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Effect of Source-Sink Manipulation on Yield Components and Photosynthetic Characteristic of Wheat Cultivars (*Triticum aestivum* and *T. durum* L.)

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Abstract: To investigate the effect of source-sink manipulation on photosynthetic characteristics and yield components of wheat cultivars, a research was carried out in the greenhouse at the College of Agriculture, Shiraz University, Shiraz, Iran, during 2008-2009 growing season. Five wheat cultivars including Shiraz, Bahar, Pishtaz, Sistan (as bread wheat) and Yavaros (as durum wheat) were grown in 5 kg plastic pots. The source-sink manipulation treatments including defoliation of all leaves, defoliation of all leaves except the flag leaf, removal of 25% of spikelets and removal of 50% of spikelets were applied at anthesis. Results showed that number of grains per spike was significantly decreased by defoliation treatment in Shiraz, Bahar and Yavaros cultivars, so that in Shiraz and Bahar cultivars, source restriction reduced the number of grains per spike by 18.97 and 11.07%, respectively. In Shiraz cultivar, defoliation of all leaves decreased main stem grain yield by 40.75%, which demonstrated that Shiraz was very sensitive to source restriction. The little response of main shoot grain yield to defoliation in Pishtaz cultivar indicates high mobilization of photoassimilate from other parts of the crop to the grains. Under sink restriction conditions, wheat cultivars (except Pishtaz) had potential to increase their 100-grain weight; moreover, Pishtaz yield appeared to be more sink rather than source-limited. Removal of all leaves except the flag leaf at 8 and 18 DAA, in Pishtaz and Yavaros cultivars, had no significant effect on net photosynthesis rate (P_n) and in all cultivars except Pishtaz, sink restriction significantly decreased P_n rate. Further research, is recommended for improving our understanding on source-sink relationship in Iranian wheat cultivars.

Key words: Sink or source restriction, wheat yield components, net photosynthesis rate, 100-grain weight

INTRODUCTION

Wheat (*Triticum aestivum* L.) is regarded as the most important cereal crop of the world in view of both areas under cultivation and production level. About two-thirds of the world population lives on wheat grain (Emam, 2007). In crops, the physiological basis of dry matter production depends on the source-sink relationship, where the source is the potential capacity for photosynthesis and the sink is the potential capacity to store or metabolize the photosynthetic products. When the sink is small, higher yield could not be achieved and even if the sink is large, the yield might not be high, when the source capacity is limited (Alam *et al.*, 2008; Emam and Seghatoleslami, 2005; Borras *et al.*, 2004).

Optimizing the source and its proper utilization by the economic sink is important for improvement of yield potential in wheat crop (Alam *et al.*, 2008; Shekoofa and Emam, 2008). According to Richards (1996) the modern high yielding cultivars of wheat are sink-limited and this

has posed problem in yield increase. Borras *et al.* (2004) reviewed the literature on the magnitude of the mean grain weight response as a function of the assimilate availability during grain filling period to test quantitatively whether source or sink limitation in wheat grain growth period was predominant. They concluded that under most conditions grain growth in wheat was apparently more sink, than source-limited.

Artificial reduction in grain number per spike (Borras *et al.*, 2004) or defoliation (Bingham *et al.*, 2006) or early use of chloromequat chloride (Emam and Karimi, 1996; Emam and Dastfal, 1997; Emam *et al.*, 1997; Shekoofa and Emam, 2008) have been employed in several studies to provide clear evidence on whether grain yield in wheat is more source or sink limited (Emam, 2007). Some researchers concluded that wheat final grain weight was limited by the ability of the source to provide assimilate during grain filling. For example, Fischer and Lambers (1978) reported that final weight per grain was increased when grains per spike were reduced

artificially, suggesting a degree of limitation of grain weight by the photoassimilate supply during grain filling. In contrast, data from other investigations have suggested that the wheat yield is more sink-limited during the grain filling (Savin and Slafer, 1991; Borrás *et al.*, 2004; Shekoofa and Emam, 2008). Also, Aggarwal *et al.* (1990) reported that whole plant defoliation treatments had no significant effects on wheat grain yield in most cases. Finally, there are some reports suggesting that grain growth in wheat might be limited by both assimilate supply (source limitation) and assimilate demand (sink limitation) (Ahmadi *et al.*, 2009).

Source and sink manipulation might be regulated by plant physiological processes such as net photosynthesis and features as stomatal conductance and transpiration rate of wheat (Ahmadi *et al.*, 2009; Rohi and Siose Mardeh, 2008) however, the direction and magnitude of the regulation varies with time and cultivar (Rohi and Siose Mardeh, 2008; Ahmadi and Joudi, 2007). The grain growth of wheat mainly depends on formation, translocation, partitioning and accumulation of photosynthates during the grain filling. Therefore, both photosynthetic activity of leaves (source) and storage ability of grains after anthesis (sink) are factors limiting the grain yield of wheat (Wang *et al.*, 1997; Emam, 2007).

Detrimental effects of defoliation on yield components might be related directly to reductions on the photosynthetic capacity of the remaining tissue (Macedo *et al.*, 2006). Zhu *et al.* (2004) reported that defoliation of wheat at late tillering increased main shoot grain yield and harvest index 7.3 and 10.7%, respectively and enhanced stomatal conductance and net photosynthesis rate of remaining leaves at anthesis. In another investigation on wheat, Yin *et al.* (1998) found that at the initial grain filling stage, the large-grain cultivar was sensitive to source reduction, leading to an increased net photosynthesis rate by 10%, however, source reduction had no impact on small grain cultivar.

The effects of source and sink manipulation on Iranian wheat cultivars has not yet been fully understood. The present study was undertaken to investigate the effect of source and sink manipulation on yield components and photosynthetic characteristics of five wheat cultivars.

MATERIALS AND METHODS

In order to investigate the effect of source-sink manipulation on photosynthetic characteristics and yield components of five wheat cultivars, a pot experiment was carried out in the greenhouse at the College of Agriculture, Shiraz University, (29° 50' N, 52° 46' E) 12 km

North of Shiraz, Iran, on a fine mixed, mesic typical Calcixerpets soil during 2008-2009 growing season. Five wheat cultivars including Shiraz, Bahar, Pishtaz, Sistan (as bread wheats) and Yavaros (as durum wheat) were grown in 5 kg plastic pots filled with fertilized soil at 20 mg kg⁻¹ nitrogen as urea. A completely randomized design with four replications was used. Ten uniform seeds of each cultivar were sown in each pot, on 21 December 2008 and thinned to five seedlings at two-leaf stage. The pots were watered when necessary to avoid water stress. The greenhouse temperature was 25°C (±5), with 70% (±10) relative humidity and light intensity varied in the range of 600-1000 μmol/m²/sec.

The source-sink manipulation treatments including control, defoliation of all leaves, defoliation of all leaves except the flag leaf, removal of 25% of spikelets (one out of every four spikelets) and removal of 50% of spikelets (every alternate spikelets) were applied at anthesis on 12 March 2009. Also, at anthesis, the plants were de-tillered to avoid becoming alternative sinks for mobilized carbohydrates (Emam, 2007).

Measurements of the net photosynthesis rate (P_n) and closely related processes, such as stomatal conductance (g_s), intercellular CO₂ concentration (C_i) and transpiration rate (E), were recorded from the flag leaf of main shoot on each plant using a portable photosynthesis system (IGRA model LCA4-ADC, Hoddeson, UK) at 8 days (initial grain filling stage) and 18 days (rapid grain filling stage) after anthesis (DAA).

At physiological maturity, plants of each pot were harvested and oven-dried at 80°C, then the number of grains per spike, main shoot yield, 100-grain weight and spike compactness (spikelet number per spike divided by spike length) was measured (Emam, 2007). The collected data were subjected to analysis of variance and the means were separated with LSD test ($p = 0.05$) using SAS software (SAS, 2000).

RESULTS

Effects of source-sink manipulation on wheat yield components: The number of grains per spike was found to be affected significantly by defoliation of all leaves and all leaves except the flag leaf treatments in three cultivars of Shiraz, Bahar and Yavaros (Table 1). It was observed that in Shiraz and Bahar cultivars, source restriction caused reduction in the number of grains per spike by 18.97 and 11.07% compared to control, respectively. In all cultivars, except Pishtaz, the main shoot grain yield was decreased significantly by defoliation treatments (Table 1). In Shiraz cultivar, defoliation of all leaves decreased main shoot

Table 1: Effect of source or sink manipulation on yield components of wheat cultivars

Wheat cultivars	Source- sink manipulation treatments	No. of grains per spike		Main shoot yield (g)		100-grain weight (g)	
		Mean	Changes with control (%)	Mean	Changes with control (%)	Mean	Changes with control (%)
Shiraz	All leaves removed	30.33h	-18.97	0.88k	-40.75	2.91m	-26.88
	All leaves removed except the flag leaf	35.11cde	-6.20	1.21fg	-18.45	3.46k	-13.07
	25% spikelets removed	25.90l	-25.80	1.13h	-24.16	4.38b	10.05
	50% spikelets removed	18.69m	-50.06	0.83l	-44.28	4.44a	11.56
	Control	37.43a		1.49a		3.98cd	
Bahar	All leaves removed	28.29i	-11.07	0.88k	-25.61	3.12l	-16.35
	All leaves removed except the flag leaf	30.17h	-4.34	1.09hi	-7.42	3.61j	-3.22
	25% spikelets removed	23.51l	-25.45	0.91k	-22.65	3.87d-g	3.75
	50% spikelets removed	15.68n	-50.12	0.61o	-48.30	3.89c-f	4.29
	Control	31.54f		1.18g		3.73g-j	
Pishtaz	All leaves removed	34.04ef	-4.68	1.32d	-5.41	3.88c-f	-0.77
	All leaves removed except the flag leaf	34.11def	-4.48	1.34cd	-3.99	3.93cde	-0.26
	25% spikelets removed	25.90k	-25.48	1.01j	-24.62	3.91c-f	0.0
	50% spikelets removed	18.39m	-48.51	0.73n	-45.52	3.97cd	1.53
	Control	35.11cde		1.34cd		3.91c-f	
Sistan	All leaves removed	34.86cde	-0.91	1.27e	-7.80	3.65ij	-4.20
	All leaves removed except the flag leaf	35.03cde	-0.43	1.32d	-4.05	3.78fgh	-0.79
	25% spikelets removed	27.18j	-24.36	1.12h	-18.84	4.12b	7.29
	50% spikelets removed	17.87m	-50.29	0.77m	-44.20	4.31a	12.24
	Control	35.18bcd		1.38bc		3.81e-h	
Yavaros	All leaves removed	33.15f	-8.50	1.23f	-15.56	3.71hij	-7.71
	All leaves removed except the flag leaf	35.64bc	-1.63	1.37bc	-6.03	3.84d-g	-4.48
	25% spikelets removed	26.63lk	-25.49	1.10i	-24.65	4.13b	2.74
	50% spikelets removed	18.18m	-49.82	0.80lm	-45.07	4.40a	9.45
	Control	36.23b		1.46a		4.02bc	

Means with the same letter in each column are not significantly different, using LSD test (0.05)

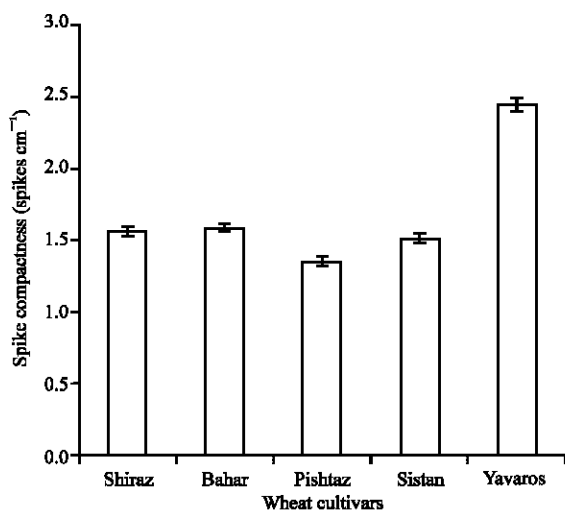


Fig. 1: Comparison of spike compactness in wheat cultivars (Vertical bar represented \pm SE)

grain yield by 40.75%, compared to control and this demonstrated that Shiraz cultivar was sensitive to source restriction. In the present investigation, removal of all leaves decreased the grain yield and its components more drastically, compared to leaving the flag leaf treatment (Table 1).

On the other hand, comparison of spike compactness in wheat cultivars showed that, Pishtaz had the minimum

spike compactness (1.35 compared to 2.44 spikelet cm^{-1} in Yavaros, Fig. 1). This might be associated with more sunlight penetration to the spike of this cultivar. Yavaros cultivar had maximum spike compactness (Fig. 1) and defoliation treatment affected yield and yield components of this cultivar negatively (Table 1). Furthermore, Pishtaz cultivar had large awns (8.2 cm) and awn photosynthesis might have contributed to grain filling under source restriction conditions. In Shiraz, Bahar, Sistan and Yavaros cultivars, 100-grain weight was significantly affected by defoliation of all leaves. In contrast, in Pishtaz the 100-grain weight was not affected by source restriction (Table 1).

Response to sink manipulation, by removal of 50 and 25% of spikelets, is shown in Table 1. As expected, in all cultivars, the number of grains per spike was decreased (24.36 in Sistan to 50.12% in Bahar cultivar) significantly by sink restriction treatments. In the present investigation, removal of 50% of spikelets caused reduction in number of grains per spike and main stem yield by 50.12 and 48.30% in Bahar cultivar, respectively.

Effects of source-sink manipulation on photosynthetic characteristics: In all cultivars except Pishtaz, sink restriction significantly decreased P_n rate (Table 2). Among the wheat cultivars, Yavaros showed minimum P_n rate after removing 50% of spikelets at 18 DAA (Table 2). In Pishtaz, stomatal conductance (g_s) of flag leaf was not

Table 2: Effect of source or sink manipulation on net photosynthesis rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (C_i) and transpiration rate (E) of wheat cultivars at 8 and 18 days after anthesis (DAA)

Wheat cultivars	Source-sink manipulation treatments	P_n ($\mu\text{mol CO}_2/\text{m}^2/\text{sec}$)		g_s ($\text{mol H}_2\text{O}/\text{m}^2/\text{sec}$)		C_i ($\mu\text{mol}/\text{CO}_2/\text{mol air}$)		E ($\text{mol H}_2\text{O}/\text{m}^2/\text{sec}$)	
		8 (DAA)	18 (DAA)	8 (DAA)	18 (DAA)	8 (DAA)	18 (DAA)	8 (DAA)	18 (DAA)
Shiraz	All leaves removed except the flag leaf	24.31a	25.11a	1.47b	1.61c	178.96c	210.31b	3.53b	3.67c
	25% spikelets removed	19.37i	18.44j	1.12f	1.01kl	150.14gh	148.73g	2.61e	2.52e
	50% spikelets removed	17.11l	16.81k	1.06gh	0.99l	147.97hi	131.21i	2.33g	2.12g
	Control	21.13e	22.86d	1.31c	1.53d	161.53e	202.32c	2.75c	2.94d
Bahar	All leaves removed except the flag leaf	19.93gh	19.98h	1.23e	1.75d	132.16k	167.94e	2.21h	2.93d
	25% spikelets removed	18.70k	18.33j	1.15f	1.09i	112.21l	110.25m	2.09i	2.12g
	50% spikelets removed	18.68k	18.51j	1.03ghi	1.02k	108.37m	101.43n	2.02i	1.87i
	Control	19.16ij	21.81e	1.11f	1.60d	113.27l	125.67j	2.11i	2.21f
Pishtaz	All leaves removed except the flag leaf	20.41fg	20.01h	1.13f	1.53d	176.92c	188.63d	1.83l	1.57j
	25% spikelets removed	20.3f	20.14h	1.02hi	1.55d	170.27c	180.25d	1.81l	1.62j
	50% spikelets removed	20.07fgh	20.12h	0.99ij	1.53d	171.12c	181.86d	1.80l	1.61j
	Control	20.46f	19.89h	1.07g	1.57d	176.37c	189.63d	1.83l	1.66j
Sistan	All leaves removed except the flag leaf	23.56c	23.89c	1.35c	1.39e	191.72b	203.83c	2.11i	2.25f
	25% spikelets removed	21.32e	21.09f	0.96j	0.86n	152.35g	121.96k	1.44n	1.13k
	50% spikelets removed	19.87h	19.21i	0.95j	0.78o	131.46k	117.45l	1.31o	1.13k
	Control	22.16d	23.17d	1.12f	1.14h	158.62f	168.99e	1.91k	2.03h
Yavaros	All leaves removed except the flag leaf	24.11ab	24.32b	1.33c	1.72d	205.85a	215.65a	3.66a	3.94a
	25% spikelets removed	16.86l	15.36l	1.14f	0.92m	113.52l	100.44n	2.53f	2.51e
	50% spikelets removed	16.12m	15.13l	1.03ghi	0.77o	109.66m	100.32n	2.21h	2.13g
	Control	23.91bc	24.63b	1.27d	1.68b	171.30d	181.84d	2.67d	3.73b

Means with the same letter in each column are not significantly different, using LSD test (0.05)

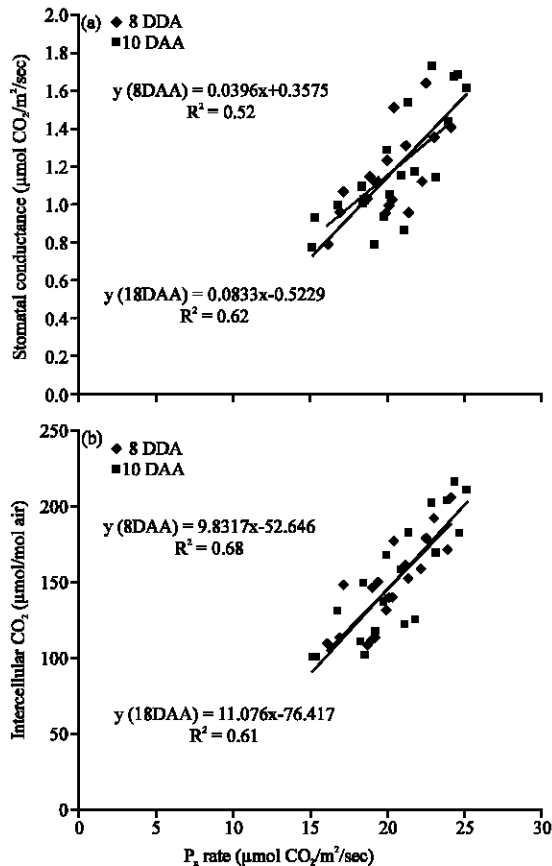


Fig. 2: Relationship between photosynthesis rate (P_n) of flag leaf with (a) stomatal conductance and (b) intercellular CO_2 concentration of wheat cultivars at 8 and 18 days after anthesis (DAA) under sink or source manipulation

affected by sink or source limitation after 18 DAA (Table 2). In addition, in other cultivars at 18 DAA, sink restriction decreased and source restriction enhanced g_s of the flag leaf. A significant positive relationship was found between P_n rate and g_s at 18 DAA ($R^2 = 0.62$) (Fig. 2a). Also, the relationship between P_n rate and C_i at 8 ($R^2 = 0.68$) and 18 DAA ($R^2 = 0.71$) was highly significant (Fig. 2b).

DISCUSSION

Among the cultivars, Sistan had the least reduction in the number of grains per spike (0.43 to 0.91%) under source restriction treatments after anthesis (Table 1). In the similar study, Chowdhary *et al.* (1999) reported that removal of all leaves in spring wheat caused reduction of 17.17 and 13.27% for number of grains per spike and 100-grain weight, respectively. Also, Singh and Singh (2002) studied the effects of defoliation of all leaves in wheat and reported 30 to 40% reduction in grain yield of the main shoot. Furthermore, Zhenlin *et al.* (1998) observed that removing one-half of the wheat leaves decreased main shoot yield by 15%.

The small response of main shoot yield to defoliation in Pishtaz cultivar (Table 1), suggests that photoassimilate supply by other parts of the crop has probably met most of the demand by the grains in this cultivar. Ahmadi *et al.* (2009) also noticed that Ghods wheat cultivar had a large spike with long awns and photoassimilate translocation from the leaf sheath, peduncle and lower internodes could support yield under source restriction. In this study, it appeared that the solar radiation could be utilized more

efficiently in Pishtaz cultivar by the spike parts (i.e., glumes, lemma, etc.) when the compactness of the ear is lower.

Removal of all leaves in Shiraz, was associated with the maximum reduction of 100-grain weight (26.88%). In a study with 20 wheat cultivars, Alam *et al.* (2008) found that Agrani and SAN-127 wheat cultivars showed high reduction in 100-grain weight, however, SAN-119, Shotabdi and Agrani cultivars were highly affected by defoliation treatments for number of grains per spike. Also, the cultivars SAN-119, Agrani and Shotabdi showed a significant decrease in grain yield of main shoot by defoliation treatments.

Under sink restriction conditions, the 100-grain weight of all cultivars except Pishtaz, was increased compared to control. This finding was in agreement with the result of Simmons *et al.* (1982), who reported that reduction in kernel number per spike of wheat increased the final seed weight, whereas defoliation reduced it. Alam *et al.* (2008) also declared that removal of 50% of spikelets decreased the number of grains per spike and main shoot yield by 41.03 and 37.01%, respectively; it also increased the 100-grain weight by 9.44%. Furthermore, they reported that removal of 25% of spikelets reduced the number of grains per spike and main shoot yield by 25.13 and 23.38%, respectively. This treatment also increased 100-grain weight by 4.08%. Roy and Salahuddin (1994) studied the effect of spikelet removal at anthesis in wheat and reported that spikelet removal increased the mean grain weight by 14%. Present results showed that under sink restriction conditions, all wheat cultivars except Pishtaz, had potential for further increase in their sink size i.e. increased 100-grain weight. Indeed, the lower response of Pishtaz cultivar to changes in assimilate availability might suggest that grain yield of this cultivar is more regulated by sink rather than the source size (Table 1).

Similar to our results, Ma *et al.* (1990) in an investigation with wheat crop, found that the partial degrading (removal of spikelets) decreased the number of grains per spike significantly (by 51%). Also, Ferdous and Shamsuddin (2001) also reported that removal of 50% of spikelets in spring wheat crop decreased the number of grains per spike and grain yield by 47.56 and 42.03%, respectively.

Indeed, the enhanced g_s of the flag leaf following source restriction, was due to feed back effect of the demand for assimilate by the sink (i.e., developing grains), also noted by other researchers (Ahmadi and Joudi, 2007; Emam and Seghatoleslami, 2005). Ahmadi and Joudi (2007) reported that leaf removal appeared to stimulate P_n rate and g_s of the remaining flag leaves. Similar results have

been reported by Wang *et al.* (1997), who declared that source restriction by partial defoliation of Winter wheat plants increased P_n rate of most leaves, however, the range of increase differed among cultivars. While, some cultivars like Lumai and Shannong showed slightly (not more than 10%) increase in P_n rate, in others, such as Hesheng and DO41 cultivars, defoliation markedly increased P_n rate. Our results suggest that photosynthetic characteristics including P_n rate, g_s , intercellular CO_2 concentration (C_i) and transpiration rate (E) differed among the cultivars and in Pishtaz at 8 and 18 DAA, C_i and E of flag leaf was not affected by source or sink restriction (Table 2).

According to our results, Rohi and Siose Mardeh, (2008) in the similar study with 20 wheat genotypes declared that P_n rate of flag leaf had strong positive relationship with g_s ($R^2 = 0.77$) and C_i ($R^2 = 0.73$) under drought stress conditions. Also, Koc *et al.* (2003) reported that increased P_n rate, was associated with increased g_s particularly at rapid grain filling stage, in durum wheat cultivars.

CONCLUSION

Generally, the present investigation demonstrated that in all cultivars, except Pishtaz, reduced source size was associated with reduced sink development, including grain number per spike, mean grain weight and consequently the grain yield. On the other hand, reducing sink size, by removal of spikelets had an increasing effect on mean grain weight, indicating the possibility of further increase in grain weight, if sufficient source is provided. Photosynthesis characteristics of flag leaf of Shiraz, Bahar, Sistan and Yavaros, were sensitive to source or sink manipulation. Pishtaz wheat cultivar, responded to source or sink manipulation slightly. This cultivar had large spike with long awns and the low spike compactness, probably photosynthesis by spike during the grain growth has had an important role in carbohydrate supply to the grain growth in defoliated plants, which is worthy of further explorations.

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