PHOTOSYNTHETICA 35 (3): 453-459, 1998

Source-sink manipulation effects on postanthesis photosynthesis and grain setting on spike in winter wheat

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Abstract

Source-sink manipulation could regulate the net photosynthetic rate (P_N) of winter wheat after anthesis, however, the direction and magnitude of the regulation varied with time after anthesis. The P_N was significantly increased by source reduction at the initial time of grain filling, but sink reduction had little influence on the P_N, which suggested that the sink (spike) limitation did not occur at this time. Source-sink relation markedly affected P_N during rapid grain filling. The P_N was increased by source reduction and decreased by sink reduction significantly, which indicated that P_N was closely associated with the change of source or sink size. The effect of source-sink manipulation on P_N had some relationship with the occurrence of plant senescence at the time of late grain filling. Source reduction accelerated the senescence and dropped the P_N, meanwhile, sink reduction delayed the senescence and promoted the P_N. A direct relation between the effect of source-sink manipulation on P_N and stomatal limitation was not found. Removing one quarter of leaves (RQ) had little influence on spike development after anthesis. In this case there was enough compensation in source production through photosynthesis. Removing one half of leaves (RH) made grain mass per spike and mass of grains lowered, especially the grain mass in the top and base positions of spike declined markedly. The source supply was grain-limiting. Removing one quarter of spikelets (RS) was beneficial to grain-setting in the remaining spikelets, leading to the increase of grain mass. Thus promoting the source supply of photosynthates after anthesis is of major importance for grain to set and to develop.

Additional key words: dry matter accumulation; intercellular CO_2 concentration; leaf removal; senescence; spikelet; stomatal conductance; *Triticum aestivum* L.

Introduction

Photosynthesis of winter wheat after anthesis is the key subject on which many

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Received 29 September 1997, *accepted* 20 January 1998.

researchers have focused, because a close positive correlation exists between the production of photosynthates and grain yield (Evans *et al.* 1975, Patterson and Moss 1979, Guo *et al.* 1995). Therefore, promoting the postanthesis photosynthesis, leading to the increase in dry matter accumulation, is an effective approach to obtain higher yields (Yu 1990, Guo *et al.* 1995, Yue *et al.* 1996).

Source-sink relation, by which many physiological processes including photosynthesis are influenced, is important for the establishment of wheat grain yield (Patterson *et al.* 1980, Biswas *et al.* 1987, Guitman *et al.* 1991, Wang *et al.* 1997). Evans *et al.* (1975) showed that a large proportion of grain saccharides is derived from CO_2 fixation during the grain filling period, and there is a linear relationship between postanthesis leaf area duration and yield in wheat grown in a range of environments. However, some researchers suggest that wheat grain yield may be sink limited, but not source limited, during grain filling over a wide array of environments (Shanaha *et al.* 1984, Slafer and Savin 1994). Other papers demonstrate that wheat cultivars may be divided into two groups, the source-limited and the sink-limited, according to the response of wheat to source-sink manipulation in the formation of grain yield (Ma *et al.* 1990, Wang *et al.* 1996). The objectives of this research, therefore, were to (*1*) determine the effect of source-sink manipulation on the photosynthesis of wheat plant at different stages of grain filling, and (*2*) investigate the effect of source sink manipulation on the grain setting and grain mass distribution on spike at maturity, which would constitute the basic part of the theory for obtaining higher grain yields in wheat.

Materials and methods

A winter wheat cultivar, Lumai 22, with high-yielding potential was selected. Seeds of this cultivar were sown at the basal seeding rate of 8 g m^{-2} in a field at the Experimental Station of Shandong Agricultural University on 5 October 1994. Before planting, fertilizer was applied at 6 kg m^{-2} farmyard manure, 20 g m^{-2} N, 13 g m^{-2} P_2O_5, and 10 g m^{-2} K_2O. 20 g m^{-2} N was top-dressed at the stem elongation stage of wheat in the spring. The precise high-yielding cultivation system of Yu (1990) was used. At anthesis, the following treatments were made on at least 120 culms: removing one half of leaves (RH), removing one quarter of leaves (RQ), and removing one quarter of spikelets (RS). For control (C), the culms were left intact.

P_N, stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured in 8-10 flag leaves 5 (initial grain filling), 20 (rapid grain filling), and 30 (late grain filling) d after anthesis (DAA), respectively, with the *LI-6200* portable photosynthesis system (*Li-Cor*, Lincoln, NE, USA). Total chlorophyll (Chl) concentration in the flag leaves was determined in 80 % acetone according to Arnon (1949). A 1 cm^3 aliquot of leaf homogenate was taken before centrifugation and added to 4 cm^3 acetone. The solution was stored at 4 °C in the dark for 10 h, then centrifuged, and absorbance was measured spectrophotometrically. The total nitrogen concentration in flag leaves was measured by a semimicro-Kjeldahl method. The sample of 40 culms for each treatment was taken at maturity. The spike traits including grain setting and grain size distribution on spike were investigated according to Grieve *et al.* (1992) in order to ascertain the source-sink manipulation effect on spike yield components.

Results and discussion

Source-sink manipulation effects on photosynthesis

P_N: Postanthesis P_N of wheat was regulated by source-sink manipulation, but the direction and magnitude of this regulation markedly varied with time after anthesis (Fig. 1). At 5 DAA, P_N was very sensitive to source reduction. RQ and RH made P_N increase by 13 and 18 %, respectively, over control. Sink reduction (RS) had little influence on P_N, which suggested that the sink (spike) limitation did not occur at this time. During rapid grain filling (20 DAA), the source-sink relation was more apparent: compared with control, the P_N was increased by 16-17 % after source reduction and decreased by 10 % after sink reduction, which indicated that the P_N was closely associated with the change of source or sink size. At 30 DAA, the RQ and RH treatments slowed P_N of the leaf by 9 and 23 %, respectively, as compared with control. RS could delay leaf senescence and caused P_N rise by 12 % over control (Fig. 1). Hence the effect of source-sink manipulation on P_N was in a certain extent related to leaf senescence.

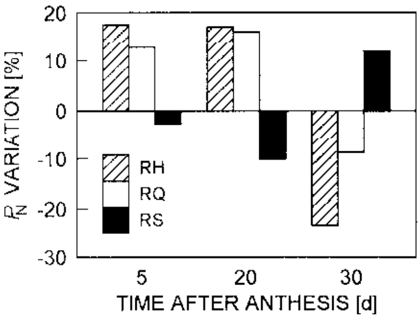

Fig. 1. Effect of source-sink manipulations (RH = half of leaves removed, RQ = quarter of leaves removed, RS = quarter of spikelets removed) on net photosynthetic rate (P_N) after anthesis as compared with control (0).

P_N variation with time after anthesis may reflect the senescence process of wheat. Source-sink manipulation significantly regulated P_N variation with time after anthesis (Fig. 2). During the early period of grain filling, P_N variation of source or sink reduction treatment was similar to that of control. P_N reached a peak for each treatment at 20 DAA, which was about 10 % higher than that at 5 DAA. Thereafter, P_N declined and source reduction induced a marked effect: at 30 DAA, P_N was only 48 or 60 % of that at 5 DAA in RQ or RH treatments. Sink reduction, on the contrary, was beneficial in keeping P_N high (86 % of that at 5 DAA in the RS treatment).

Table 1. Stomatal conductance (g_s) [cm s^{-1}] and intercellular CO$_2$ concentration (C_i) [cm^3 m^{-3}] in the leaves of winter wheat after anthesis (DAA = d after anthesis). C = control, RH = half of leaves removed, RQ = quarter of leaves removed, RS = quarter of spikelets removed.

Treatment	g_s			C_i		
	5 DAA	20 DAA	30 DAA	5 DAA	20 DAA	30 DAA
RH	4.71	4.53	2.29	299.7	297.4	318.0
RQ	4.91	4.27	1.92	294.3	288.1	322.1
C	4.82	4.23	2.91	303.2	298.4	312.3
RS	4.93	4.33	3.01	308.7	314.7	301.8

g_s and C_i: The effect of source-sink manipulation on P_N was related to changes of g_s and C_i to a certain degree (Table 1). The differences in values at 5 DAA were very small and thus g_s or C_i were not P_N-limiting. At 20 DAA the sink reduction caused C_i to increase obviously, which indicated that P_N decrease was associated with the decline of photosynthetic activity in mesophyll cells when sink was reduced. At 30 DAA in source reduction treatments compared with control, C_i rose a little although g_s dropped evidently, and after sink reduction g_s slightly increased and C_i slightly decreased. Thus the P_N decrease after source reduction may be induced by the decline of photosynthetic activity in mesophyll cells, and *vice versa.*

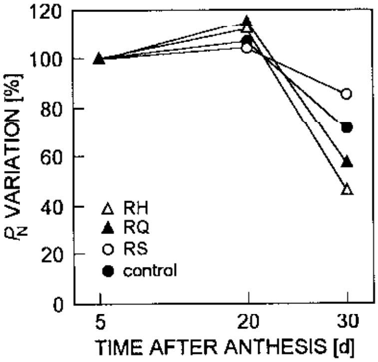

Fig. 2. Effect of source-sink manipulations (C = control, RH = half of leaves removed, RQ = quarter of leaves removed, RS = quarter of spikelets removed) on net photosynthetic rate (P_N) variation related to the 5th d after anthesis.

The responses of Chl and N concentrations in leaves to source-sink manipulation were similar (Fig. 3), negligible at 5 DAA and more expressed afterwards, when the source reduction caused the concentrations of Chl and N in leaves to drop sharply, which indicated accelerated senescence. Meanwhile, the concentrations of Chl and N declined slowly after 20 DAA in the RS treatment, which was beneficial to prolong the leaf function and delay senescence. There was a significant positive correlation between the concentrations of Chl or N and P_N at 30 DAA (Fig. 4) which demonstrated a large effect of source-sink manipulations on these characteristics.

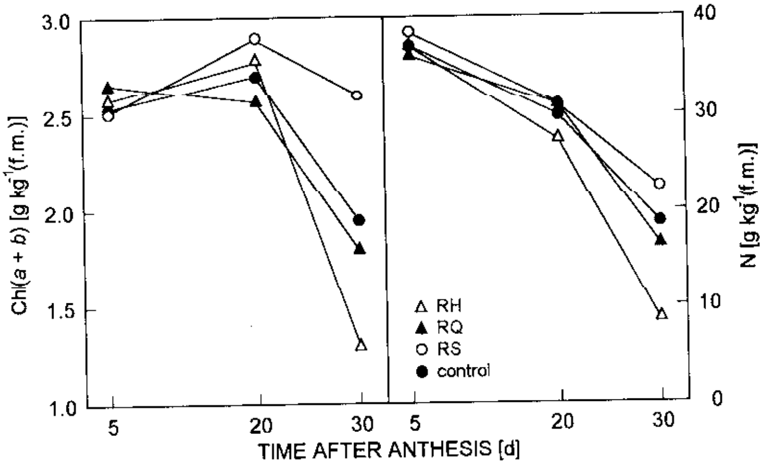

Fig. 3. Effect of source-sink manipulations (C = control, RH = half of leaves removed, RQ = quarter of leaves removed, RS = quarter of spikelets removed) on chlorophyll (Chl) and nitrogen (N) contents in flag leaf of wheat.

Source sink manipulation effects on spike characteristics

Spikelet number and grain number per spike: There was little influence of source reduction on spikelet number and grain number per spike (SPS and GPS). Sink reduction induced a significant decrease in GPS, but the magnitude of the decrease was less than 20 % of control although 25 % of spikelets on spike were removed at the very onset of flowering (Table 2). Thus a compensatory response in GPS to sink reduction existed to a certain extent.

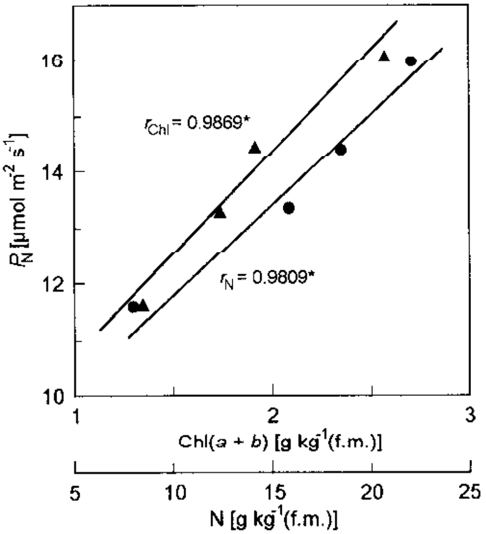

Fig. 4. Relation of net photosynthetic rate (P_N) to contents of chlorophyll (Chl) and nitrogen (N) at 30 d after anthesis in flag leaf of wheat. *Significant at $p = 0.05$.

Table 2. Effects of source-sink manipulation on spike characteristics of winter wheat. SPS = spikelets per spike, GPS = grains per spike, MPS = grain mass per spike [g(d.m.)], MPG = mass per grain [mg(d.m.)], C = control, RH = half of leaves removed, RQ = quarter of leaves removed, RS = quarter of spikelets removed. Means followed by the same letter are not significantly different at $p = 0.05$.

Treatment	SPS	GPS	MPS	MPG
RH	19.43 a	45.22 a	1.98 a	43.01 a
RQ	19.86 a	45.78 a	2.29 b	50.65 b
C	20.14 a	45.66 a	2.35 b	51.10 b
RS	15.17 b	37.78 b	2.07 a	55.21 c

Grain mass per spike and mass per grain: The effect of source reduction on grain mass per spike (MPS) and mass per grain (MPG) varied with the magnitude of source reduction. MPS and MPG were unaffected by RQ, but significantly reduced by RH. In the RS treatment, the MPS was significantly lower and MPG significantly higher than in the control (Table 2).

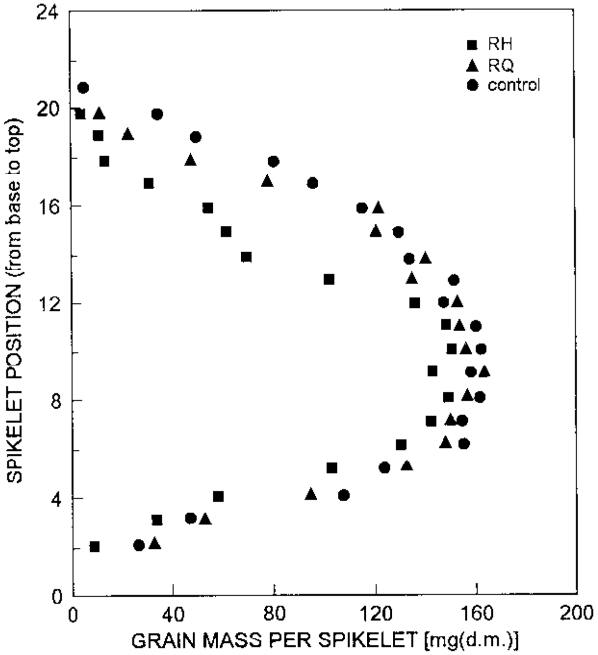

Fig. 5. Effect of source reduction on grain mass per spikelet on spike. C = control, RH = half of leaves removed, RQ = quarter of leaves removed.

Grain mass distribution: The MPS in the middle parts of spike in the RQ and RH treatments was not significantly different from that of control. These grains were a predominant sink in dry matter accumulation, especially when the source supply was limited. As for the upper spikelets on spike, RQ had no striking influence on MPS except the up-most three spikelets, in which the grain mass was significantly reduced by RQ. RH resulted in a marked decrease of MPS in the upper spikelets on spike. Source reduction also decreased MPS in the base spikelets on spike in a similar way (Fig. 5). The effect of source reduction on MPS is in the order upper>base>middle spikelets on spike in this study. Thus we can conclude that promoting the source supply of photosynthates after anthesis is of most importance for grains to set and to develop, which is necessary for obtaining higher grain yield of winter wheat. The sink capacity and source strength in wheat are highly independent similarly as in maize (Wang *et al.* 1996).

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