Inheritance studies for post-anthesis mobilization of assimilates in wheat under rainfed condition

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Abstract

Wheat (*Triticum aestivum* L.) is the most widely grown crop of the world and staple food of about 35% of world population. Photosynthate or current assimilates are the primary carbon source for grain filling, but under moisture stress these may not be available. Hence, the stem and other plant parts reserves are an essential carbon source for grain filling under stress conditions. Analysis of variance exhibited significant genotypic differences for all the traits under study. Under the treated condition, genotype LLR-21 showed the highest translocation of dry matter and translocation efficiency among parents, while LLR20 showed the highest percentage of contribution of pre-anthesis assimilates to grain. Among crosses, cross LLR-22 x CB-42 showed the highest value for translocation of dry matter and translocation efficiency, while Nazcozari x LLR22 showed the highest percentage for contribution to pre-anthesis assimilates. Combining ability analysis revealed that the traits showed different behavior under stress conditions than the control condition. GCA mean squares for the dry matter at anthesis, dry matter at maturity, translocation of dry matter and contribution of pre-anthesis assimilates to grain was lower than SCA, suggesting the presence of a non-additive type of gene action under control conditions. GCA mean squares for translocation of dry matter, translocation efficiency and contribution of pre-anthesis assimilates to grain was lower than SCA, suggesting the presence of a non-additive type of gene action under control conditions. The dry matter at anthesis and dry matter at maturity showed additive type of gene action under-treated conditions.

Keywords: Stem reserve translocation; photosynthetic assimilates; GSC; SCA; combining ability

Abbreviations: GSA: General Combining Ability, SCA: Specific Combining Ability WSC: water-soluble carbohydrates

Introduction

Due to climate change, most of the world has been facing water scarcity and drought for the last two decades, mainly due to changing rains patterns and increasing temperatures(Mahmood et al., 2020; Naeem et al., 2015; Nazir et al., 2021). Production of wheat, both in irrigated and rain-fed areas, is being hampered due to this climate change (Rauf et al., 2013). The world's ever-increasing population needs more resources and is subjected to food security issues every passing day. To overcome foodsecurity issues, breeders are in the quest to minimize the effects of stresses by evolving high yielding crop varieties with increased stress tolerance and having maximum water use efficiency in utilizing the optimum available resources (Mahmood et al., 2013; Naeem et al., 2016; Nowsherwan et al., 2018; Sarfraz et al., 2020). To evolve a variety resistant to biotic and abiotic stresses, breeding for stem reserves is essential. Stem reserves play a significant role in increasing the yield by improving grain filling (Blum et al., 1989). Many researchers mentioned that stem reserve mobilization plays an essential role under stress conditions (Bidinger et al., 1977; Blum et al., 1989; Ehdaie & Waines, 1989; Nazir et al., 2021). Stem reserves are water-soluble carbohydrates, and their availability depends highly on environmental conditions

and cultivars. Under any biotic or abiotic stress, stem reserves can play an essential role during grain filling. Hence, stress loss can be minimized with the cultivars having better mobilization efficiency of stem reserves (Nazir et al., 2021). The two vital sources for stabilizing grain yield are the capacity for photosynthetic assimilates storage and the efficiency of its remobilization to the grain (Moayedi et al., 2009). Under dryland conditions, as compared to irrigated conditions, only 50% of the WSC (water-soluble carbohydrates) were available for translocation during grain filling (Hussain & Rivandi, 2007; Nazir et al., 2021). Stem reserve storage is affected by the stem length, controlled by height genes (Rht1 and Rht2), which reduced reserve storage by 35% and 39% as the length was reduced to 21% (Borrell et al., 1993; Naeem et al., 2015). The decline of photosynthesis after anthesis has been reported by Johnson et al. (1981), limiting the contribution of current photosynthates to the grain (Naeem et al., 2016; Nazir et al., 2021; Sarfraz et al., 2020). Severe drought stress may reduce grain filling, leaf desiccation and reduced photosynthesis. The study's objective was to identify efficient genotypes for both extremes of stem reserve mobilization to grain and find out the best combiner for stem reserve translocation in wheat.

Materials and Methods

The experimental materials comprised six wheat varieties/lines viz, Nacozari, LLR-22, LLR-20, CB-42, Parula and LLR-21, screened for stem reserves mobilization efficiency and direct crosses 50 lines were screened for Stem reserve mobilization under stress-induced conditions. The screening was done for the total dry matter at anthesis (g), total dry matter at maturity (g) translocation of dry matter (g), translocation efficiency percentage, the contribution of post-anthesis assimilate associated with stem reserve mobilization and morphological characters.

The screening study was carried out during the wheat season of 2015-16 (planted in autumn-2015 and harvested in spring 2016). Combining ability studies was planted in fall 2016 and harvested in spring 2017. All the experiments were conducted in the Department of Plant Breeding and Genetics, PMAS Arid Agriculture University Rawalpindi. All the F1 hybrids and their parents were planted in the field in a randomized complete block design (RCBD) with three replications. Two sets of this experiment were sown under rain-fed condition; one was kept as control while the other was treated with potassium iodide at 50% anthesis stage to create chemical desiccation. Row length was kept 5.0 m and distance between rows and plants 30cm and 15cm, respectively. Two seeds per hole were sown with the help of a dibbler and later thinned to one seedling per hill after germination; other cultural and agronomic practices were kept uniform, i.e., seed treatment, time of sowing, weeding, thinning, fertilization, etc. for the whole experiment. Ten guarded plants from each replication were selected randomly to record the traits' data at maturity.

Collection of Data

The data were recorded for the following traits at the required stage from ten guarded plants randomly selected from each replication.

Aerial plant biomass treated (g)

At maturity, ten randomly selected un-thrashed plants were harvested from the plot, treated with potassium iodide, and weighed with the help of electric balance in grams. Some derived parameters were also calculated related to biomass and translocation of stem reserves with the help of the following formulae.

Mobilization of dry matter (mg per plant) = dry matter at anthesis - dry matter at maturity.

Translocation efficiency (%) = (Mobilization of dry

matter /dry matter at anthesis) ×100.

Contribution of assimilates to grain (%) = (Mobilization of dry matter/grain weight) $\times 100$ (Papakosta & Gagianas, 1991).

Aerial plant biomass for control (g)

Aerial plant biomass of plants grown under rain-fed conditions was measured according to the method for aerial plant biomass for treated.

Statistical Analysis

The data collected for all the traits were subjected to analysis of variance according to (Steel, 1997). The correlation coefficient was also calculated. The combining ability analysis was worked out by the procedure suggested by Griffing (1956) Method-2, Model-11.

Results

The value of different plant traits of 21 genotypes, including 6 parental lines and 15 direct cross combinations, was subjected to variance analysis. Twofactor analysis of variance was conducted. The results showed highly significant (P < 0.01) differences among all genotypes for all the traits (Table 1). Analysis of variance also depicted significant differences among control and treated condition. Similarly, interaction Genotype x treatment was also found significant. Analysis of variance (combining ability) for treated (treated with potassium iodide to cause stress) conditions showed significant GCA and SCA results. GCA of the control condition was nonsignificant for all the traits except for dry matter at anthesis, while SCA was observed with a significant value of dry matter at anthesis. Detailed results and discussions are discussed further as follows (Table 3).

Results indicated that the GCA effects of parents for Dry matter at anthesis under control condition (rain-fed condition) were significant for LLR 20 and Nacozari and non-significant for the rest of the parents. LLR 22 was found highly responsible for dry matter at anthesis undertreated conditions. However, the parents CB 42, Parula and LLR 21showed negative GCA values and are responsible for less dry matter at anthesis. The magnitude of SCA effects is shown in table 1. Out of 15 crosses, cross numbers 2, 6,8,12 and 13 showed the significant positive value of SCA under rain-fed conditions, while crosses Nacozari x LLR 22, Nacozari x LLR 20, Nacozari x LLR 21, LLR 22 x LLR 20, LLR 22 x CB 42, LLR 20 x Parula, LLR 20 x LLR 21 and CB 42 x LLR 21 were observed with significant value of SCA for treated condition.

The GCA effects of parents for Dry matter at maturity under control conditions (rain-fed condition) were nonsignificant for all the parents. For treated conditions (treated with potassium iodide to induce stress), LLR 22, LLR 20 and Nacozari showed significant positive value for GCA and the remaining showed negative value for general combining ability. Results indicated that LLR 22 was highly responsible for dry matter at maturity. However, the parents CB 42, Parula and LLR 21showed negative GCA values and were responsible for less dry matter at maturity. According to Sanjari et al., 2010, no significant differences among genotypes for the dry matter at maturity under drought stress conditions. Out of 15 crosses, cross numbers 6,12,14 and 15 showed the value of SCA under rain-fed conditions, while crosses Nacozari x LLR 22, LLR 22 x LLR 21, LLR 20 x Parula, LLR 20 x LLR 21 and CB 42 x Parula were observed with the

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Table 1	. Mean	squares	for	six	wheat	varieties	and	fifteen	F1	crosses

	Df	DMA	DMM	TDM	ТЕ	СРА
Replication	2	2334.381 ns	2971.341 ns	9122.198 ns	3.133 ns	7.41 ns
Treatment	1	243.056 **	38006177.786**	10549093.3 **	11600.643 **	43260.51**
Error	2	1811.937	278.167	2468.865	7.198	0.872
Genotype	20	1835737.2 **	2096902.058**	1045662.36 **	1160.817 **	2246.031**
treat x genotype	20	748.772 **	212916.902**	242712.465 **	322.716 **	639.084 **
Error	80	1661.159	636.312	5210.865	4.009	5.298

** Significant at P< 0.01

DMA= total dry matter at anthesis (g), DMM= total dry matter at maturity (g), TDM=translocation of dry matter (g), TE%= translocation efficiency percentage, CPA= contribution of post-anthesis assimilate

FABLE 2. Mean values of interaction for treatments and genotype	s (treatment x genotype) for all the traits under control	condition and treated conditions
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Genotypes	Control con	dition	Treated condition							
	DMA	DMM	TDM	ТЕ	СРА	DMA	DMM	TDM	ТЕ	СРА
Nacozari	3068.00	5425.00	314.00	9.01	11.75	3064.00	4009.30	1190.60	38.70	55.80
LLR 22	3803.30	5714.60	754.00	19.35	28.28	3771.00	4415.30	1623.00	42.60	72.10
LLR 20	3323.00	4037.60	1016.00	30.18	58.70	3307.00	3411.00	978.00	29.40	91.70
CB 42	2826.60	4956.60	83.00	2.36	3.75	2828.00	3346.60	954.66	33.70	64.70
Parula	2750.00	4227.60	508.30	18.25	25.59	2769.00	3052.60	1064.30	38.60	77.80
LLR 21	2775.60	4298.30	847.30	30.53	35.75	2730.00	3053.30	1679.60	60.50	85.80
Nacozari x LLR22	3244.00	4013.60	1180.30	36.12	60.52	3236.60	3743.60	835.33	25.70	62.50
Nacozari x LLR 20	3414.00	4179.60	645.00	18.79	45.72	3427.30	3694.30	793.00	23.20	73.80
Nacozari x CB 42	3376.00	4953.60	-12.30	0.21	0.00	3358.60	3522.30	1173.60	34.70	88.90
Nacozari x Parula	2256.30	3876.00	413.30	18.16	20.32	2250.60	3456.60	459.00	20.30	27.60
Nacozari x LLR 21	2424.60	5234.00	-617.60	0.00	0.00	2415.00	4054.60	251.66	10.30	13.30
LLR 22 x LLR 20	2235.30	4271.60	-64.60	0.00	0.00	2283.30	3264.00	416.33	18.60	28.70
LLR 22 x CB 42	2146.30	3980.00	625.30	27.94	25.41	2132.60	2841.30	1327.00	61.80	65.60
LLR 22 x Parula	3484.60	5426.00	414.30	11.41	17.59	3486.00	4347.30	973.33	27.90	53.00
LLR 22 x LLR 21	2914.60	4854.00	-499.30	0.00	0.00	2933.30	3634.30	240.33	8.24	24.90
LLR 20 x CB 42	2254.30	4385.30	100.30	4.46	4.49	2237.60	2827.00	1223.30	54.20	68.10
LLR 20 x Parula	2391.00	4582.30	401.00	16.67	15.47	2367.60	3411.30	1117.30	46.70	52.20
LLR 20 x LLR 21	2687.30	5069.60	109.60	4.37	4.40	2666.60	3971.00	191.66	7.13	12.90
CB 42 x Parula	2609.30	4991.60	-526.30	0.00	0.00	2641.30	3478.30	399.33	15.20	31.40
CB 42 x LLR 21	1715.60	3314.00	655.00	37.52	29.06	1740.00	1998.00	1161.00	67.60	80.40
Parula x LLR 21	2010.30	3468.60	562.60	27.84	27.84	2006.30	2660.60	1009.30	50.20	60.80
LSD	30.52	42.44	117.52	3.27	3.71	30.52	42.44	117.52	3.27	3.71

** Significant at P< 0.01 > ns

DMA= total dry matter at anthesis (g), DMM= total dry matter at maturity (g), TDM=translocation of dry matter (g), TE%= translocation efficiency percentage, CPA= contribution of post-anthesis assimilate

Table 3. Estimates of GCA and SCA effects of six parents and their direct crosses for traits directly associated with stem reserve translocation under contr	ol
condition	

GCA Effects		Control Con	dition (Rainfo	ed condition)		Treated condition				
Parents	DMA	DMM	TDM	TE %	CPA	DMA	DMM	TDM	TE	CPA
Nacozari	165.43 *	142.86 ns	63.57 ns	0.19 ns	2.01 ns	289.44 **	154.15 **	290.87 **	5.49 **	13.29 **
LLR 22	-53.44 ns	-120.64 ns	33.65 ns	2.23 ns	2.02 ns	309.82 **	320.78 **	-47.88 **	-6.98 **	0.43 ns
LLR 20	144.06 *	109.32 ns	55.44 ns	0.91 ns	2.00 ns	79.44 **	48.99 **	-151.21**	-6.36 **	-3.86 **
CB 42	-64.74 ns	-41.22 ns	-29.18 ns	-1.91 ns	-2.02 ns	-173.5 **	-164.72**	107.12 **	6.75 **	2.89 **
Parula	69.81 ns	-16.72 ns	-15.93 ns	0.28 ns	0.61 ns	-165.18**	-105.22**	-97.54 **	-0.85 ns	-5.44 **
LLR 21	-261.1 **	-73.60 ns	-107.56 ns	-1.71 ns	-4.62 ns	-339.9 **	-253.9 **	-101.3 **	1.95 **	-7.31 **
SCA EFFECTS (Cros	sses)									
Nacozari x LLR 22	-55.78 ns	-70.43 ns	80.43 ns	0.92 ns	-0.70 ns	426.39 **	502.63 **	472.29 **	10.08 **	1.62 *
Nacozari xLLR 20	284.39 **	-394.72 *	142.97 ns	2.07 ns	11.07 *	192.76 **	-229.9 **	-69.38 **	-3.83 **	25.47 **
Nacozari x CB 42	-538.5 **	-195.85 ns	-422.7 **	-6.44 ns	-12.21 *	-33.24 **	-80.54 **	-351.1 **	-12.58 **	-8.24 **
Nacozari x Parula	-123.70 ns	103.32 ns	-196.99 ns	-1.14 ns	-7.58 ns	-100.6 **	-434.0 **	-36.71 ns	-0.05 ns	13.20 **
Nacozari x LLR 21	-213.78 *	82.86 ns	-97.36 ns	-5.57 ns	-9.64 *	35.18 **	-284.6 **	582.45 **	18.96 **	23.03 **
LLR 22 x LLR 20	548.60 **	556.78 **	238.22 ns	1.02 ns	7.54 ns	292.72 **	-113.2 **	84.37 **	2.46 **	20.51 **
LLR 22 x CB 42	149.05 ns	138.32 ns	121.85 ns	1.16 ns	0.75 ns	477.05 **	-71.50 **	206.70 **	0.89 ns	28.79 **
LLR 22 x Parula	584.18 **	-10.84 ns	265.26 *	1.10 ns	13.05 **	-639.3 **	-196.6 **	-303.3 **	-5.93 **	-24.13 **
LLR 22 x LLR 21	-125.57 ns	136.03 ns	-360.4 **	-9.73 **	-10.82 *	-300.2 **	550.08 **	-506.8 **	-18.70 **	-36.56 **
LLR 20 x CB 42	-377.1 **	73.70 ns	-140.61 ns	-5.10 ns	-11.18 *	-518.5**	-480.7**	463.37 **	27.32 **	9.79 **
LLR 20 x Parula	-845.3 **	-689.1 **	-166.53 ns	5.34 ns	-3.59 ns	826.39 **	965.79 **	314.37 **	1.04 ns	5.50 **
LLR 20 x LLR 21	773.26 **	464.41 **	447.76 **	4.98 ns	17.01 **	448.51 **	401.54 **	-414.8 **	-21.46 **	-20.69 **
CB 42 x Parula	590.14 **	-112.93 ns	326.10 *	5.22 ns	17.66 **	-38.95 **	243.50 **	200.04 **	6.73 **	-2.00 **
CB 42 x LLR 21	-124.28 ns	40.28 ns	-296.61 *	-5.61 ns	-6.63 ns	434.85 **	951.92 **	-721.8 **	-35.67 **	-39.40 **
Parula x LLR 21	-113.15 ns	225.11 ns	3.14 ns	-4.62 ns	-7.41 ns	-500 **	-1080.5**	452.20 **	32.47 **	36.37 **
$\sigma^2 g \sigma^2 V$	-0.03401	-0.09602	-0.19979	-0.15229	-0.18394	0.56791	0.047462	0.089573	-0.07126	-0.10258

** Significant at P< 0.01 > ns

DMA= total dry matter at anthesis (g), DMM= total dry matter at maturity (g), TDM=translocation of dry matter (g), TE%= translocation efficiency percentage, CPA= contribution of post-anthesis assimilate

significant value of SCA for treated condition. The remaining cross products also showed significant value, but the negative highest value for SCA under-treated conditions was shown by cross LLR 20 x Parula.

According to results, for translocation of dry matter (TDM), The GCA effects of parents for the control condition (rain-fed condition) were non-significant for all the parents. For treated conditions (treated with potassium iodide to induce stress), nacozari and CB-42 showed significant positive value for GCA, and the remaining showed negative value for general combining ability. Results indicated that nacozari was highly responsible for dry matter at maturity. However, the parents LLR 22, LLR 20, Parula and LLR 21showed negative GCA values and were responsible for less dry matter at maturity. Out of 15 crosses, cross LLR 22 x Parula, LLR 20 x LLR 21, CB 42 x Parula showed the significant positive value of SCA under rain-fed condition, while Nacozari x LLR 22, Nacozari x LLR 21, LLR 22 x LLR 20, LLR 22 x CB 42, LLR 20 x CB 42, LLR 20 x Parula, CB 42 x Parula and Parula x LLR 21 were observed with significant value of SCA for treated condition. The remaining cross-products also showed significant value but were negative. The highest value for SCA under-treated conditions was shown by Nacozari x LLR 21.

The GCA effects of parents for Translocation efficiency (TE %) under control conditions (rain-fed condition) were non-significant for all the parents. For treated conditions (treated with potassium iodide to induce stress), nacozari, CB-42 and LLR 21 showed significant positive value for GCA and the remaining showed negative value for general combining ability. Results indicate that CB 42 was highly responsible for translocation efficiency. However, the parents LLR 22, LLR 20 and Parula showed negative GCA values and are responsible for less translocation efficiency. Under control conditions, none of the crosses showed nonsignificant results, while the cross number Nacozari x LLR 22, Nacozari x LLR 21, LLR 22 x LLR 20, LLR 20 x CB 42, CB 42 x Parula and Parula x LLR 21 were observed with significant value of SCA for treated condition. The remaining cross products also showed significant value, but the negative highest value for SCA under-treated conditions was shown by Parula x LLR 21.

The GCA effects of parents for the contribution of pre-anthesis assimilates to grain under control condition (rain-fed condition) were non-significant for all the parents. For treated conditions (treated with potassium iodide to induce stress), nacozari and CB-42 showed significant positive value for GCA, and the remaining showed negative value for general combining ability. Results indicated that Nacozari was highly responsible for pre-anthesis assimilates to grain. However, the parents LLR 20, LLR 21 and Parula showed negative GCA values and are responsible for less contribution of pre-anthesis assimilates to grain. Under control conditions, the crosses Nacozari x LLR 20, LLR 22 x Parula, LLR 20 x LLR 21 and CB-42 x Parula showed significant positive results. In contrast, the cross Nacozari x LLR 20, Nacozari x Parula, Nacozari x LLR 21, LLR 22 x LLR 20, LLR 22 x CB 42, LLR 20 x CB 42, LLR 20 x Parula and Parula x LLR 21 were observed with significant value of SCA for treated condition. The highest value for SCA under-treated conditions was shown by Parula x LLR 21.

Discussion

The study, as mentioned above, was conducted to find out the best general and specific combiner under rainfed conditions for stem reserve translocation. The results indicate the presence of variability under control and treated conditions. Stem reserve translocation and associated traits were highly influenced by the stressinduced condition, clearly indicating the association of translocation of water-soluble carbohydrates is an essential source of grain filling under stress conditions. Mobilization of stem reserve is the varietal character as suggested by (Blum et al., 1989; Mahalakshmi et al., 1993; Pirzado, Jatoi, et al., 2021; Pirzado, Sutahar, et al., 2021). Higher mobilization efficiency resulted in better pre-anthesis stored reserves for grain filling under stress-induced conditions. The line LLR21 was the best general combiner because of it performance in a series of crosses for translocation of dry matter, translocation efficiency and contribution of pre-anthesis assimilates to grain As it is evident that the best general combiner is mostly not the best specific combiner, the results confirm the statement (Xie et al., 2003).

Conclusion

The cross combination Nacozari x LLR-22 showed the best performance as a specific combiner for translocation of dry matter under stress conditions and the cross Parula x LLR 21 showed the best performance as a specific combiner for translocation efficiency. The cross LLR 20 x Parula showed the highest value of SCA for the total dry matter at anthesis and total dry matter at maturity; similarly, cross Parula x LLR 21 showed the highest SCA for the contribution of pre-anthesis assimilates to grain. LLR 21 was found best general combiner for translocation of dry matter, translocation efficiency and contribution of pre-anthesis assimilates to grain filling.

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