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Terminal heat stress in Indian mustard (*Brassica juncea* L.): Variation in dry matter accumulation, stem reserve mobilization, carbohydrates translocation and their correlation with seed yield

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The rapeseed mustard is one of the most important sources of edible oil in India and contributes 28.6% in total oilseed production. The mustard growing areas in India are experiencing the vast diversity in the agro climatic conditions. Here, we studied forty-nine advanced breeding lines of *Brassica juncea* L. for two consecutive years (2016-18) to examine the variations in the remobilization of assimilates from flowering to maturity stage and their contribution to seed filling under stressed environment. Further, we investigated the impact of high temperature on dry matter accumulation and partitioning from source to sink in Brassica germplasm. The synchronization between the seed filling stage and the onset of heat spell is critical event that determines the overall yield. Imbalances caused due to miss-matching of above events created hindrance in source-sink translocation, thus resulted in yield losses. Amount of remobilized dry matter, remobilization efficiency and remobilization percentage increased significantly, while the dry matter accumulation, total carbohydrates content and seed yield per plant declined in the late sown genotypes during both crop seasons. Reduced accumulation of photo assimilates under stress and higher sink demand resulted in more number of shriveled seeds leading to yield depression. The higher remobilization efficiency in late sown genotypes was strongly associated with dry matter at flowering that consequently tended to affect the final seed weight. This study will provide insights for better understanding of source-sink relationships in Indian mustard under heat stress and the differential remobilization efficiencies in the advanced breeding lines.

Keywords: Abiotic stress, Assimilates, Remobilization, Source-sink translocation, Yield depression

India is an agriculture based subcontinent with 12% arable land supporting about 26% of world's agricultural population with 7.4% share in oilseeds, 5.8% in oils and 6.1% in oil mean production and 9.3% of oil consumption in the world economy[1]. Oilseed Brassica achieved significant growth in India with 23.5% area and 24.2% production[2]. Rapeseed mustard is the third most important source of edible oil next to soybean and groundnut in India[3]. The northern part of country particularly i.e. Punjab, Haryana and Rajasthan accounted for highest acreage in terms of field crop[4]. However, productivity is still low due to large cultivation under rainfed situation, further accentuated by biotic and abiotic stresses. The yields of field crops were expected to decline by 3-7% for each one-degree rise in temperature[5]. Country is facing an acute shortage of edible oil and current production meets only 57% of the domestic requirements. The situation demands concrete efforts to increase production and productivity of edible oils under changing agro-climatic conditions[6]. Sowing of mustard usually delayed due to multiple cropping system, which exposes the terminal stage of crop to the heat stress and finally resulting to yield losses[7].

Interception of solar radiation and its chemical conversion triggers carbohydrates synthesis and other biomolecules required for metabolic activity. It also determines leaf efficiency for dry matter accumulation (DMA)[8]. Early planting of mustard encounters heat stress at seedling stage thus hampering seedling establishment[9] and with delayed planting, seed filling stage faces high temperature thus, restricting assimilatory supplies to the developing seeds or sink strength is reduced[10]. Sink strength is the product of sink capacity and sink activity, which is determined by photo assimilates supply to sink[11]. At seed filling stage, the total carbon reserve come via two routes i.e. from current photosynthetic activity and stem reserve remobilization[12]. Heat stress reduces leaf photosynthesis

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and overall carbohydrates accumulation resulting in impaired seed filling[13]. Under normal conditions, the contribution of stem reserves varied from 20 to 40% of grain weight[14], which can go up to 70% under stressed conditions[15]. The remobilization of assimilates and their contribution to grain weight is meager in Brassica under terminal heat stress. Therefore, in the present study, we investigated the variation in dry matter accumulation, remobilization of assimilates and total carbohydrates at flowering and maturity along with the correlation of these traits with seed yield.

Material and Method

Cultivar tested and management

Field experiments was performed at an experimental farm, Oilseed Section, Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana during two consecutive winter season (November to April) 2016-17 and 2017-18. Ludhiana is situated at 30°56′N, 75°48′E at an elevation of 262 meters above the mean sea level. A set of forty-nine advanced breeding lines were tested at two sowing dates. Genotypes were sown in paired rows with 5 m row length at recommended time (timely sown) and at one month interval thereafter (late sown) in randomized block design (RBD) in three replications. Pre sowing irrigation (10-12cm) was given before seeding and two irrigations at 35 and 65 DAS thereafter. The ½ nitrogen and full phosphorous and potassium were applied before sowing and the remaining ½ N with the first irrigation as per agronomic recommendation. All the plant protection measures were taken to raise healthy crop stand.

Meteorological observation

The weather data was recorded at the meteorological observatory of Department of Climate Change and Agricultural Meteorology, PAU Ludhaina, located about 1.0 km from the experimental site. The trial site was describe by sub-tropical, semi-arid kind of climate with scorching and dry summer from April to June followed by sweltering and humid periods from July to September and cold winter (December and January). Monsoon rains were received during July, August and September. The mean air temperature (T_{min} and T_{max} °C), mean relative humidity, total rainfall, total evaporation, average sunshine hours and wind velocity during cropping seasons (2016-18) are present in Table 1.

Dry matter accumulation

The aerial stem part of five plants from each genotype per replication was up-rooted at flowering and maturity stage. Leaves and shoot were stored separately. The stored samples were dried in hot air oven at 40°C until completely dried. Measured stem dry weight (SDM) at both the stages as dry matter accumulation per plant.

Remobilization of assimilates

The aerial stem part of each genotype was randomly selected at two stages [flowering (F) and maturity (M)] to record stem biomass. The amount of remobilized dry matter(ARDM) was computed by the method of *Cox et al.* [16][ARDM (g plant^{-1}) = SDM (F) – SDM (M)], remobilization efficiency (REE) by Papakosta & Gagianas[17][ARDM (g plant^{-1})/ SDM (F)×100] and remobilization percentage (REP) or contribution of dry matter to the grain was determined using equations of Arduini *et al.*[18][ARDM (g plant^{-1}) / seed yield (g plant^{-1}) ×100] where, SDM (F): Stem dry matter at flowering stage, SDM (M): Stem dry matter at maturity stage (in g) except from seed weight

Table 1 — Mean value of minimum and maximum temperature (°C), mean relative humidity (%), total rainfall (mm), total evaporation (mm), average sunshine hours and wind velocity (km/hr) during two crop stages and sowing time

Year	Crop stages	T_{min}	T_{max}	RH_{avr}	Total rainfall	Rainfall events	Total evaporation	Sunshine hours	Wind velocity
Timely sown									
2016-17	F	6.9	19.5	69.1	5.6	1.0	51.2	5.2	2.8
	S	8.4	20.8	70.3	51.2	4.0	130.0	5.9	3.2
	M	14.1	28.7	58.2	47.0	5.0	174.4	8.8	4.3
2017-18	F	6.2	19.0	74.2	18.4	1	57.8	5.3	2.9
	S	8.5	21.7	70.6	45.4	5.0	149.5	7.0	3.3
	M	15.1	32.2	55.9	0.0	0.0	5.16	8.0	4.6
Late sown									
2016-17	F	9.5	21.3	74.6	45.6	3.0	49.9	5.48	3.41
	S	9.5	23.2	68.5	27.0	1.0	71.4	7.90	3.6
	M	16.5	33.3	49.9	62.0	2.0	237.4	9.75	4.3
2017-18	F	9.5	23.2	67.8	46.0	2.0	130.2	7.62	3.1
	S	11.5	31.6	66.3	27.0	4.0	130.7	8.1	3.6
	M	16.7	36.5	59.8	0.0	0.0	178.3	8.4	3.9

[F, Flowering; S, Siliquing; and M, Maturity]

Total carbohydrates

The total sugar content was evaluated utilizing anthrone-sulfuric acid method[19]. The dry leaf and stem sample (0.1 g) were homogenized in 2 mL of 80% ethanol, refluxing the concentrate at 80°C for 30 min in hot water bath and afterward supernatant was collected. Repeat this step twice. Collect supernatant and make total volume to 5 mL and estimate total sugars. To the sugar free residue (pellet) add 3 mL of 50% perchloric acid and 2 mL of distilled water, kept it overnight. Centrifuge the content and collect the supernatant. Starch was estimated using method of Clegg[20]. The concentration of sugar and starch was calculated using standard curve value of glucose. Starch concentration was calculated by multiplying the glucose concentration by 0.9. Total carbohydrates were computed by the sum of total sugar and starch content and expressed as mg g^{-1} DW.

Seed yield/plant

Five plants were randomly selected from each replication, harvested, dried and threshed for seed yield. Seed yield of five plants per replication was converted to per plant. The obtained seed yield per plant from the three replications were pooled and averaged for further calculations.

Statistical analysis

The data information investigated by using analysis statistical software CPCSI developed by the Department of Statistics, Mathematics and Physics, Punjab Agricultural University, Ludhiana[21] for analysis of variance (ANOVA) using randomized block design. Means for treatment effects were isolated based on the critical difference (CD) using ANOVA. The treatments were compared by computing the student's t-test at 5% ($P \leq 0.05$) level of significance. The two years data was pooled and Pearson correlation between seed yield and studied traits were calculated using OPSTAT software programme.

Results

Dry matter accumulation

Significant variation existed over two years for genotypes and environment and their interactive effect (G x E) was significant (Table 2). SDM was reduced significantly in the late sown genotypes at flowering (31.0%) and maturity (56.1%) over the years as compared to timely sown genotypes (Table 3). The reduction in late sown genotypes was primarily related to lower accumulation and translocation of photo-assimilates from source to stem. The reduction in dry matter from flowering to maturity in late sown genotypes was also higher (47.0%) as compared to timely sown (16.7%) indicated more stem reserve translocation and utilization as temperature increases at terminal stage in delayed sowing. Correlation analysis indicated positive and significant correlation between SDM at flowering with SDM at maturity (r=0.761**) and ARDM (r=0.287*) while SDM (M) had negative but significant relation with ARDM (r= -0.404**), REE (r= -0.602**) and REP (r= -0.400**) in timely sown condition whereas in late sown SDM (F) had significant correlation with ARDM (r=0.732**), REE

Table 2 — Statistical significance of dry matter accumulation, remobilization of assimilates and total carbohydrates accumulation in Indian mustard during two crop season and two sowing times

Source of variance	SDM (F)	SDM (M)	ARDM	REE	REP	SY $plant^{-1}$	Total carbohydrates		
							Flowering		Maturity
							Leaves	Stem	Stem
2016-17									
E	0.70	0.69	0.62	0.80	18.8	0.34	0.731	0.643	0.46
G	3.46	3.41	3.11	3.99	93.1	1.72	3.62	3.18	2.28
ExG	4.90	4.82	4.40	5.65	131.8	2.44	5.12	4.50	3.23
2017-18									
E	0.69	0.76	0.59	0.96	18.5	0.24	0.61	0.68	0.72
G	3.42	3.76	2.95	4.78	91.9	1.19	3.05	3.41	3.59
ExG	4.84	5.31	4.18	6.76	130.0	1.69	4.31	4.82	5.08
Pooled mean									
Y	0.48	0.51	0.43	0.62	13.2	0.23	0.477	0.47	0.42
E	0.48	0.51	0.43	0.62	13.2	0.23	NS	0.47	0.42
YxE	0.68	0.73	NS	0.88	18.7	NS	0.67	0.66	0.60
G	2.41	2.55	2.12	3.09	65.0	1.18	2.36	2.34	2.12
YxG	3.41	3.61	3.00	4.37	92.5	1.67	3.33	3.31	3.00
ExG	3.41	3.61	3.00	4.37	92.5	1.67	3.33	3.31	3.00
YxExG	4.82	5.11	4.25	3.18	130.9	2.36	4.72	4.68	4.24

[Y, Year; E, Environment; G. Genotype. Level of significance at 5% ($P \leq 0.05$) using student's 't' test] (r=0.439**) and REP (r=0.544**) while dry matter at maturity had negative but significant relationship with ARDM, REE and REP (Table 4). The negative correlation of SDM (M) with remobilization of dry matter under both sowing conditions indicated the antagonistic effects of above said parameters.

Amount of remobilized dry matter

The amount of remobilized dry matter (ARDM) is the demand for consuming stem reserve, which increased in late sown genotypes as photosynthesis (source) was affected with increased temperature. Genotypes varied significantly in both the environments over the years however Y x E interaction was non-significant indicating that in both cropping season environment had non-significant influence on ARDM (Table 2). The dry matter remobilization is the difference in the dry matter (DM) at flowering and maturity. The value of ARDM was higher in late sown genotypes due to less difference between the DM of flowering and maturity stages. Further, in late sown condition, source is the limiting factor and the seed filling is highly dependent on stem reserve that is why the DM accumulation was less in late sown condition. The amount of dry matter mobilization was 47.2% higher over two years in late sown genotypes (Table 3).ARDM was positively and significantly correlated with REE and REP under both sowing conditions, however week but positive association existed for seed yield per plant (r= 0.031) in late sown while negative in timely sown (r=-0.077) genotypes. The strong association existed for ARDM with REE and REP as indicated by regression analysis (Fig. 1 A and B).

Remobilization efficiency (REE)

Heat stress distinctly affected the dry matter remobilization efficiency, leading to an increase of

Table 3 — Mean of stem dry matter (SDM), amount of remobilized dry matter (ARDM), remobilization efficiency (REE), remobilization percentage (REP) and seed yield per plant (SY plant^{-1})

	2016-17			2017-18			Pooled mean		
	Timely sown	Late sown	CV	Timely sown	Late sown	CV	Timely sown	Late sown	CV
SDM (g plant^{-1}) (F)	37.0	27.4	7.66	35.7	22.7	8.34	36.4	25.1	7.96
SDM (g plant^{-1}) (M)	29.9	15.0	10.83	30.5	11.7	12.67	30.3	13.3	11.72
ARDM (g plant^{-1})	7.11	12.4	22.65	5.22	11.0	25.93	6.17	11.7	24.09
REE (%)	19.2	44.1	8.98	14.2	46.4	11.23	16.7	45.3	10.09
REP(%)	158.9	620.9	17.01	124.8	780.5	14.45	141.8	700.7	15.65
SY/plant (g plant^{-1})	5.48	2.30	31.51	4.32	1.65	29.0	4.90	1.97	30.92

Table 4 — Correlation between SDM at flowering (F) and maturity (M), remobilization of assimilates, total carbohydrates in stem and leaves and seed yield/plant in timely sown (below diagonal) and late sown (above diagonal)

						Total carbohydrates			
	SDM (F)	SDM (M)	ARDM	REE	REP	Leaves (F)	Stem (F)	Stem (M)	SYplant^{-1}
SDM (F)	1	0.219	0.732**	0.439**	0.554**	0.007	–0.133	0.072	0.033
SDM (M)	0.761**	1	–0.504**	–0.755**	–0.381**	–0.177	–0.091	–0.099	–0.002
ARDM	0.287*	–0.404**	1	0.916**	0.756**	0.130	–0.054	0.133	0.031
REE	0.042	–0.602**	0.948**	1	0.710**	0.191	–0.044	0.100	0.002
REP	0.186	–0.400**	0.852**	0.846**	1	–0.003	–0.123	0.020	–0.370**
Leaves (F)	–0.018	0.037	–0.079	–0.107	0.005	1	–0.256	0.037	0.111
Stem (F)	0.177	0.198	–0.043	–0.122	–0.075	–0.334*	1	0.066	0.235
Stem (M)	0.010	0.129	–0.177	–0.144	–0.138	–0.014	0.117	1	0.160
SY/plant	0.011	0.063	–0.077	–0.093	–0.497**	–0.120	-0.016	0.025	1

[** and* represent significant at *P* ≤0.05 and *P* ≤0.01, respectively]

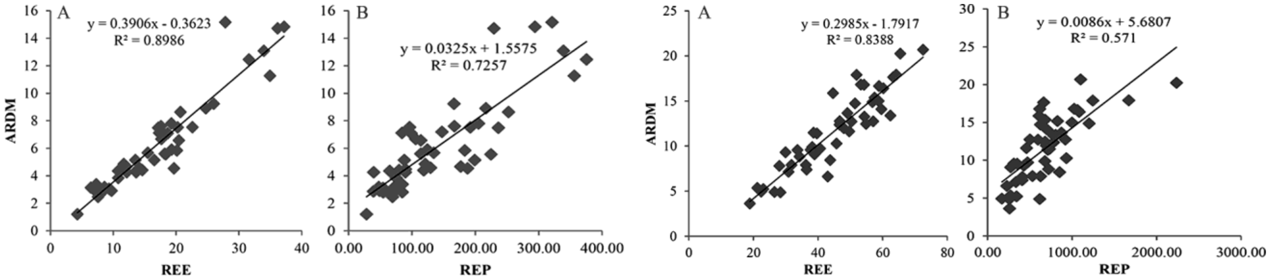

Fig. 1 — A and B — Relationship between ARDM, REE and REP under (A) timely sown; and (B) late sown condition.

63.1% with late sowing. Stored stem reserve serves, as a source of carbon for seed filling and the reserve utilization was more in the late-sown genotypes, which were prone to terminal heat stress. REE varied significantly among genotypes and environment. The interactive effects over the years also showed significant effects (Table 2). Positive association of dry matter remobilization efficiency existed with ARDM (r=0.948**) and dry matter at flowering (r= 0.042) whereas negative with dry matter at maturity (r=-0.602**) in timely sown while in late sowing significant and positive association existed for dry matter at flowering (r= 0.439**) and ARDM (r=0.916**) but negative with dry matter at maturity (r= -0.755**). The higher efficiency in late sown genotypes was strongly associated with dry matter at flowering which is the main contributing factor to final seed weight while regression analysis indicated strong association with REP (R^2=0.714) in timely sown and (R^2=0.503) in late sown (Fig. 2 A and B).

Remobilization percentage

Growing conditions greatly influenced the remobilization percentage. The dry matter of late sown genotypes had more contribution to grain. As temperature increases and senescence proceeds plant tends to complete its life cycle before the termination of grain filling. In timely sown genotypes, there is sufficient time and photo assimilates to fulfill the required demand at sink, while in late sowing both are limiting factor and rate of grain filling increases while duration decreases leading to production of more number of shriveled seeds. The remobilization percentage was 79.7% higher in delayed sowing over the years (Table 3). REP was positively associated with dry matter at flowering and significant with ARDM and REE, but negative significant association existed with dry matter at maturity under both sowing conditions.

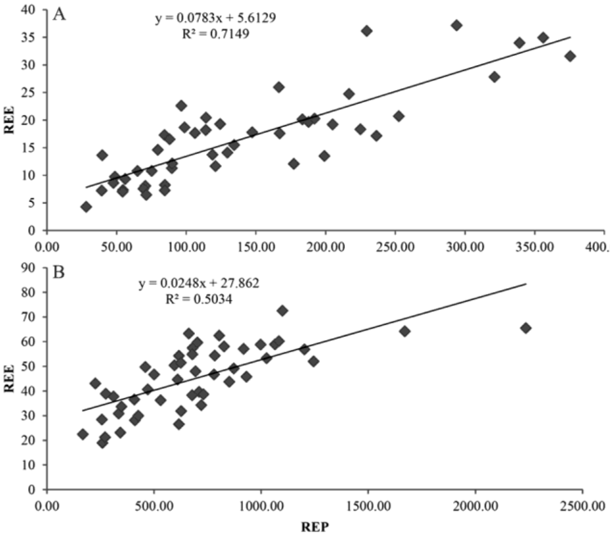

Fig. 2 — A and B- Relationship between REE and REP under (A) timely sown; and (B) late sown conditions (mean of two years)

Total carbohydrates

Carbohydrates content at flowering stage (Fig. 3) was reduced by 18.5% in the leaves and 27.1% in stem of late sown genotypes over the year. At maturity stem carbohydrates were reduced by 44.0% with delay in sowing. The lower carbohydrates content in late sown genotypes at flowering stage is directly linked with reduction of photo assimilates at source level (leaves) and with reduced mobilization from source to stem and hence imbalance in partitioning. Positive but non-significant correlation existed for leaves (r= 0.111) and stem (r= 0.235) at flowering stage and with stem (r= 0.160) at maturity stage in late sown genotypes (Table 4).

Seed yield

Significant variation existed for seed yield per plant among genotypes and planting time in both crop seasons; however non-significant variation existed for

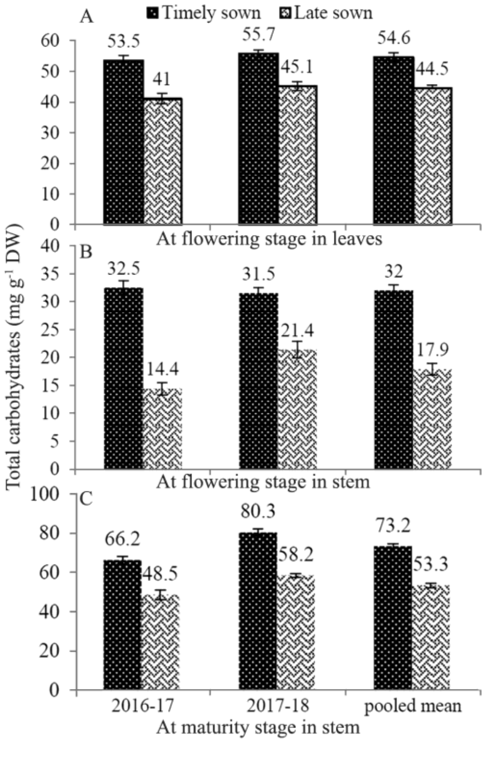

Fig 3 — Total carbohydrate content at different crop stage during two crop season at two sowing dates. [Data represent mean±Standard Error]

Y × E interaction indicated that seed yield per plant had negligible variation over the years and environment (Table 2). Late sown genotypes had 58.0% reduction during first and 61.8% in second crop season (Table 3). The negative but significant correlation of seed yield existed for REP (r= –0.497**) in timely sown (r= –0.370**) and in late sown. Although remobilization percentage was higher but seed weight was not elevated with higher remobilization percentage in brassica genotypes.

Table 5 shows performance of the selected promising genotypes based on the mean values of the period of study (two years) and the two sowing times, viz. timely sown and late sown.

Discussion

Heat stress in *Brassica* accelerated plant development from flowering to maturity resulting in prematurely ended reproductive stage causing significant yield losses. The threshold temperature for Brassica was 29.5°C past, which seed yield decline[22]. Grain filling is the critical stage for Brassica crop as it faces terminal heat stress leading to yield losses. New cultivars that are more competent for mobilizing assimilates to the developing grain/ seed, however, the equilibrium between source and sink along with the distribution of more assimilates to vegetative and reproductive organs affects harvest index[11]. The photosynthetic carbon source for grain filling is reliant upon the light absorption by the green leaf area; consequently, source is limited characteristics by natural leaf ages along with different stresses, further the demand for photo assimilates for grain filling increases along with increased plant biomass. Stem reserve is an important source of carbon for grain filling (Fig. 4). Therefore, for improving the capability of seed/ grain filling, the study of stem reserve is an important goal under abiotic stresses, particularly in drought and heat stress.

Reduction in dry matter accumulation (DMA)

Heat stress during seed filling negatively affects the dry matter production of genotypes. In Indian mustard the higher percentage of biomass was allocated to stem at 120 DAS while at maturity stage the higher percent of biomass was allocated to siliquae (reproductive product).The total dry matter production was more in timely sown crop (26th October) followed by late sown (5th and 15th November)[23]. In the present study, DMA was more at flowering stage as compared to maturity stage (except reproductive product) under both sowing conditions but late sown genotypes had lower accumulation at both the stages investigated as compared to timely sown. High temperature exposure resulted in shorter and thinner stems of canola cultivars, which resulted in production of smaller thicker leaves with lower biomass as compared to cultivars grown under optimum temperature[24]. Potential stem storage as a sink is determined by stem length and stem weight density in wheat[25]. The reduced accumulation of dry matter is mainly due to reduced production and accumulation of photo assimilates in rice under heat stress[26]. The dry matter of rice grain is mainly dependent upon the photosynthetic outcome of leaves after the heading stage[27]. High temperature stress seriously limits the photosynthetic production capability of rice, which mainly begins from the higher declining rates of leaf photosynthesis under high temperature stress. This is a significant factor for reduced grain yield. In wheat, 38% reduction in DMA

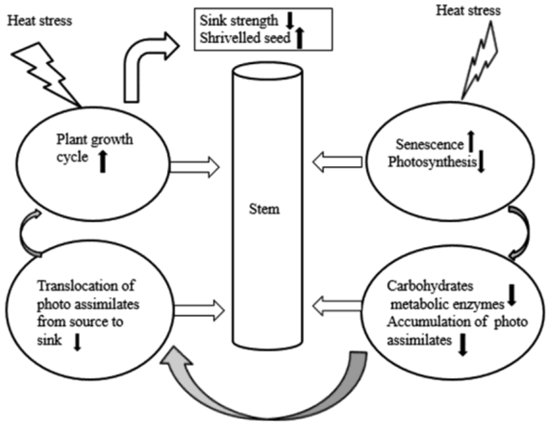

Fig 4 — Imbalance in source sinks relationship in Indian mustard genotypes under high temperature stress.

Table 5 — Performance of promising genotypes based on pooled mean of two years and sowing times

Genotype	Sowing time	SDM (g plant^{-1})		ARDM (g plant $^{-1}$)	REE (%)	REP (%)	Total carbohydrates(mg g^{-1} DW)		
		Flowering	Maturity				Flowering		Maturity
							Leaves	Stem	Stem
MCN-08-14	Timely sown	37.4	32.3	5.1	13.5	199.1	69.6	70.3	32.9
	Late sown	25.3	12.6	12.7	50.4	595.3	50.0	49.4	14.7
B-326	Timely sown	45.3	41.9	3.5	7.3	84.6	49.4	79.8	28.0
	Late sown	15.5	8.9	6.6	43.0	226.3	44.4	71.7	15.4

was at anthesis stage while at maturity stage it was 37% with delayed planting[28]. In an another study, shortened development phase due to heat stress caused a significant reduction in total above-ground biomass in wheat[29].

Heat stress caused increase in rate of remobilization of assimilates

The remobilized dry matter and utilization (efficiency) were higher in the stressed genotypes and so the more percentage/rate (REP) value. The mobilization of photosynthetic product or the photosynthates from source to sink is related to the production capacity of photo assimilates on one hand and utilization capacity of sink on the other hand. Disparity between these two factors resulted in the yield decline. The source-sink relationship forms a two-segment framework, but investigation of this does not always clearly recognize the yield limiting process The unknown de synchronization between remobilized assimilates rates and the actual effect of remobilized assimilates to seed yield has been observed in Indian mustard. Present investigation shows evident enhancement of remobilized dry matter (ARDM), remobilized efficiency (REE) which prompts us to think whether seed yield may also have to complement effect; however, there is a visible decrement. This scenario is indicator of physiological condition where the sink capacity reduced by heat stress resulting in lesser and smaller kernels in wheat[30] and in Indian mustard number of shriveled seeds were more due to terminal heat stress[31]. Reduction in source and sink activity greatly affected the growth and yield[32]. The amount of remobilized dry matter, remobilized efficiency and remobilization percentage were higher in late sown genotypes due to heat stress and drought stress[33] in wheat. Pre-anthesis reserve (PSR) mobilization to final grain weight was higher in heat sensitive late sown genotypes, while heat tolerant genotypes had lowest stem reserve mobilization[34]. Remobilization efficiency (REE) increased under water stress conditions when the current photosynthesis was inhibited. The remobilization percentage under normal conditions was 37.1% and increased to 42.6% in the water stress genotypes. The stem reserve utilization rate was higher in wheat genotypes grown under rainfed than irrigated conditions[35]

Reduction in total carbohydrates

Decline in amount of total carbohydrates under present investigation was higher in late sown genotypes as heat stress reduced photosynthetic activity and induced premature senescence, resulting in decrement in synthesis and distribution of assimilates to developing organs. The balance between storage and movable carbohydrates is crucial for carbon allocation. The reduction in the sucrose synthesizing enzyme activity in late sown wheat genotypes is possibly due to the altered sucrose to starch metabolizing enzymes[36] This fact can be correlated well with the present investigation where leaves (source) possess higher carbohydrates content however possibly the stored carbohydrates were restricted to source only; their transportation to sink may be hindered in late sown condition. Stem being a photosynthetic organ in Brassica also possessed lower carbohydrates content in late sown genotypes, which may not be able to fulfill the demand required at sink. The impairment in carbohydrates metabolism was likewise explained in chickpea[37] where ascend in temperature (30 to 35°C) reduced leaves sucrose metabolism and hindered sucrose delivery to developing seeds which may be an essential elucidation of shriveled seeds due to heat stress. The declined amount of chlorophyll in the leaf was strongly coordinated with carbohydrates and nitrogen content in proso millet (*Panicum miliaceum* L.) and impacted well on remobilization efficiencies[38]. Decline in seed yield was due to reduced starch accumulation amounting to 65% of seed dry weight, which accounted for starch in wheat[39]. Additionally decline in carbohydrates content in culms and kernel of wheat under heat stress has also been reported[29].

Seed yield per plant and correlation analysis

Leaf senescence accelerated by high temperature at seed filling stage, which reduced photosynthetic activity leading to declining in growth and yield attributes. Seed yield (g plant^{-1}) was reduced by 4.88% and test weight by 10.1% in Indian mustard during terminal heat stress[40]. The decrease in seed yield is directly connected with sink strength which was evident from less number of seeds or more number of shriveled seeds produced, which intended for reduced sink capacity and overall reserves which may remain immobilized and stored in the stem. In the present investigation reduced sink strength was due to reduced seed weight which led to more stem reserve mobilization or efficiency as observed in late sown genotypes. During grain filling stage in wheat, mobilization of soluble carbohydrates contributed 20% to final grain weight in non-stress conditions while it rose to 70.0% or more under drought stress[41].

Soluble carbohydrates were significant and positively correlated with accumulation efficiency and grain filling efficiency in wheat under drought stress[42]. Our result also showed consistency with the above findings as positive correlation existed for total carbohydrates with seed yield. In wheat positive correlation existed for test grain weight and stems reserve mobilization under rainfed and irrigated conditions[8], however in present investigation positive correlation existed between seed yield and stem reserve utilization in late sown condition only.

Conclusion

Terminal heat stress (≥30°C) during seed filling not only influenced stem reserve accumulation but mobilization and translocation as well. The remobilization of assimilates increased under late sowing in the two identified MCN-08-14 and B-326 promising genotypes. Stem dry matter (SDM) accumulation reduced significantly at flowering and maturity however, the reduction was higher in B-326 genotype. Increase in ARDM was 45%, REE by 73% and REP by 62% in late sown genotypes; which however was not reflected in the seed yield. There might be an unknown factor that desynchronizes overall carbohydrates transportation. The differential behavior of same set of genotypes was observed when grown under normal and late sown conditions as the later faces terminal high temperature stress, which may be the result of asynchronous genetic function due to late sowing leading to yield losses. The genetic potential of the genotypes when sown late can be further tested at locations with relatively higher temperature where the terminal heat stress will invariably affect the translocation and channelization of photo assimilates resulting in differential remobilization responses. Further, the enzymes kinetics related to carbohydrate metabolism under terminal heat stress can be the extended part of the present study and to explore the sink strength and hindrance in source to sink relationship. To enhance the remobilization of assimilates or the reserves, the ‘source to sink’ can be an important strategy for improving seed filling in Brassicas to ensure sustainable production.

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Conflicts of interest

Authors declare no competing interests.

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