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Effects of source/sink manipulation on net photosynthetic rate and photosynthate partitioning during grain filling in winter wheat

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Abstract

Source-sink relationship, which was influenced by both genotype and environmental factors, contributed to the variation in photosynthesis and photosynthate partitioning of wheat. Source reduction by partial defoliation increased leaf net photosynthetic rate (P_N), and sink reduction decreased P_N of irrigated wheat. However, the change in P_N varied among genotypes. Source reduction enhanced photosynthate translocation into grain in irrigated wheat. However, the enhancement was more evident in cv. Lumai 215953 than in cv. Lumai 15. Sink reduction had little effect on the translocation of photosynthate into grain in cv. Lumai 15, but decreased the translocation of photosynthate into grain and increased it into stem in cv. Lumai 215953. In rainfed, non-irrigated wheat, the source or sink manipulation influenced P_N only slightly. The source reduction decreased the partitioning of photosynthates into the upper parts (including grains) of plant. However, very little effects of sink reduction on the production of photosynthates occurred in rainfed wheat. This showed that grain sink size was not a factor limiting the production of photosynthates, but controlled the partitioning of photosynthates. Sink reduction decreased photosynthate translocation into grains, and increased it into upper parts of rainfed wheat plant.

Additional key words: assimilates, cultivar differences, irrigation, translocation, *Triticum aestivum* L.

Introduction

The grain yield of wheat mainly depends on the formation, translocation, partitioning and accumulation of photosynthates during the grain filling. So, photosynthetic activity of leaves (source), and storage ability of grains after anthesis (sink) are the factors limiting the grain yield of wheat (Evans *et al.* 1975, Ma *et al.* 1990, Wang *et al.* 1996). Interrelationship between source and sink was found to

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Abbreviations: P_N - net photosynthetic rate, *RH, RQ* - plants with one half or one quarter of leaves removed, respectively, *RS* - plants with one quarter of spikelets removed.

differ among genotypes and under different environmental conditions (Xu 1985, 1987, Wu 1988, Wang *et al.* 1994, Wang 1996). Evans *et al.* (1975) reported that the leaf area duration was linearly related to the grain yield of wheat. Gifford *et al.* (1984, 1989) found that the increase in wheat grain yield depended mainly on increased translocation of photosynthate into sink. Austin and Bingham (1980) got similar results comparing the main winter wheat cultivars in England since 1970.

Source/sink relationship varies in different ecological conditions (Shanahan *et al.* 1983, Xu 1985, 1987, Wang *et al.* 1996). Shanahan *et al.* (1983) reported the limitation of sink size on grain yield of wheat genotypes at different places and under different nitrogen supply.

The aim of this paper was to characterise the effects of sink-source manipulation on net photosynthetic rate and photosynthate partitioning in irrigated and rainfed wheat during grain filling. We analysed the function of sink and source during grain formation and filling in different wheat cultivars to provide theoretical basis for growing the high-yielding wheat under irrigated or rainfed conditions.

Materials and methods

Plants and treatments: The chosen cultivars of high-yielding wheat (*Triticum aestivum* L.) were grown under usual agrotechnics in a randomized block design (plots 10 m^2) in a field at the experimental farm of the Shandong Agricultural University. Experiments with irrigated wheat cultivars Lumai 215953, Shannong 48-2, Lumai 15, Laizhou 953, Hesheng 2, DO41 and Tai 780 were performed in 4 replicates in vegetation periods 1993-1994 and 1994-1995, experiments with rainfed wheat cultivars Lumai 215953, Laizhou 953 and Hesheng 2 in 3 replicates in 1994-1995. At flowering, the following treatments were done on 40 stems: removal of one half of leaves (*RH*), removal of one quarter of leaves (*RQ*), and removal of one quarter of spikelets (*RS*); intact plants were controls.

Net photosynthetic rate: P_N was measured in 6 - 8 flag leaves at grain filling with portable photosynthesis apparatuses (*LCA-3, ADC,* Hoddesdon, England and *LI-6200, Li-Cor,* Lincoln, NE, USA). The whole plants of all variants were sampled at maturity and the dry matter partitioning into various parts was measured.

Partitioning of ^{14}C-photosynthates: The experiments with irrigated high-yielding cultivars Lumai 215953 and Lumai 15 were performed in 1989 and 1990. The same treatments were used as in measurements of P_N. Flag leaves of selected plants in all treatments were pulse-labelled with $^{14}CO_2$ at grain filling. Each leaf was enclosed into a chamber of transparent polyethylene film filled with 10 cm^3 of $^{14}CO_2$ (generated by acidifying $NaH^{14}CO_3$ solution with an excess of 50 % lactic acid; radioactivity 925 kBq dm^{-3}) and was left to photosynthesise for 30 min (10.00 local time) under natural light. Samples, including stem, leaf sheaths and ears, were harvested 3 d after labelling, killed at 105 °C, oven-dried at 80 °C and ground into powder. Samples (50 mg) were then used for determining the analysis of ^{14}C. The radioactivity of plant samples was determined by *FJ-2101* liquid scintillometer and calculated per unit dry mass of organ. The % radioactivity in each part was then determined.

Results and discussion

Source and sink manipulation effects on net photosynthetic rate

Irrigated wheat: Source reduction by partial defoliation increased P_N of most leaves, but the size of the increase differed among cultivars (Fig. 1). Some cultivars like Lumai 215953, Shannong 48-2, Lumai 14 and Laizhou 953 possessed slightly increased P_N, generally by not more than 10 % over control. In the other cultivars (Lumai 15, Hesheng 2, DO41, Tai 780) markedly increased P_N was found. P_N of *RQ* plants generally increased by 10 %, sometimes by nearly 20 %. P_N of *RH* plants rose by about 20 %.

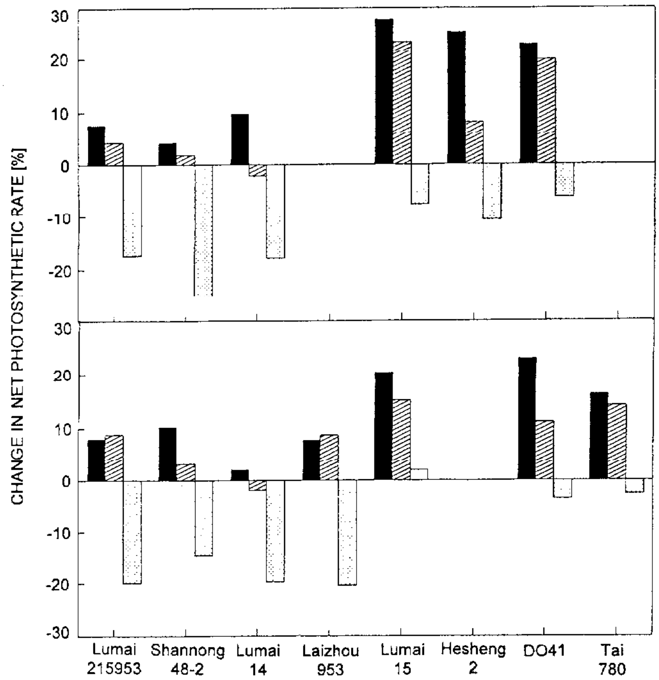

Fig. 1. Effects of sink and source manipulation on net photosynthetic rates in leaves of different cultivars of irrigated wheat in vegetation periods 1993-1994 (*top*) and 1994-1995 (*bottom*). *Full columns: RH* plants, *hatched columns: RQ* plants, *dotted columns: RS* plants. 0 - control.

The sink reduction by removal of some spikelets induced decline in P_N, different among cultivars (Fig. 1). In some cultivars like Lumai 15, Hesheng 2, DO41 and Tai 780 a 10 - 20 % increase in P_N was found. In the other cultivars, P_N varied in the range of -6 to 2 % of the control.

The above results allow to distinguish wheat cultivars into 2 types: sensitive cultivars (Lumai 14, Lumai 215953, Shannong 48-2 and Laizhou 953) and slowly reacting cultivars (Lumai 15, Hesheng 2, DO41 and Tai 780).

Rainfed wheat: The response of leaf photosynthesis to defoliation in rainfed wheat was similar to that of irrigated wheat. P_N of leaves slowly changed with source reduction. P_N of *RQ* in Lumai 215953, Laizhou 953, Hesheng 2 *etc.* was similar as in control. P_N of *RH* slightly rose.

Sink reduction slightly affected P_N of rainfed wheat (Table 1). P_N of *RS* in Lumai 215953 was similar to control. In cv. Laizhou 953 and Hesheng 2, only about 6 % decrease in P_N was found. Although only some cultivars were sensitive to sink reduction, P_N of majority of cultivars in rainfed wheat responded to partial sink removal. This indicates that water supply influenced the effects of source and sink manipulation on P_N. However, it seems that P_N in rainfed wheat depended more on other factors than on cultivars.

Table 1. Effects of source and sink manipulation on net photosynthetic rate, P_N, of leaves in rainfed wheat [μmol m^{-2} s^{-1}].

Treatment	Control	RH	RQ	RS	$LSD_{0.05}$
Lumai 215953	17.9	18.8	17.4	18.1	0.796
Laizhou 953	16.5	17.2	16.7	15.6	0.989
Hesheng 2	18.1	19.3	18.2	17.0	0.701

Source and sink manipulation effects on the partitioning of photosynthates

Irrigated wheat: There was a higher portion (50 - 60 %) of photosynthates translocated into grains at grains filling, but a certain portion (40 - 50 %) was translocated also into stem, sheath and leaves (Fig. 2). At this stage, partitioning of photosynthates varied significantly among cultivars. In Lumai 15, flag leaves supplied more photosynthates to grains, and less photosynthates to stem or sheaths

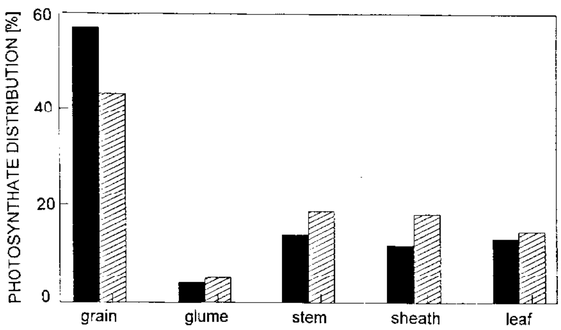

Fig. 2. Partitioning of ^{14}C photosynthates into different parts of wheat plants. *Full columns:* cv. Lumai 215953, *hatched columns:* cv. Lumai 15.

than those in Lumai 215953. There was similar partitioning of photosynthates into leaves of both cultivars. Source reduction increased the partitioning of photosynthates to leaves (Fig. 3). The grains of *RH* and *RQ* got particularly more photosynthates. However, the photosynthate amount varied among cultivars. Grains of Lumai 15 got less than 10 % more, and grains of Lumai 215953 nearly 20 % more photosynthates. Little variation of the translocation of photosynthates into glume occurred consistently between both cultivars after source was reduced. However, both cultivars indicated markedly lower amount of photosynthates translocated into stem and sheath. Yet source reduction had less effects on the translocation of photosynthates into leaf sheath in Lumai 15.

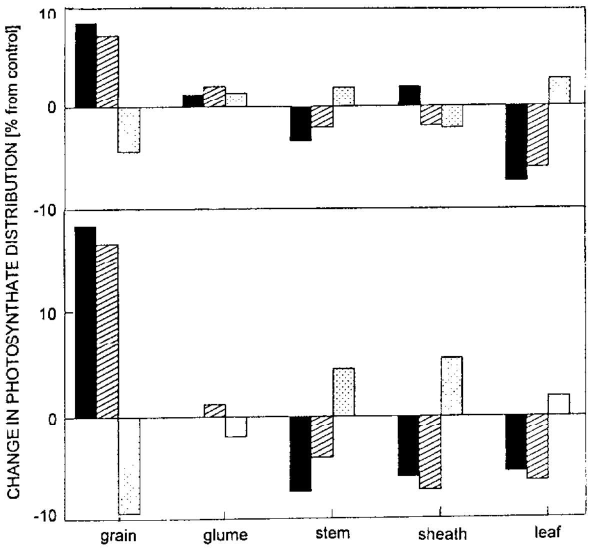

Fig. 3. Effects of sink and source manipulation on ^{14}C photosynthate partitioning in irrigated wheat plants of cv. Lumai 15 (*top*) and cv. Lumai 215953 (*bottom*). *Full columns: RH* plants, *hatched columns: RQ* plants, *dotted columns: RS* plants. 0 - control.

There were markedly different effects of sink reduction on the partitioning of photosynthates among cultivars (Fig. 3). Sink reduction had little effect on the translocation of photosynthate into grain in cv. Lumai 15, but decreased the translocation of photosynthate into grain and increased it into stem in cv. Lumai 215953 (Fig. 3).

Rainfed wheat: Plant dry mass of *RQ* at maturity declined by 8.4 - 10.1 % and grain mass by 10.1 - 14.1 % (Table 2). This was mainly due to the decreased translocation of photosynthates into grains, the 1st and 2nd internodes under ear, flag leaf sheath and leaf sheath under flag leaf. Plant dry mass of *RH* at maturity declined by 8.4 - 10.1 % and grain mass by 10.1 - 14.1 %. This agreed with *RQ*, but *RH* possessed more conspicuous effects of source reduction. In *RH* plants, the translocation of photosynthates into grains, internodes under ear, the 2nd internodes under ear and flag leaf sheath improved, while that into the other parts changed very little. This indicated the sensitive response of rainfed wheat to source reduction. The grain mass declined more rapidly than biological output after source reduction during grain formation. This indicates that the grain yield was more sensitive to source reduction

Table 2. Effects of source reduction on the partitioning of dry matter in rainfed wheat [mg per culm]. C - control.

Treatment		Lumai 215953				Laizhou 953				Hesheng 2			
		C	*RH*	*RQ*	*RS*	C	*RH*	*RQ*	*RS*	C	*RH*	*RQ*	*RS*
Grain		1301	1033	1117	1054	1505	1287	1353	1309	1601	1331	1391	1357
Glume		362	374	381	349	507	496	484	492	578	534	567	541
Internodes*	1	187	172	165	218	215	178	214	235	224	189	233	237
	2	194	166	168	218	195	161	187	211	207	172	192	214
	3	146	137	154	137	158	129	117	142	166	121	150	159
	4	104	98	110	107	136	119	121	137	109	111	97	103
	5	75	74	61	82	87	79	92	95	89	87	91	79
Sheaths*	1	142	124	132	182	151	121	157	178	191	148	184	217
	2	84	72	64	107	108	98	121	129	109	92	98	132
	3	52	48	57	45	79	72	80	67	57	73	65	71
	4	24	29	37	25	54	59	62	72	41	48	54	39
Leaves*	1	115	47	75	107	110	61	85	102	104	44	75	113
	2	75	40	51	84	98	42	67	114	76	37	56	94
	3	46	20	34	52	71	39	57	82	55	39	44	64
	4	13	11	20	21	39	19	21	27	35	21	32	44
Total		2920	2445	2626	2788	3513	2960	3218	3392	3642	3047	3329	3464

* from top to bottom

than biological output. There showed the same tendency of little effects of sink reduction (*RS*) on dry mass at maturity among cultivars of rainfed wheat. It is possible that other factors than sink size influenced dry matter production. Sink reduction resulted in 13.0 - 19.0 % decrease in grain mass and varying increase of internode under ear, the 2nd internodes under ear, flag leaf and the 2nd leaf sheath under ear. Sink reduction played little function in the partitioning of photosynthates in the middle and low parts.

Hence, sink size could affect the partitioning of photosynthates at grain forming of rainfed wheat. Sink reduction induced markedly decreased photosynthate partitioning to grain and increased it to the other shoot parts.

References

Austin, R.B., Bingham, J.: Genetic improvement in winter wheat yields since 1900 and associated physiological change. - J. agr. Sci. 94: 675-689, 1980

Evans, L.T., Wardlaw, I.F., Fischer, R.A.: Wheat. - In: Evans, L.T. (ed.): Crop Physiology. Pp. 101-149. Cambridge University Press, London - New York - Melbourne 1975.

Gifford, R.M., Thorne, J.H., Hitz, W.D., Giaguinta, R.T.: Crop productivity and photosynthate partitioning. - Science **225**: 801-808, 1984.

Krenzer, E.G., Moss, D.N.: Carbon dioxide enrichment effects upon yield components in wheat. - Crop Sci. **15**: 71-74, 1975.

Ma, Y.Z., Mackown, C.T., Van Sanford, D.A.: Sink manipulation in wheat: Compensatory changes in kernel size. - Crop Sci. **30**: 1099-1105, 1990.

Shanahan, J.F., Smith, D.H., Welsh, J.R.: An analysis of post anthesis sink limited winter wheat grain yields under various environments. - Agron. J. **76**: 611-615, 1983.

Wang Shuan, Wang Jihua, Liang Zhenxing: [Study on basic performance of source-sink in hybrid wheat.] - Acta agron. sin. **20**: 426-431, 1994. [In Chin.]

Wang Zhenlin, Yin Yanping, He Mingrong: [Partitioning of ^{14}C-photosynthate during grain filling, yield components and their relation to source-sink manipulation of late-sown winter wheat.] - Scientia Agr. sin. **29**: 50-58, 1996. [In Chin.]

Wu Jimin, Wu Zhaosu: [Evolution changes in the sink-source characters of wheat cultivars grown in the lower Yangtze valley.] - J. Nanjing Agr. Univ. **11**: 9-13, 1988. [In Chin.]

Xu Feng: [Ecological regularity of sink and source in wheat cultivars.] - J. Anhui agr. Coll. **10**: 1-12, 1985. [In Chin.]

Xu Feng: [Source-sink Structure and Photosynthetic Types of Wheat Cultivars, Advance on Theory and Practice of Wheat Breeding.] - Science Press, Beijing 1987. [In Chin.]

Yu Songlie: [Wheat in Shandong Province.] - Agricultural Press, Beijing 1990. [In Chin.]