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Wheat (*Triticum aestivum* L.) grain filling and dry matter partitioning responses to source:sink modifications under postanthesis water and nitrogen deficiency

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ABSTRACT. Re-translocation of stem and spike reserves was investigated in source:sink restricted wheat subjected to water and nitrogen deficiency during seed filling. Either sink or source restriction significantly decreased the amount of current photosynthesis and its contribution to grain yield. Furthermore, source limitation increased stem and spike reserves contribution to seed filling process. Higher amount of stem reserve mobilization in source restricted vs. control and sink restricted plants indicates that at rapid grain filling stage (14 days after anthesis to physiological maturity), stem dry matter decreases to provide assimilates for kernel after defoliation. In spike halved plants, drought stress significantly decreased grain yield, indicating that when the sink is restricted, postanthesis drought stress can increase sink limitation through lower grain filling rate and dry matter allocation to grain two weeks after anthesis at the beginning of rapid grain filling stage. On the other hand, in spike halved plants, more nitrogen supply at anthesis increased grain yield because more dry matter allocation to grain is not associated with more current photosynthesis. But when all the leaves were removed except flag leaf, more postanthesis nitrogen could not increase dry matter allocation to grain filling process, showing that postanthesis nitrogen supply increases grain yield by decreasing sink limitation, and not by increasing source strength.

Key words: current photosynthesis, dry matter allocation, grain filling rate, stem reserves, wheat (*Triticum aestivum* L.).

RESUMO. Enchimento de grãos de trigo (*Triticum aestivum* L.) e respostas da partição de matéria seca às modificações fonte:dreno sob deficiência de água e nitrogênio após a antese. A retranslocação de reservas do colmo e espiga foi investigada com relação às restrições de fonte e dreno em plantas submetidas à deficiência de água e nitrogênio durante o enchimento de grãos. A fotossíntese e a sua contribuição para a produtividade foram reduzidas por ambas restrições. As restrições na fonte aumentaram a contribuição das reservas do colmo e da espiga. A maior mobilização de fonte sob restrição versus o controle e o dreno sob restrição indica que, no período de maior enchimento, a matéria seca do colmo foi reduzida por fornecer os assimilados após a restrição. Nas espigas reduzidas, a produtividade foi afetada pelo estresse hídrico indicando que após a antese o estresse pode aumentar a limitação por causa de taxas mais altas de enchimento e translocação de matéria seca duas semanas após a antese. Nas espigas reduzidas, o maior fornecimento de nitrogênio durante a antese elevou a produtividade porque maior translocação de matéria seca não está associada à maior fotossíntese. O nível mais alto de nitrogênio não foi capaz de aumentar a translocação quando todas as folhas, exceto a bandeira, foram removidas. Isso demonstra que o fornecimento de nitrogênio, após a antese, aumenta a produtividade por reduzir a limitação do dreno e não por aumentar a força da fonte.

Palavras-chave: fotossíntese corrente, alocação de matéria seca, taxa de enchimento de grãos, reservas do colmo, trigo (*Triticum aestivum* L.).

Introduction

Improving the capacity for supporting grain filling by stem and spike reserves is an important physiological trait and breeding target in wheat (BLUM)

(BLUM, 1998). Ehdaie et al. (2006) noted that wheat crops in dry land areas may depend more on stem reserves for grain filling than on current photosynthesis. Palta et al. (1994) found that total grain carbon with fast development of water deficit was

reduced by 24% relative to slow rate, whereas postanthesis assimilation was reduced by 57% while remobilization of reserves was increased by 36%. Postanthesis nitrogen and drought stress decrease grain yield of wheat through sink strength and source capacity (YANG et al., 2002; SCHAPENDONK et al., 2007). So, wheat breeding programs for developing wheat genotypes that can recover from postanthesis stresses require improved understanding of source:sink relationship physiological process and modeling research on source:sink interactions that determine the magnitude of multiple stresses on grain growth (SPIERTZ et al., 2006; GARCIA DEL MORAL et al., 2007). On the other hand, narrowing the gap between genetic potential and phenotypic expression need knowledge about the effects of source:sink manipulation on net photosynthetic rate and photosynthate partitioning during grain filling in winter wheat (BARNABAS; FEHER, 2008; REYNOLDS; TRETOWAN, 2007).

Wang et al. (1997) showed that source reduction caused a decrease in the allocation of dry matter to the sheath and stem, and promoted the reserve photosynthates to be reallocated to grain. The effect of sink reduction was contrary, indicating that grain sink size was not a factor limiting the production of photosynthates, but controlled the partitioning of photosynthates. Avaro et al. (2007) noted that defoliation did not alter dry matter translocation from the main stem, as the reduction in translocation of leaf blades was compensated with translocation increases from the chaff. Sink demand determined Dry matter translocation that was mostly regulated by the stem. Yang et al. (2001) reported that at maturity, 75 to 92% of pre-anthesis carbon stored in straw was reallocated to grain under Postanthesis drought stress. Yang et al. (2000) concluded that senescence induced by controlled soil drying during grain filling can promote the remobilization of presorted assimilates to the grains, accelerate grain filling, and improve yield in cases where senescence is unfavorably delayed by heavy use of nitrogen. An increased knowledge of the source:sink regulatory mechanisms controlling plant nitrogen and water economy is vital for improving nitrogen and water use efficiency and for reducing excessive input of fertilizers and irrigation, while maintaining an acceptable yield. Hence, the objective of this study was to investigate re-translocation of stem and spike reserves in source:sink restricted wheat subjected to water and nitrogen deficiency during seed filling stage. On the other hand, there is strong evidence for sink limitation in modern wheat cultivars under postanthesis drought stress, and it appears that

postanthesis nitrogen supply increases grain yield by decreasing sink limitation, and not by increasing source strength. So, in wheat, traits associated with spike fertility appear to be more usable than source strength related traits for routine screening of postanthesis drought stress tolerance and nitrogen deficiency adaptation (BRUCKNER; FROBERG, 1991). This hypothesis was tested using both source and sink restriction treatments.

Material and methods

Plant material and growth conditions

This study was conducted for an improved understanding of source-sink relationship under postanthesis environmental stresses in Chamran winter wheat cultivar. The experiment was carried out in Ramhormoz, Iran, during 2008. The site is located at 31°16' N latitude, 49°36' E longitude, with an altitude of 151 m above the sea level. This region has a semi-arid climate (329 mm rainfall yearly). The soil of the experimental site was clay loam with a clay type of montmorillonite, low in nitrogen (0.04 - 0.05%), low in organic matter (0.9 - 1%) and alkaline in reaction with a pH of 7.8 and $E_c = 0.44 \text{ dS m}^{-1}$.

Experimental design

The experiment was laid out in a randomized complete block design with split factorial arrangement with three replications. Soil water contents were allotted to main plots. Source:sink restriction and postanthesis nitrogen supply were allotted to subplots.

Water control in the soil

Gypsum blocks, consisting of two rectangular electrodes embedded in a block of gypsum with wires attached to each electrode, extruded from gypsum block and compared to the tensiometer, were used for measuring the soil water tension. Gypsum blocks located at several depths in the soil near fibrous root zone were used to determine when to begin and when to turn off the irrigation depending on the irrigation strategy. For installation of the gypsum blocks, the hole was augured at angles of 45 degrees to the horizontal plane to prevent preferential water penetration down the backfilled augured hole.

Postanthesis drought stress treatment

Before anthesis, all the experimental units were irrigated uniformly when the water soil content reached 75% of field capacity (FC)-wilting point (WP). After anthesis, control and under-water stress plots were irrigated when the soil water content

decreased to 75 and 25% of field capacity (FC) - wilting point (WP), respectively.

Postanthesis nitrogen deficiency treatment

In all three nitrogen deprivation levels, a quarter of total nitrogen was top dressed at planting and a quarter of it at tillering. In N1, N2 and N3, 0, 25 and 50% of remaining needed nitrogen was applied at anthesis, respectively.

Source:sink manipulation treatment

Source:sink restriction at anthesis consisted of four defoliation levels (control, removal of flag leaf, removal of all leaves but not the flag leaf, and removal of all leaves) and one spike halving.

Experimental units and agronomic practices

A subplot size of 2 x 5 m, having 4 rows 5 m long was used and sowing was done on both sides of hills at the rate of 450 plants per square meter. Uniformity of sowing depth was achieved by using a hand dibbler to make 3-5 cm deep holes. The spaces between rows were 50 cm wide. Within each plot, an area of 2 m² was hand harvested to estimate grain yield. After anthesis to physiological maturity, a weekly random sample of 30 plants was chosen from two middle rows to record biomass accumulation and its allocation to stem and leaf, grain and straw of spike during seed filling period. Dry weights were recorded after the plant material had been oven dried at 70°C for 48 hours.

Growth parameters measurement:

The following formulas were used for calculating some physiological traits:

1. Amount of stem reserves mobilization to grain (t ha^{-1}) = maximum stem dry matter after anthesis (t ha^{-1}) - stem dry matter at maturity (t ha^{-1});
2. Amount of spike reserves mobilization to grain (t ha^{-1}) = maximum straw of spike dry matter after anthesis (t ha^{-1}) - straw of spike dry matter at maturity (t ha^{-1});
3. Stem reserve contribution to grain yield (%) = (amount of stem reserves mobilization to grain (t ha^{-1}) / grain yield (t ha^{-1})) \times 100;
4. Spike reserve contribution to grain yield (%) = (amount of spike reserves mobilization to grain (t ha^{-1}) / grain yield (t ha^{-1})) \times 100;
5. Amount of current photosynthesis for grain filling (t ha^{-1}) = grain yield (t ha^{-1}) - amount of stem and spike reserves mobilization to grain yield (t ha^{-1});
6. Current photosynthesis contribution to grain yield (%) = (amount of current photosynthesis for grain filling (t ha^{-1}) / grain yield (t ha^{-1})) \times 100;
7. Stem reserves utilization for grain filling

(%) = (amount of stem reserves mobilization to grain (t ha^{-1}) / maximum stem dry matter after anthesis (t ha^{-1})) \times 100;

8. Spike reserves utilization for grain filling (%) = (amount of spike reserves mobilization to grain (t ha^{-1}) / straw of spike dry matter after anthesis (t ha^{-1})) \times 100.

Statistical analysis

Collected data was statistically analyzed using analysis of variance technique appropriate for randomized complete block design with postanthesis nitrogen supply and source:sink restriction factors split on irrigation strategy, and Duncan's multiple range test ($p < 0.05$) was employed for mean separation when F values were significant.

Results and discussion

Our results indicate that future yield improvements may be achieved by strengthening the sink capacity. Either sink or source restriction significantly decreased the amount of current photosynthesis and its contribution to grain yield (Tables 1 and 2). This confirmed the hypothesis that photosynthetic rate is apparently underutilized in modern cultivars and that radiation use efficiency (RUE) during grain filling can be increased through increasing number of grains per spike. In addition, it has recently been reported that increased post-anthesis biomass can be achieved by increased sink strength through positive feedback to photosynthesis (REYNOLDS et al., 2005).

Source limitation increased stem and spike reserves contribution to seed filling process (Tables 1 and 2). The findings indicate that, while the demand by the growing kernel is increasing and current assimilation is diminishing due to natural senescence and the effect of various stresses (BLUM, 1998), an important source of carbon for grain filling is the stem and spike reserves. Neither source nor sink restriction had any impact on the amount of total stem and spike reserves mobilization to grain, but source-restricted plants had a higher amount of both stem and spike reserves mobilization to grain yield vs. control and sink restricted ones (Tables 1 and 2). Our results suggest that the demand by the grain yield sink is a primary factor in determining stem reserve mobilization. Thus, shading of barley plants after anthesis promoted the use of stem reserves for grain filling (BONNETT; INCOLL, 1992) and when wheat plants were shaded during grain filling, up to 0.93 gram of grain was produced per gram of

assimilates exported from the stem (GENT, 1994). Source:sink ratios had no impact on maximum stem dry matter after anthesis (14 days after anthesis), showing that at the initial grain filling stage, the current photosynthesis was enough for kernel demand (Tables 1 and 2). But Yin et al. (1998) reported that at the first half of grain filling period, wheat was sensitive to source reduction leading to an increase of net photosynthetic rate by 10%; however, little effect of sink reduction was observed. Higher amount of stem reserve mobilization in source restricted vs. control and sink restricted plants indicates that at rapid grain filling stage (14 days after anthesis to physiological maturity), stem dry matter decreases to provide assimilates for kernel after defoliation (Tables 1 and 2). Grain yield of wheat is determined in part by kernel weight, which is a function of the rate and duration of grain fill (MOU; KRONSTAD, 1994). But in our study, source:sink ratio had no influence on seed filling period and rate (Tables 1 and 2), indicating that the grain mass was strictly regulated by source/sink changes.

However, Alvaro et al. (2007) reported that

degraining increased grain weight by up to 15%. Either source or sink restriction increased dry matter allocation to stem and leaf and decreased its allocation to grains two weeks after anthesis (Tables 1 and 2). It seems both source and sink reduction promote the allocation of dry matter to the sheath and stem, and decrease the reserve photosynthates to be reallocated to grain. No difference was noted between control and source:sink manipulated plants for allocation of dry matter to straw of spike at the beginning of rapid grain filling stage, but maximum straw of spike dry matter after anthesis significantly decreased after source:sink manipulation (Tables 1 and 2), indicating that glumes and awns can be effective on grain growth during first half of seed filling period, but after this period, demand of kernel needs a stronger dry matter supporter, i.e. stem reserves.

So, the stem reserves contribution to grain yield in control plants was 15.20 times more than spike reserves contribution (Table 2). Stem reserve utilization for grain yield was affected by neither source nor sink restriction (Tables 1 and 2).

Table 1 Mean squares of source:sink manipulation at anthesis, postanthesis nitrogen and water supply effects on some agronomic and physiological traits of winter wheat (*Triticum aestivum* L.).

S.O.V	d.f	Current photosynthesis contribution to grain yield (%)	Stem and spike reserve contribution to grain yield (%)	Stem reserve contribution to grain yield (%)	Spike reserve contribution to grain yield (%)	Amount of current photosynthesis for grain filling (t ha ⁻¹)	Amount of stem and spike reserve mobilization to grain (t ha ⁻¹)	Amount of stem reserve mobilization to grain (t ha ⁻¹)	Amount of spike reserve mobilization to grain (t ha ⁻¹)	Stem reserve utilization for grain filling (%)	Spike reserve utilization for grain filling (%)
Replication	2	137.032ns	136.283ns	127.099ns	0.191ns	0.208ns	0.927ns	0.274ns	0.0001ns	61.445ns	0.942ns
W	1	25284.488**	25659.00**	22749.414**	66.936**	86.031**	0.514ns	1.352ns	0.0001ns	617.922ns	3.269ns
Error (Ea)	2	92.681	88.407	81.726	0.480	0.171	0.690	0.177	0.0001	39.572	2.164
N	2	378.488**	368.297**	320.334**	2.479*	1.478**	0.223ns	0.008ns	0.0001ns	0.024ns	3.613ns
S	4	2546.149**	2559.418**	2188.563**	14.023**	12.941**	0.322ns	0.584**	0.005**	51.518*	24.168**
W × N	2	12.580ns	14.102ns	12.586ns	0.109ns	0.155ns	0.477ns	0.056ns	0.001ns	0.891ns	5.365ns
W × S	4	1235.888**	1218.772**	1136.499**	3.756**	7.814**	1.912**	1.591**	0.006**	303.921**	23.849**
N × S	8	53.322ns	52.216ns	49.263ns	1.593*	0.337**	0.166ns	0.109ns	0.001ns	42.009ns	5.190ns
W × N × S	8	84.993ns	81.906ns	68.583ns	1.713*	0.286*	0.235ns	0.106ns	0.002**	15.689ns	6.106ns
Error (Eb)	56	53.430	52.195	47.128	0.629	0.113	5.257	0.0603	0.0001	17.338	3.632

W, N and S: postanthesis water supply, postanthesis nitrogen supply and source: sink manipulation at anthesis, respectively; **, * and NS indicate significance at 0.01, 0.05 and lack of significance at 0.05, respectively.

Table 2. Mean comparison of some agronomic and physiological traits of winter wheat (*Triticum aestivum* L.) as affected by postanthesis water supply, postanthesis nitrogen supply and source:sink manipulation at anthesis.

	Maximum straw of spike dry matter after anthesis (t ha ⁻¹)	Grain Yield (t ha ⁻¹)	Grain filling period (day)	Grain filling rate (mg day ⁻¹)	Dry matter allocation to straw of spike two weeks after anthesis (%)	Dry matter allocation to grain two weeks after anthesis (%)	Dry matter allocation to stem and leaf two weeks after anthesis (%)	Maximum stem dry matter after anthesis (t ha ⁻¹)
W1	1.56a	4.19a	25.95a	1.58a	13.72b	18.08b	68.15a	9.09a
W2	1.41b	2.48b	25.21a	1.33b	16.28a	14.23a	69.49a	8.14b
N1	1.46b	3.19b	25.77a	1.47a	14.90a	15.48b	69.62a	8.73a
N2	1.47ab	3.25b	25.02a	1.50a	14.92a	16.04ab	69.01a	8.58a
N3	1.53a	3.57a	25.96a	1.40a	15.18a	16.93a	67.84a	8.53a
S1	1.64a	4.46a	25.76	1.41b	15.21a	20.08a	64.62b	8.49a
S2	1.53b	3.81b	24.85a	1.45b	14.66a	17.15b	68.15a	9.01a
S3	1.43c	2.95c	25.16a	1.44b	14.79a	14.82c	70.39a	8.78a
S4	1.39c	2.50d	25.43a	1.36b	15.29a	13.75c	70.96a	8.35a
S5	1.45c	2.97c	26.69a	1.61b	15.05a	14.97c	69.98a	8.45a

W1 and W2: postanthesis moderate irrigation and postanthesis water deficiency, respectively; N1: 25% planting, 25% tillering, 0% anthesis (50% postanthesis nitrogen deficiency); N2: 25% planting, 25% tillering, 25% anthesis (25% postanthesis nitrogen deficiency); N3: 25% planting, 25% tillering, 50% anthesis (0% postanthesis nitrogen deficiency); S1, S2, S3, S4, and S5: not source-sink manipulation, removal of flag leaf, removal of all leaves but not flag leaf, removal of all leaves and ear halving, respectively; *Means of the same category followed by different letters are significantly different at 0.05% levels of probability using Duncan test.

In any way, source restricted plants had greater reserves remobilization efficiency from stem to grain than sink restricted plants (Table 2). Source size significantly increased spike reserves utilization for grain filling process but sink restriction had no impact on it (Table 2). Sufficient nitrogen supply significantly increased the amount of current photosynthesis and its contribution to grain yield and decreased both stem and spike reserves contribution to grain yield, but it had no impact on seed filling rate and period (Tables 1 and 2). This might indicate that at higher rates of nitrogen availability, nitrogen does not need to be translocated from vegetative plant parts to filling grains as efficiently as in the case where nitrogen could not be taken up from the soil and the higher enzyme content of Rubisco in leaves increase radiation use efficiency (MUURINEN et al., 2006). Similarly, Gebbing and Schnyder (1999) showed that partitioning of pre-anthesis C among the grain fractions was strongly dependent on the carbon/nitrogen ratio in mobilized pre-anthesis biomass ($r^2 = 0.92$). On the other hand, more nitrogen supply after anthesis increased dry matter allocation to grain two weeks after anthesis (Tables 1 and 2). Hence, it seems that significantly lower grain yield under postanthesis nitrogen deficiency is mostly related to decreased fertile florets, i.e. the number of grains per spike, rather than decline in grain weight. It may be occurred more limited sink than source under conditions of both water and nitrogen limitation, in particular after flowering. It can be explained by the fact that the increased number of grains per unit area is attributed to greater survival of floret primordia (ARAUS et al., 2007). Thus, the higher survival of floret primordia under stress and unstressed conditions is the most important factor leading to higher yield potential.

Nitrogen supply had no influence on maximum stem dry matter after anthesis and dry matter allocation to it two weeks after anthesis, but increased maximum straw of spike without any effect on dry matter allocation to it (Tables 1 and 2). This result suggests that more postanthesis nitrogen supply at anthesis increases the current photosynthesis and decreases demand for stem and spike reserves. Postanthesis nitrogen supply had no impact on the amount of spike or stem reserves mobilizations to grain and their reserves utilization for grain filling process (Tables 1 and 2). Drought stress increased both stem and spike reserves contribution to grain yield and decreased current photosynthesis contribution to grain

demand and its amount for grain filling, but had no impact on the amount of reserves mobilization from these organs to grain and their reserves utilization for grain filling process (Tables 1 and 2). However, Ehdaie et al. (2006) believed that drought increased mobilization efficiency, expressed as percentage of maximum dry matter mobilized, in the peduncle. Drought stress had no effect on dry matter allocation to stem and leaf two weeks after anthesis at beginning of rapid seed filling period but decreased maximum stem dry matter two weeks after anthesis (Tables 1 and 2). Both dry matter allocations to grain and straw of spike increased under postanthesis drought stress, but grain filling rate and maximum straw of spike dry matter after anthesis decreased (Tables 1 and 2). It seems that early senescence caused by postanthesis water deficit reduces current photosynthesis and grain filling rate, and eventually results in reduction of grain weight. Inoue et al. (2004) reported that remobilization of pre-anthesis assimilates to the grain was increased and the contribution of pre-anthesis assimilates to the grain decreased under non-irrigated treatment. Flag leaf removal under postanthesis drought stress had no significant effect on current photosynthesis distribution to grain yield but under moderate irrigation, it significantly decreased this trait, indicating that source strength is not limited under water stress conditions (Table 3). Hence, it seems that determination of postanthesis source limitation does not appear to be a usable technique of routine screening of diverse wheat germplasm for postanthesis drought stress tolerance due to a poor association of source limitation and postanthesis drought stress (MUURINEN et al., 2007). On the other hand, ear halving decreased dry matter allocation to grain two weeks after anthesis in both irrigation strategies, indicating that sink strength is limited in all soil water contents (Table 3). In spike halved plants, drought stress significantly decreased grain yield, which indicates that when the sink is restricted, postanthesis drought stress can increase sink limitation through lower grain filling rate and dry matter allocation to grain two weeks after anthesis at the beginning of rapid grain filling stage (Table 3). On the other hand, in spike halved plants, more nitrogen supply at anthesis increased grain yield, because it caused more dry matter allocation to grain, but not more current photosynthesis (Table 3).

It showed that additional top-dressing nitrogen is applied between the panicle primordia initiation stage and the late stage of spikelet initiation, appears to be the most effective for floret and spikelet production. However, when all the leaves were removed except flag leaf, more postanthesis nitrogen could not increase dry

matter allocation to grain filling process (Table 3), which shows that postanthesis nitrogen supply increases grain yield through decrease in sink limitation, rather than increase in source strength.

Table 3. Mean comparison of some agronomic and physiological traits as affected by postanthesis water supply and postanthesis nitrogen supply interactions with source: sink manipulation at anthesis.

	Grain Yield (t ha ⁻¹)	Current photosynthesis contribution to grain yield (%)	Dry matter allocation to grain two weeks after anthesis (%)	Grain filling rate grain (mg day ⁻¹)
Postanthesis water supply x source sink manipulation at anthesis				
W1 x S1	5.84a	81.64a	22.61a	1.44b
W1 x S2	4.75b	64.34b	17.61bc	1.56ab
W1 x S3	3.73c	41.23c	16.94bc	1.67a
W1 x S4	2.85d	30.98d	15.38c	1.50ab
W1 x S5	3.81c	63.39b	17.84b	1.71a
W2 x S1	3.07d	27.31d	17.56bc	1.39bc
W2 x S2	2.86d	24.92de	16.69bc	1.34bc
W2 x S3	2.17e	18.73e	12.70d	1.20c
W2 x S4	2.15e	19.20e	12.12d	1.22c
W2 x S5	2.14e	23.80de	12.09d	1.50ab
Postanthesis nitrogen supply x source sink manipulation at anthesis				
N1 x S1	4.26b	51.95ab	15.34ab	1.47abcd
N1 x S2	3.54c	38.26cd	16.43ab	1.53abc
N1 x S3	3.06d	30.18de	15.92ab	1.55abc
N1 x S4	2.33f	22.49e	13.86ab	1.36cd
N1 x S5	2.77de	42.87c	12.96b	1.44bcd
N2 x S1	4.42ab	53.73ab	15.67ab	1.40bcd
N2 x S2	3.51c	41.74c	13.69b	1.52abc
N2 x S3	2.82de	29.03e	14.16ab	1.40bcd
N2 x S4	2.74e	24.49e	16.23ab	1.51abc
N2 x S5	2.75de	40.41c	14.84ab	1.66ab
N3 x S1	4.68a	57.75a	14.61ab	1.37cd
N3 x S2	4.38b	53.89ab	13.87ab	1.30cd
N3 x S3	2.96de	30.73de	14.30ab	1.37cd
N3 x S4	2.43f	28.28e	15.78ab	1.22d
N3 x S5	3.41c	47.52bc	17.36a	1.73a

W1 and W2: postanthesis moderate irrigation and postanthesis water deficiency, respectively; N1: 25% planting, 25% tillering, 0% anthesis (50% postanthesis nitrogen deficiency); N2: 25% planting, 25% tillering, 25% anthesis (25% postanthesis nitrogen deficiency); N3: 25% planting, 25% tillering, 50% anthesis (0% postanthesis nitrogen deficiency); S1, S2, S3, S4, and S5: not source-sink manipulation, removal of flag leaf, removal of all leaves but not flag leaf, removal of all leaves and ear halving, respectively; *Means of the same category followed by different letters are significantly different at 0.05% levels of probability using Duncan test.

The results from different nitrogen treatments in this study did not support the assumption that lower postanthesis nitrogen supply would result in lower source strength and current photosynthesis. It seems that a higher rate of nitrogen availability, nitrogen taken up from the soil is immediately used by developing the grains rather than first being incorporated into leaf photosynthetic proteins. In not source:sink manipulated and ear halved plants, under both postanthesis water soil contents, more nitrogen supply after anthesis did not enhance the grain yield (Table 4) because in these treatments, the source size is so much that it is not necessary to increase the source actively with more nitrogen supply to earn a strength source and current photosynthesis is enough for kernel demand in all nitrogen levels. In removed flag leaf plants, more nitrogen supply after anthesis inhibited further decrease in current photosynthesis under

postanthesis water stress and enhanced the grain yield vs. postanthesis nitrogen deficiency conditions (Table 4).

Table 4. Mean comparison of grain yield (t ha⁻¹) as affected by postanthesis water stress x postanthesis nitrogen deficiency x source: sink manipulation.

	postanthesis moderate irrigation			postanthesis water deficiency		
	N1	N2	N3	N1	N2	N3
S1	5.56bc	6.12a	5.84ab	2.96gh	2.72hi	3.53ef
S2	4.52 d	4.44d	5.30c	2.55hij	2.58hij	3.45ef
S3	3.76 e	3.59ef	3.82c	2.36ijk	2.05klm	2.10klm
S4	2.91 gh	2.72hi	2.91gh	1.76m	2.76hi	1.94klm
S5	3.64ef	3.24fg	4.55d	1.90lm	2.26jkl	2.27jkl

N1: 25% planting, 25% tillering, 0% anthesis (50% postanthesis nitrogen deficiency); N2: 25% planting, 25% tillering, 25% anthesis (25% postanthesis nitrogen deficiency); N3: 25% planting, 25% tillering, 50% anthesis (0% postanthesis nitrogen deficiency); S1, S2, S3, S4, and S5: not source-sink manipulation, removal of flag leaf, removal of all leaves but not flag leaf, removal of all leaves and ear halving, respectively; Means of the same category followed by different letters are significantly different at 0.05% levels of probability using Duncan test.

Ahmadi and Baker (2001) reported that water stress and nitrogen deficiency caused premature grain desiccation, resulted in a marked decline in grain sucrose, and reduced grain weight. Insufficient source size in more intense defoliation levels was the reason for non-significant effect of more postanthesis nitrogen supply on grain yield (Table 4); because nitrogen is a source activity enhancer and when there is not enough leaf area index (LAI), the nitrogen supply will not have an impact on source strength and current photosynthesis (Table 4). Mazaheri et al. (2005) noted that net assimilation rate (NAR) i.e. source activity during seed filling period was a poor predictor of grain yield, while leaf area index (LAI) i.e. source size at early seed filling stage affected crop growth rate (CGR), total dry matter accumulation and grain yield.

Conclusion

These results suggest that in rain-fed, non-irrigated wheat, especially with sufficient nitrogen supply after anthesis, breeders must concentrate their programs on increasing sink activity, but under high water soil contents especially when nitrogen input is low, they must try to increase both the source and the sink strength.

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