sheets

Supplementary table 1: Accumulation of water-soluble carbohydrates (WSC) (mg/g DW) in stem internodes of wheat ILs, parent and check under irrigated (IR) and rain-fed (R) conditions

Mean of WSC at three stages (0DAA, 15DAA and maturity) in:					
Lines	Irrigation	(B _{int})	(M _{int})	(U _{int})	(Ped)
PBW725	Irrigated	223 ^c	204 ^{de}	215 ^{cd}	214 ^b
	Rain-fed	238 ^{bc}	225 ^{bcd}	234 ^{abc}	237 ^{ab}
DS5U ^t (5A)	Irrigated	242 ^{bc}	247 ^{ab}	218 ^{cd}	219 ^b
	Rain-fed	245 ^{ab}	249 ^{ab}	249 ^a	251 ^a
5U-24	Irrigated	225 ^c	215 ^{cd}	223 ^{bcd}	218 ^b
	Rain-fed	247 ^{ab}	233.7 ^{bc}	228 ^{abc}	235 ^{ab}
5U-26	Irrigated	193 ^d	189 ^e	202 ^{de}	183 ^c
	Rain-fed	263 ^a	264 ^a	243 ^{ab}	251 ^a
5U-27	Irrigated	238 ^{bc}	242 ^{ab}	191 ^{ef}	187 ^c
	Rain-fed	248 ^{ab}	247 ^{ab}	224 ^{bcd}	250 ^a
5U-31	Irrigated	200 ^d	207 ^{de}	186 ^{ef}	176 ^{cd}
	Rain-fed	195 ^d	201 ^{de}	175 ^f	154 ^d

Data represent mean $\pm$ S.D. of three replicates. Values without parentheses are for irrigated conditions and those with parentheses are for rain-fed conditions.

Supplementary table 2: Mobilization of water-soluble carbohydrates (WSC) (mg/g DW) in stem internodes of wheat ILs, parent and check under irrigated (IR) and rain-fed (R) conditions

Mobilized WSC in:					
Lines	Irrigation	(B _{int})	(M _{int})	(U _{int})	(Ped)
PBW725	Irrigated	288 ^{cdef}	286 ^{bc}	282 ^{cd}	291 ^{bc}
	Rain-fed	331 ^b	321 ^a	325 ^a	325 ^a
DS5U ^t (5A)	Irrigated	272 ^{def}	282 ^{bcd}	263 ^{def}	263 ^{cde}
	Rain-fed	353 ^{ab}	328 ^a	316 ^a	303 ^{ab}



5U-24	Irrigated	238 ^g	233 ^f	232 ^g	214 ^f
	Rain-fed	300 ^c	262 ^{cde}	284 ^{bcd}	262 ^{cde}
5U-26	Irrigated	265 ^{efg}	258 ^{def}	246 ^{efg}	247 ^{de}
	Rain-fed	348 ^{ab}	331 ^a	309 ^{abc}	317 ^{ab}
5U-27	Irrigated	291 ^{cde}	289 ^b	261 ^{def}	265 ^{cd}
	Rain-fed	363 ^a	342 ^a	311 ^{ab}	325 ^a
5U-31	Irrigated	261 ^{fg}	249 ^{ef}	238 ^{fg}	210 ^f
	Rain-fed	297 ^{cd}	280 ^{bcd}	270 ^{de}	233 ^{ef}

Data represent mean $\pm$ S.D. of three replicates. Values without parentheses are for irrigated conditions and those with parentheses are for rain-fed conditions.

Supplementary table 3: Percent stem reserve mobilization (SRM) (%) after defoliation treatment under irrigated and rain-fed conditions

Lines	Treatment	SRM (%)
PBW725	Irrigated	93.44 ^f
	Rain-fed	94.24 ^{ef}
DS5U^h(5A)	Irrigated	94.04 ^{ef}
	Rain-fed	97.16 ^{bc}
5U-24	Irrigated	92.03 ^g
	Rain-fed	94.59 ^e
5U-26	Irrigated	96.50 ^{cd}
	Rain-fed	98.91 ^a
5U-27	Irrigated	95.70 ^d
	Rain-fed	97.70 ^b
5U-31	Irrigated	93.84 ^{ef}
	Rain-fed	89.96 ^h

Means with the different letter are significantly different.

