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Stem Reserve Mobilization in Relation to Yield under Different Drought and High Temperature Stress Conditions in Wheat (*Triticum aestivum* L.) Genotypes

Kirpa Ram*, Rajkumar, Sunita and Renu Munjal

Department of Botany and Plant Physiology, CCS Haryana Agricultural University, Hisar (HRY)-125004, India

**Corresponding author*

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A B S T R A C T

Pre-anthesis carbon accumulation in stem as reserve material an important source of mobilization during grain development stage (post anthesis) and directly influenced by drought and high temperature. The effect of different drought and high temperature conditions on stem reserve mobilization in relation to yield in wheat genotypes, viz., AKAW-3717, C-306, DHTW-60, HD-2967, HTW-11, KUNDAN, WH-730 and WH-1105 was studied during *rabi* season of mid-November to April, 2015-16 and 2016-17 in randomized block design with three replications. For control (irrigated) and drought-stressed condition, genotypes were sown at optimum planting date (timely sown), while for heat-stressed experiment sowing date was delayed by one month from the date of timely sown. Faster mobilization in accumulated dry matter was observed in all tested genotypes with increasing drought intensity in combination with high temperature both in peduncle and penultimate internodes. Under delayed sowing with combination of different drought condition, faster remobilization was observed in genotype DHTW-60, HD-2967 followed by WH-1105 and genotype AKAW-3717 had minimum remobilization value under all tested environment. The genotypes were found with high reserve mobilization value showed yield stability under all drought and high temperature environment. However, stem reserves mobilization (SRM) for grain filling time had great importance because current photosynthetic source that are mobilized to grain at post grain filling period and stress condition.

Introduction

Carbon requirements for grain filling in wheat are mainly from current assimilation by photosynthesis and remobilization of reserves from the stems (Yang *et al.,* 2000). Remobilization of assimilates is an active process that involves translocation of stored reserves from stems and sheaths to grains (Gupta *et al*., 2015). Stem reserves contribute 20 to 40% weight of the grain in non-stressed condition (Vignjevic *et al.,* 2015) and this can be up to 70% under stressed conditions during grain filling (Rebetzke *et al.,* 2008). Drought and high temperature induced earlier mobilization of non-structural reserve carbohydrates from stem and leaf sheaths, which provided a greater proportion of grain dry weight at maturity. It can account for 70-92 % of grain dry matter, under conditions of drought (Yang *et al.,* 2002; Pradhan *et al.*, 2012). Accumulation of photosynthetic products depends on the environmental conditions, and it starts from internode elongation and continue up to grain filling stage in wheat (Dreccer *et al.,* 2009). Heat (Wang *et al.,* 2012) or water stress (Ehdaie *et al.,* 2008; Gupta *et al.,* 2011) can reduce water soluble carbohydrates and its mobilization to the grain growth.

But under heat stress, plants can only partially compensate for reduced stem carbohydrates content by increasing mobilization efficiency (Wang *et al.,* 2012). Mobilization of photosynthate (water soluble carbohydrates) from the upper part of stem (such as peduncle and penultimate internode) appears to start at 21 DAA (days after anthesis) when the grain is about one third of its final mass.

However, such mobilization is started earlier at 10 DAA from the lower part of stem through peduncle in wheat (Ehdaie *et al.*, 2006, 2008). There is a strong positive correlation between stem dry matter and stem WSC content, which suggests that post-anthesis changes in stem dry weight in wheat could be an effective indirect method to estimate the amount of stem reserves accumulated and mobilized to grain (Ehdaie *et al.,* 2008).

Materials and Methods

Raising of crop and plant material

Presents study was carried out in field and laboratory of Wheat and Barley section, Department of Genetics and Plant Breeding, College of Agriculture, CCS HAU, Hisar in winter season of mid-November to April, 2015-16 and 2016-17 with eight selected wheat genotype *viz.*, AKAW-3717, C-306, DHTW-60, HD-2967, HTW-11, Kundan, WH-730 and WH-1105. In control (irrigated) and drought-stressed experiments (with pre-sowing irrigation only), genotypes were sown at optimum planting date, while for heat-stressed experiment sowing date was delayed.

Treatments

Drought conditions was achieved by withholding the irrigation at different stages (40 days after sowing (DAS), 80 DAS, 40+80 DAS (Both at 40 and 80 days after sowing) and for complete drought no irrigation was given throughout the year).

Timely sowing was done on 17 November, 2015 and 13 November, 2016; late sowing on 14 December, 2015 and 16 December, 2016 and very late sowing 13 January, 2016 and 11 January, 2017.

Stem reserve mobilization

Stem reserve mobilization was calculated by the method suggested by Cox *et al.,* (1986). Five stems (penultimate and peduncle without spike) from randomly selected plants from each plot at anthesis and maturity were separated into penultimate and peduncle and were dried in an oven at 80 °C for 72 hrs. The weight of stem parts was recorded with the analytical balance (Afcoset, ER-200A) and stem reserve mobilization was calculated using following formula.

$$\textbf{SRM}\ (\%) = \frac{\text{DMSHT (Ant)} - \text{DMSHT (Mat)}}{\text{DMSHT (Ant)}} \times 100$$

SRM is stem reserve mobilization (g/plant); DMSHT (Ant) is above-ground dry matter of stem parts at anthesis stage (g); DMSHT (Mat) is aboveground dry matter of stem parts at maturity stage (g). SRM from stem part (penultimate and peduncle) was calculated separately.

Grain yield (g) per square meter

Grain yield was recorded after harvesting and threshing the plants in per meter square. The threshed grains were cleaned and yield was recorded in gram.

Results and Discussion

Stem reserve mobilization (%)

Stem reserve mobilization (%) in peduncle and penultimate internode recorded under different drought and delayed sowing condition shown in Table 1 and 2.

Peduncle reserve mobilization

Application of drought showed faster remobilization in timely, late and very late sown conditions and highest stem reserve mobilization (Table 1) was found in complete drought situation (29.1 %) under very late sown condition followed by late sown drought condition (24.2 %) whereas lowest stem reserve mobilization was observed in control (irrigated) (20.2 %) under timely sown condition.

Average stem reserve mobilization in peduncle for different drought stress condition ranged from 13.3 to 24.9 % (timely sown), 16.7 to 29.7 % (late sown) and 21.3 to 34.8 % (very late sown). The drought situation of D40+D65 and complete drought resulted significant maximum stem reserve mobilization 24.1 and 24.9 % (timely sown), 28.4 and 29.7 % (late sown) and 33.4 and 34.8 % (very late sown) respectively. Significant difference was observed in peduncle for reserve mobilization in all genotypes and different drought stress environments. Significant difference was observed among genotypes under timely sown, late sown and very late sown condition. Average peduncle reserve mobilization for genotypes ranged from 16.0 to 25.2 (timely sown), 19.5 to 30.0 % (late sown) and 24.3 to 34.5 % (very late sown). Genotype WH-1105 (25.2 %) followed by HD-2967 (22.7 %) had highest stem reserve mobilization under timely sown condition. Combined effects of heat and drought stress showed that DHTW-60 (30.0 %) and HD-2967 (27.7 %) followed by WH-1105 (25.6 %) had high peduncle reserve mobilization under late sown condition and genotypes DHTW-60 (34.5 %) and HD-2967 (33.2 %) followed by HTW-11 (30.6 %) under very late sown condition.

Penultimate internode reserve mobilization

Table 2 showed significant penultimate internode remobilization in all genotypes under drought stress and delayed sown condition.

Average penultimate internode reserve mobilization for different drought stress condition varied between 6.6 to 15.1 % (timely sown), 10.2 to 19.2 % (late sown) and 15.7 to 25.3 % (very late sown). The drought situation of D40+D65 and complete drought resulted significantly highest in penultimate internode reserve mobilization 14.1 and 15.1 % (timely sown), 18.4 and 19.2 % (late sown) and 24.0 and 25.3 % (very late sown) respectively. Significant difference was observed for penultimate internode reserve mobilization in all genotypes under different drought stress condition.

Interaction of drought and genotypes was found significant under timely sown, late sown and very late sown condition. Average penultimate internode reserve mobilization for genotypes varied from 8.9 to 14.8 % (timely sown), 10.4 to 20.4 % (late sown) and 16.1 to 26.8 % (very late sown). Genotype WH-1105 (14.8 %) followed by HD-2967 (14.1 %) had highest stem reserve mobilization under timely sown condition.

Table.1 Response of wheat genotypes to drought and high temperature for stem reserve mobilization (%) in peduncle under timely, late and very late sown conditions

Genotypes	Timely sown						Late sown						Very late sown					
	Control	Time of drought application				Mean (G)	Control	Time of drought application				Mean (G)	Control	Time of drought application				Mean (G)
		D40	D65	D40+D65	DR			D40	D65	D40+D65	DR			D40	D65	D40+D65	DR	
AKAW 3717	9.1	13.6	17.0	19.7	20.7	**16.0**	12.5	16.7	20.2	23.4	24.9	**19.5**	15.8	20.1	26.2	29.4	30.0	**24.3**
C-306	11.6	16.1	20.1	23.1	23.9	**19.0**	15.1	18.8	22.9	26.4	27.4	**22.1**	17.1	21.5	27.9	30.0	31.4	**25.6**
DHTW-60	16.0	19.9	23.7	26.4	27.3	**22.7**	21.6	27.2	31.7	34.0	35.5	**30.0**	26.7	31.6	35.1	38.8	40.2	**34.5**
HD-2967	17.1	20.8	24.5	27.2	28.0	**23.5**	19.8	23.9	29.0	32.0	33.6	**27.7**	26.4	30.1	34.5	37.0	38.1	**33.2**
HTW-11	11.2	15.5	18.9	22.0	22.3	**18.0**	16.8	21.6	25.1	28.9	30.4	**24.6**	23.3	27.7	31.1	34.5	36.5	**30.6**
KUNDAN	13.7	17.3	21.6	24.6	25.7	**20.6**	16.1	20.5	24.7	27.7	28.8	**23.6**	20.9	25.6	29.5	32.6	33.9	**28.5**
WH-730	10.0	13.8	17.6	20.2	20.8	**16.5**	13.3	17.3	21.3	24.9	25.8	**20.5**	18.9	23.2	28.3	31.5	32.7	**26.9**
WH-1105	17.7	22.4	26.2	29.2	30.6	**25.2**	18.0	22.1	26.5	29.7	31.5	**25.6**	21.6	26.4	30.2	33.0	35.5	**29.3**
Mean (D)	**13.3**	**17.4**	**21.2**	**24.1**	**24.9**	**20.2**	**16.7**	**21.0**	**25.2**	**28.4**	**29.7**	**24.2**	**21.3**	**25.8**	**30.4**	**33.4**	**34.8**	**29.1**
CD at 5%	**D = 1.36, G = 1.46, DxG= 1.73**						**D = 1.42, G = 1.23, DxG = 1.86**						**D = 1.49, G = 1.50, DxG= 2.03**					

D40- Drought at 40 days after sowing (DAS), D65- Drought at 65 DAS, D40+D65- Drought both at 40 and 65 DAS, DR- Complete drought, G-Genotypes and D- Drought

Table.2 Response of wheat genotypes to drought and high temperature for stem reserve mobilization (%) in penultimate internode under timely, late and very late sown conditions

Genotypes	Timely sown						Late sown						Very late sown					
	Control	Time of drought application				Mean (G)	Control	Time of drought application				Mean (G)	Control	Time of drought application				Mean (G)
		D40	D65	D40+D65	DR			D40	D65	D40+D65	DR			D40	D65	D40+D65	DR	
AKAW 3717	3.8	7.6	9.5	11.6	12.2	**8.9**	5.4	9.2	11.9	13.7	13.7	**10.8**	11.1	14.7	16.7	18.5	19.7	**16.1**
C-306	5.9	9.5	11.9	13.1	14.5	**11.0**	9.0	12.3	14.0	15.8	16.9	**13.6**	12.2	15.0	17.5	19.4	20.8	**17.0**
DHTW-60	8.2	11.1	13.5	15.5	16.2	**12.9**	14.8	18.0	21.3	23.6	24.3	**20.4**	21.7	25.3	27.1	29.1	30.9	**26.8**
HD-2967	9.3	12.1	14.7	16.6	17.9	**14.1**	13.5	17.7	19.5	22.2	23.4	**19.3**	20.6	24.4	26.1	28.8	29.4	**25.9**
HTW-11	4.7	7.9	10.8	12.6	13.4	**9.9**	10.5	14.4	16.7	19.4	20.3	**16.3**	16.9	21.4	25.3	27.0	28.5	**23.8**
KUNDAN	6.7	10.1	12.9	14.5	15.3	**11.9**	9.9	13.7	15.5	17.2	18.8	**15.0**	14.1	17.0	20.2	23.8	24.5	**19.9**
WH-730	4.4	7.8	9.7	12.0	12.7	**9.3**	6.5	10.3	12.4	14.8	15.1	**11.8**	13.3	16.4	18.8	20.5	21.9	**18.2**
WH-1105	9.9	13.0	15.4	17.1	18.7	**14.8**	11.9	15.6	18.0	20.4	21.1	**17.4**	15.8	19.3	22.1	24.7	26.6	**21.7**
Mean (D)	**6.6**	**9.9**	**12.3**	**14.1**	**15.1**	**11.6**	**10.2**	**13.9**	**16.2**	**18.4**	**19.2**	**15.6**	**15.7**	**19.2**	**21.7**	**24.0**	**25.3**	**21.2**
CD at 5%	**D = 1.24, G = 1.31, DxG= 1.61**						**D = 1.27, G = 1.34, DxG= 1.76**						**D = 1.32, G = 1.41, DxG= 1.91**					

D40- Drought at 40 days after sowing (DAS), D65- Drought at 65 DAS, D40+D65- Drought both at 40 and 65 DAS, DR- Complete drought, G-Genotypes and D- Drought

Table.3 Mean sum of square of wheat genotypes for stem reserve mobilization (%) and grain yield per meter square in response to drought and high temperature in peduncle and penultimate internode under timely, late and very late sown condition

Source of variation	df	Stem reserve mobilization (%)		Grain yield per meter square
		Peduncle	Penultimate internode	
Replication	2	15.984**	6.653**	48690.050**
Genotype (G)	7	545.720**	465.881**	978705.423**
Drought Treatment (D)	4	3060.929**	1296.155**	3763527.001**
GxD	28	0.817**	141.216**	115109.931**
Sowing Time (S)	2	262.680*	107.530**	448805.668**
GxS	14	0.376**	13.769**	7862.076**
DxS	8	14.619**	5.550**	13767.091**
GxDxS	56	0.345**	0.934**	6047.508**
Error	238	0.086	0.09	378.091

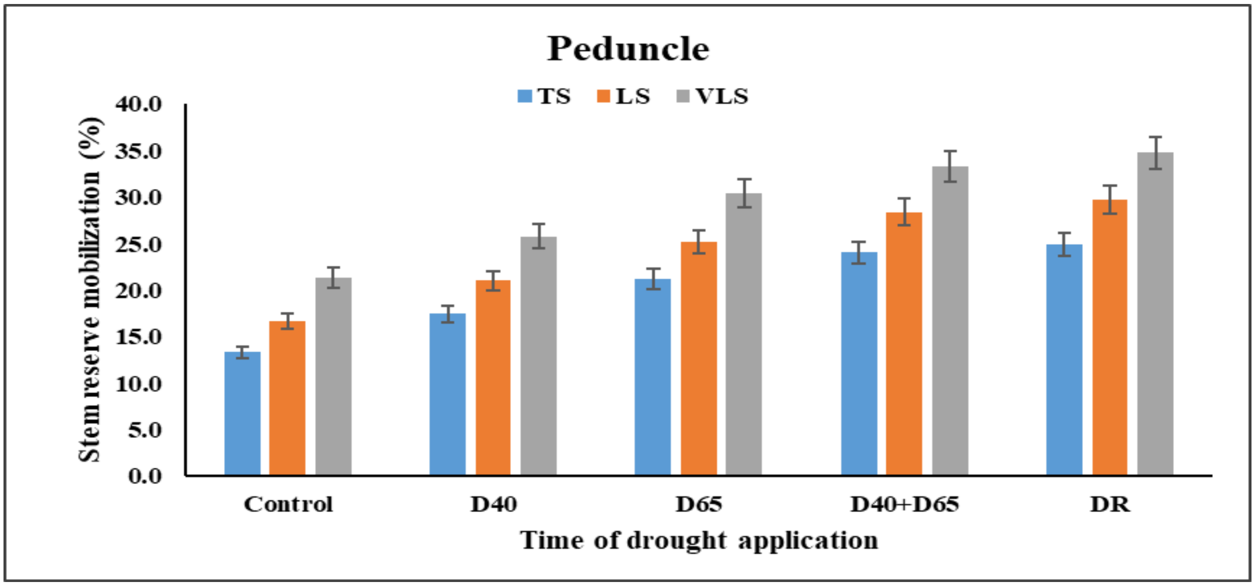
** Significant at 1% of significance

Table.4 Response of wheat genotypes to drought and high temperature for biomass per square meter (g) under timely, late and very late sown conditions

Genotypes	Timely Sown						Late Sown						Very Late Sown					
	Control	Time of drought application				Mean (G)	Control	Time of drought application				Mean (G)	Control	Time of drought application				Mean (G)
		D40	D65	D40+65	DR			D40	D65	D40+65	DR			D40	D65	D40+65	DR	
AKAW 3717	1413.0	1259.8	1197.3	1141.3	708.2	**1143.9**	940.2	752.7	621.2	550.5	238.0	**620.5**	570.7	481.5	379.9	281.5	150.0	**372.7**
C-306	1503.8	1313.6	1222.8	1150.5	978.3	**1233.8**	1020.1	767.9	622.3	589.1	353.3	**670.5**	594.0	485.3	384.8	289.7	157.1	**382.2**
DHTW-60	1576.1	1358.7	1250.0	1177.7	1041.8	**1280.9**	1313.6	911.4	751.6	616.8	529.9	**824.7**	729.9	538.0	465.2	375.5	262.0	**474.1**
HD-2967	1666.8	1376.6	1259.2	1186.4	1069.0	**1311.6**	1121.2	897.8	713.6	615.8	529.9	**775.7**	671.7	523.4	449.5	355.4	239.7	**447.9**
HTW-11	1467.4	1304.3	1222.8	1150.5	933.2	**1215.7**	1063.6	870.1	677.7	607.6	463.6	**736.5**	638.6	514.7	420.1	342.9	231.5	**429.6**
KUNDAN	1531.0	1340.8	1222.8	1177.7	1005.4	**1255.5**	1032.6	842.4	665.8	594.0	436.4	**714.2**	618.5	499.5	406.0	303.3	193.5	**404.1**
WH-730	1422.3	1277.2	1210.3	1141.3	838.0	**1177.8**	987.5	759.2	621.2	581.5	282.6	**646.4**	607.1	495.7	394.0	297.8	172.3	**393.4**
WH-1105	1811.4	1413.0	1259.2	1186.4	1096.2	**1353.3**	1104.9	881.0	687.5	612.5	485.3	**754.2**	624.5	507.6	416.8	332.1	200.5	**416.3**
Mean (D)	**1549.0**	**1330.5**	**1230.6**	**1164.0**	**958.8**	**1246.6**	**1073.0**	**835.3**	**670.1**	**596.0**	**414.9**	**717.9**	**631.9**	**505.7**	**414.5**	**322.3**	**200.8**	**415.0**
CD at 5%	**D= 35.24, G= 44.58, DxG= 99.69**						**D= 21.04, G= 26.62, DxG= 59.53**						**D= 10.79, G= 13.65, DxG= 30.53**					

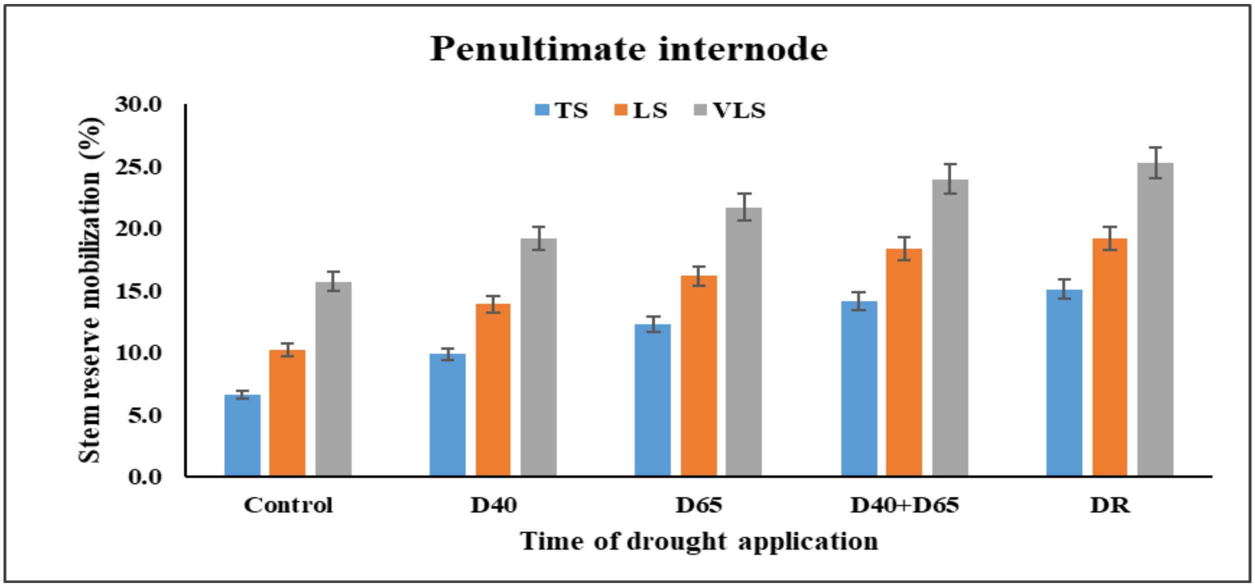
D40- Drought at 40 days after sowing (DAS), D65- Drought at 65 DAS, D40+D65- Drought both at 40 and 65 DAS, DR- Complete drought, G-Genotypes and D- Drought

Fig.1 Response of wheat genotypes to drought and high temperature for stem reserve mobilization in peduncle under timely, late and very late sown conditions



D40- Drought at 40 days after sowing (DAS), D65- Drought at 65 DAS, D40+D65- Drought both at 40 and 65 DAS, DR- Complete drought, TS- Timely sown, LS- Late sown and VLS- Very late sown

Fig.2 Response of wheat genotypes to drought and high temperature for stem reserve mobilization in penultimate internode under timely, late and very late sown conditions



D40- Drought at 40 days after sowing (DAS), D65- Drought at 65 DAS, D40+D65- Drought both at 40 and 65 DAS, DR- Complete drought, TS- Timely sown, LS- Late sown and VLS- Very late sown

Combined effects of delayed sowing and drought stress showed that DHTW-60 (20.4 %) and HD-2967 (19.9 %) followed by WH-1105 (17.4 %) had high penultimate internode reserve mobilization under late sown condition and genotypes DHTW-60 (26.8 %) and HD-2967 (25.9 %) followed by HTW-11 (23.8 %) under very late sown condition.

Genotype AKAW-3717 found lowest in average peduncle and penultimate internode reserve mobilization among all genotypes under all drought and delayed sowing conditions. Figure 1 and 2 showed increasing trends in graphical representation for stem reserve mobilization under different drought and sowing condition in peduncle and penultimate internode respectively. Significant difference in stem reserved mobilization at D40, D65, D40+D65 and complete drought situation was observed in peduncle and penultimate internode.

Grain yield per square meter (g)

Application of drought showed reduction in grain yield per square meter under timely, late and very late sown conditions and maximum reduction in grain yield per square meter were found in complete drought situation (169.4 g) under very late sown condition and minimum reduction in grain yield per square meter were observed in compete drought stress (207.6 g) under timely sown condition (Table 4). Average grain yield per square meter for different drought stress condition ranged from 207.6 to 525.7 g (timely sown), 208.1 to 402.7 g (late sown) and 169.4 to 341.7 g (very late sown). The drought situation of D40+D65, and complete drought resulted significant reduction in grain yield per square meter (355.6 and 207.6 g) under timely sown, (327.1 and 208.1 g) under late sown and (219.5 and 169.4 g) under very late sown condition respectively. Significant difference was found for grain yield per square meter in all genotypes and different drought stress condition with significant interaction effect for drought and genotypes. Average grain yield per square meter for genotypes ranged from 307.6 to 576.3 g (timely sown), 223.8 to 456.0 g (late sown) and 192.2 to 350.4 g (very late sown). Genotype WH-1105 (576.3 g) followed by HD-2967 (490.3 g) and DHTW-60 (400.7 g) had maximum grain yield per square meter under timely sown condition whereas, combined effects of heat and drought stress showed that DHTW-60 (456.0 g) and HD-2967 (427.5 g) followed by WH-1105 (367.4 g) had maximum grain yield per square meter under late sown condition and genotypes DHTW-60 (350.4 g) and HD-2967 (427.5 g) followed by HTW-11 (367.4 g) under very late sown condition.

Mean sum of square

Table 3 showed mean sum of square for stem reserve mobilization and grain yield. These results indicate that there is significant variation due to genotypes (G), drought treatments (D) *i.e* D40, D65, D40+D65 and complete drought & due to sowing time (S) *i.e* timely, late and very late. Interaction effects between genotypes, drought and sowing time was found significant. This indicated that genotypes differed in their response to drought condition and sowing time of the trait under study.

Stored stem reserves serve as a source of carbon for grain filling in wheat, particularly during stress conditions (Wardlaw, 1974) and stem is the alternative source of carbon for grain filling by re-translocating the reserve to maintain reproductive growth under stress conditions (Blum *et al.,* 1994; Wang *et al.,* 2012). Combined effect of stress showed faster remobilization of stem reserve both in peduncle and penultimate internode whereas, peduncle showed faster and higher remobilization in all drought condition and delayed sowing. Genotype DHTW-60, WH-1105 & HD-2967 showed higher SRM at different time of drought application and different sowing condition in peduncle and penultimate internode (Table 1an 2). The results of present investigation are supported by earlier finding of Gupta *et al.,* 2011; Joudi *et al.,* 2012; Zhang *et al.,* 2014). Sharifi *et al.,* (2017) found similar result in wheat genotypes under water-deficit treatments with 50 to 80 % higher mobilization than the in well-watered treatments, which indicates that water deficits promoted remobilization. Drought result in increasing mobilization efficiency, expressed as percentage of maximum dry matter mobilized, in the peduncle, penultimate and the lower internodes by 65, 11 and 5 %, respectively in wheat (Ehdaie *et al.*, 2008). Under heat stress genotypic variation exists for the contribution of stem reserves for grain filling (Yang *et al.*, 2002). Gupta *et al.*, (2011) found higher mobilization of dry matter and mobilization efficiency in the internodes of wheat genotypes C-306 and PBW-343, both under control and stress drought stress conditions, which resulted in enhanced translocation of stem reserves to the grains. Genotype DHTW-60, HD-2967, WH-1105 and HTW-11 was found maximum in yield per square meter (Table 4) under drought situation with delayed sowing. Similar findings have also been reported by various workers (Verspreet, 2015; Munjal & Dhanda, 2016; Zampieri *et al.*, 2017; and Ram *et al.*, 2017a, 2017b). Dwivedi *et al.*, (2017) also reported higher reduction in grain yield (60.3%). Maich *et al.*, (2017) reported elevated temperature caused a reduction in grain yield between 6-21% as compared normal grown varieties. Aynehband *et al.*, (2011) and Wang *et al.*, (2017) reported that grain weight depends on different dates of sowing and water availability.

It was concluded from the above results and discussion, combination of high temperature and drought during grain filling periods is more destructive than individual stress. Faster peduncle and penultimate internode reserve mobilization was responsible for higher gain yield under unfavorable conditions. Genotypes DHTW-60, HD-2967 and WH-1105 showed maximum reserve mobilization efficiency and yield in all environment (timely sown, late sown and very late sown) and all treatments (drought at 40 DAS, drought at 80 DAS, Drought at 40+80 DAS and complete drought) conditions. Genotypes with high remobilization efficiency showed maximum in grain yield per meter square. So, on the basis of this study stem reserve mobilization is best physiological strategy to selection of tolerant and high yielding genotypes for drought and high temperature prone area.

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