The impact of source or sink limitations on yield formation of winter wheat (*Triticum aestivum* L.) due to post-anthesis water and nitrogen deficiencies

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ABSTRACT

The experiments were laid out to understand the mechanisms causing yield limitations imposed by post-anthesis water and nitrogen deficiencies in plants with modified source-sink ratios. Two soil-water regimes were allotted to the main plots. At anthesis, three levels of N were applied: none, 25% and 50% of total the N supply. Spike-halving caused reduction in grain yield at both water regimes and all N supply levels, showing that the reduction in grain number can not be compensated by a higher individual grain weight. Sink reduction by trimming 50% of the spikelets reduced grain number per ear by 38.5% and increased individual grain weight by 12.0%, which shows the plasticity in grain weight and grain set of wheat if sufficient assimilates are available. Additional nitrogen supply at anthesis had no significant effect on the total aboveground biomass, but increased grain yield through more allocation of dry matter to grains. Our findings suggest that for rainfed wheat with optimum N supply and supplemental irrigation, wheat growers should choose cultivars with a high grain number per ear and manage the crop to increase grain number per unit of land (sink capacity).

Keywords: drought stress; grain number; grain weight; grain yield; Harvest-index; nitrogen availability

Wheat yields in the semi-arid regions are not only limited by inadequate water supply, but also by N shortage late in the cropping season. It becomes clear that the physiological response of genotypes to drought stress should be included in studies investigating the interaction between N and water management (Ahmadi and Baker 2001, Saint Pierre et al. 2008). Fan and Li (2001) demonstrated that depending on the level of N supply, N fertilization could increase the agronomic N-use efficiency of winter wheat, which significantly reduced with the severeness of drought stress.

Efficient N use is crucial for economic wheat production and the prevention of N emissions to ground and surface water (Spiertz et al. 2006, Spiertz 2009), therefore, optimizing irrigation regimes and nitrogen management taking into account crop phenology will produce optimum grain yields (Karam et al. 2009).

Improving attainable yields of wheat under stress conditions requires knowledge of yield-determining physiological processes such as adaptation to environments with a broad range of climatic and edaphic variation, diversity in plant traits and plasticity in source-sink relationships (Reynolds and Trethowan 2007, Barnabas et al. 2008). Fan et al. (2005) found that both leaf photosynthesis and grain starch accumulation could be promoted by nitrogen supply under drought conditions. Madani et al. (2010) demonstrated that late nitrogen supply at anthesis did increase grain yield more by alleviating sink limitations than by increasing source strength. However, there are more publications on the negative effects of N under drought (Haberle et al. 2008, Sepaskhah and Hosseini 2008, Singh et al. 2008).

Modern wheat cultivars were frequently characterised as sink-limited (Matthew and Foyer 2001, Acreche and Slafer 2009) and to attain maximum grain set and yields, these cultivars require an ample supply of N fertilizer (Kichey et al. 2007). Findings show that post-anthesis nitrogen supplies could increase grain yield by decreasing the sink limitation (Madani et al. 2010). During the grain filling period, resource availability, especially water and nitrogen, determines the extent to which sink and source contribute to yield formation. These components are grain number per unit area (sink size), amount of reserves able to be remobilized to the grains and post-floral photosynthesis and assimilation of carbon and N.

We hypothesize, that limited resource availability will mainly result in resource restrictions by reducing current photosynthesis, and less by sink limitations. Therefore, the amount of mobile reserves in the vegetative parts will determine the yield gap.

The objective of the study was to analyze the effects of drought and nitrogen deficiency on yield, biomass production, and partitioning of assimilates in winter wheat under various source-sink relationships, in order to assess the impact of source capacity and sink strength on yield levels and stability.

MATERIAL AND METHODS

Plant material and location. This study was conducted under post-anthesis water and nitrogen (N) stress with the winter wheat cultivar Chamran. The experiments were carried out in Ramhormoz, Iran, during the growing seasons of 2007–2008 and 2008–2009. The site is located at 31'16''N latitude, 49°36'E longitude, with an altitude of 151 m above the sea level.

Weather and soil. This region has a hot climate, with mean annual maximum and minimum daily air temperatures of 32.7°C and 19.5°C, respectively. The precipitation growing season of wheat was 329 mm. Long-term (1978–2008) meteorological data are shown in Table 1. The soil was a montmorillonite clay loam, low in total nitrogen (4–5 g/kg), very low in organic matter (9–10 g/kg) with a pH of 7.8 and Ec = 0.44 dS/m.

Experimental design. The field experiment was laid out in a randomized complete block-design with split factorial arrangement with three replications. Water regimes were allotted to main plots and source: sink restrictions and post-anthesis nitrogen supply to sub-plots.

Irrigation regimes and soil water control. Furrow irrigation was applied. Prior to anthesis, all the experimental units were irrigated uniformly when the water soil content reached 75% of the amount available (SWC), corresponding to the difference between the SWC at field capacity (θFC) and wilting point (θWP).

Table 1. Long-term (1978–2008) meteorological data in Ramhormoz, Iran

	Average of temperature (°C)		Monthly total of precipitation (mm)	Average of relative humidity (%)	
	minimum	maximum		minimum	maximum
Jan	8.4	17.1	85	56	86
Feb	9.5	19.9	45.6	42	77
Mar	12.9	24.4	51.2	36	70
Apr	18.4	31.9	19.7	24	56
May	24.3	39.4	0	14	36
June	27.7	44.3	0	11	29
July	30.2	46	0	12	31
Aug	29.8	45.6	0	14	35
Sep	25.9	42	0	14	34
Oct	21.5	35.7	7.3	19	41
Nov	14.6	26.6	26.9	32	63
Dec	10.3	19.8	95.5	52	81
Annual	19.5	32.7	344.5	27	53

Table 2. The mean squares of ANOVA for grain yield, total biomass, straw yield, harvest index, number of grains per spike (NGS), 1000-grain weight (TSW) and total grain weight per spike (TGWS) in combined analysis of 2007–2008 and 2008–2009 data

S.O.V	*df*	Grain yield	Total biomass	Straw yield	Harvest index	NGS	TSW	TGWS
Y	1	0.262^{ns}	7.308^{ns}	10.33^{ns}	19.33^{*}	53.89^{ns}	113.2^{ns}	0.023^{ns}
Error (a)	4	0.045	1.098	1.264	32.02	28.71	19.86	0.004
W	1	126.2^{**}	393.0^{**}	73.75^{**}	2282.6^{**}	3388.7^{**}	2476.6^{**}	11.60^{**}
YW	1	0.072^{ns}	0.063^{ns}	0.272^{ns}	0.350^{ns}	9.153^{ns}	26.65^{ns}	0.007
Error (b)	4	0.007	0.471	0.417	10.51	51.82	77.37	0.0006
N	2	2.389^{**}	1.347^{ns}	6.998^{ns}	295.1^{**}	396.4^{**}	96.67^{*}	0.221^{**}
S	4	18.61^{**}	41.86^{**}	5.468^{ns}	426.1^{**}	1123.5^{**}	288.6^{**}	1.712^{**}
WN	2	0.147^{ns}	0.729^{ns}	1.260^{ns}	65.59^{ns}	32.699^{ns}	99.41^{**}	0.013^{ns}
WS	4	4.658^{**}	38.06^{**}	18.92^{**}	114.0^{*}	217.6^{**}	93.03^{*}	0.428^{**}
NS	8	0.959^{**}	6.840^{*}	8.249^{*}	189.3^{**}	102.6^{**}	38.27^{ns}	0.088^{**}
WNS	8	1.063^{**}	10.95^{**}	6.705^{ns}	61.86^{ns}	47.89^{*}	67.65^{*}	0.101^{**}
YN	2	0.529^{**}	3.278^{ns}	3.582^{ns}	78.79^{ns}	73.66^{*}	23.51^{ns}	0.046^{**}
YS	4	0.325^{**}	2.789^{ns}	4.653^{ns}	105.7^{*}	69.81^{*}	32.14^{ns}	0.030^{**}
YWN	2	0.899^{**}	0.055^{ns}	1.208^{ns}	138.9^{*}	82.24^{*}	85.61^{ns}	0.081^{**}
YWS	4	0.024^{ns}	0.548^{ns}	0.749^{ns}	23.34^{ns}	18.36^{ns}	60.98^{ns}	0.002^{ns}
YNS	8	0.057^{ns}	3.806^{ns}	3.262^{ns}	46.40^{ns}	16.06^{ns}	32.47^{ns}	0.005^{ns}
YWNS	8	0.465^{**}	4.619^{ns}	5.944^{ns}	138.1^{**}	31.25^{ns}	35.16^{ns}	0.043^{**}
Error (c)	112	0.079	3.279	3.662	42.17	22.15	31.00	0.007

$^{**}P < 0.01$; $^{*}P < 0.05$; $^{ns}P > 0.05$; Y – year effect; W – post-anthesis water regime effect; N – post-anthesis N supply; S – effect of source-sink manipulation at anthesis; YW, WN, WS, NS, WNS, YN, YS, YWN, YWS, YNS, YWNS represent interaction terms between the treatment factors

Soil water content (SWC) = θFC – θWP,

Where: θFC and θWP are volumetric soil water contents (%), respectively.

After anthesis, the control (W1) and under water stress (W2) plots were irrigated when the soil water content reduced to 75% and 25% of the available soil water content, respectively. The volumetric water contents at field capacity (θFC) and permanent wilting point (θWP) were 42% and 20% on a per volume basis, respectively. Therefore, the available soil water content (θFC – θWP), volumetric soil water content before irrigation in deficit (θWC + 25% SWC) and fully irrigated (θWC + 75% SWC) plots were 22%, 27.5% and 36.5% on a per volume basis, respectively.

The relationship between soil resistivity (R) and volumetric water content (W) of experimental field at 25°C is found to be given as $W = 49.\ 232e^{-0,012R}$; $R^2 = 0.88$; $P < 0.01$. During the growth season, this equation is used to convert measured soil resistivity (R) by installed granular matrix sensors (Watermark Soil Moisture Sensors, Irrometer Co. Inc., Riverside, CA) to volumetric soil water content (Karam et al. 2009; Madani et al. 2010). Granular matrix sensors were located at two depths (20 and 40 cm) in the soil profile near the fibrous root zone. For sensors installations, the hole was augured at an angle of 45 degree with the horizontal plane to prevent preferential water penetration down the backfilled-augured hole. The pre-anthesis stage (sowing to anthesis) is divided to tree sub-stages consisting of sowing to tillering, tillering to stem elongation, and stem elongation to anthesis. The efficient root depths at the end of these three stages were determined by 8 cm at tillering, 17 cm at stem elongation, and 25 cm at anthesis. Hence, the net irrigation amount (NIA) for all of the plots during different reproductive stages, and the post-anthesis net irrigation amount for deficit and fully

Table 3. Means for grain yield, total biomass, straw yield, harvest index, number of grains per spike (NGS), 1000-grain weight (TSW) and total grain weight per spike (TGWS) as affected by source: sink manipulation at anthesis, post-anthesis water and nitrogen supply in combined analysis of 2007–2008 and 2008–2009 data

Treatments	Grain yield	Total biomass	Straw yield	Harvest index (%)	NGS	TSW	TGWS
		(t/ha)				(g)	
W1	4.13^{a}	11.98^{a}	7.84^{a}	35.21^{a}	31.39^{a}	41.03^{a}	1.25^{a}
W2	2.46^{b}	9.02^{b}	6.56^{b}	28.09^{b}	22.71^{b}	33.61^{b}	0.74^{b}
N1	3.09^{c}	10.67^{a}	7.58^{a}	29.27^{b}	24.34^{c}	38.58^{a}	0.93^{c}
N2	3.31^{b}	10.42^{a}	7.10^{a}	32.04^{a}	27.37^{b}	37.34^{ab}	1.00^{b}
N3	3.48^{a}	10.41^{a}	6.92^{a}	33.65^{a}	29.45^{a}	36.00^{b}	1.05^{a}
S1	4.27^{a}	12.07^{a}	7.80^{a}	35.44^{a}	34.72^{a}	37.53^{b}	1.29^{a}
S2	3.76^{b}	11.02^{b}	7.25^{a}	34.76^{a}	31.06^{b}	37.16^{b}	1.14^{b}
S3	3.03^{c}	9.91^{cd}	6.87^{a}	31.17^{b}	26.38^{c}	35.02^{b}	0.92^{c}
S4	2.45^{d}	9.28^{d}	6.83^{a}	27.31^{c}	21.65^{d}	34.97^{b}	0.74^{d}
S5	2.95^{c}	10.22^{bc}	7.26^{a}	29.5^{abc}	21.44^{d}	41.92^{a}	0.89^{c}

W1, W2 – post-anthesis moderate irrigation and severe water deficiency, respectively. N1, N2, N3 – 0, 20.5, and 41 kg/ha N at anthesis, respectively. S1, S2, S3, S4, 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 within each column of each category followed by the different letters are significantly different ($P < 0.05$) according to Duncan test

irrigated plants to bring soil water content to field capacity (θFC) was determined according to the below formula:

NAI during sowing to tillering = (1/4 SWC × RD)/(IE) = (1/4 (22) × 8)/(50) = 0.88 cm

NAI during tillering to stem elongation = (1/4 SWC × RD)/(IE) = (1/4 (22) × 17)/(50) = 1.87 cm

NAI during stem elongation to anthesis = 1/4 SWC × RD)/(IE) = (1/4 (22) × 25)/(50) = 2.75 cm

NAI for fully irrigated plots = (1/4 SWC × RD)/(IE) = (1/4 (22) × 25)/(50) = 2.75 cm

NAI for deficit irrigated plots = (3/4 SWC × RD)/(IE) = (3/4 (22) × 25)/(50) = 8.25 cm

Where: NAI, SWC, RD, and IE are net amounts of irrigation (mm), volumetric available soil water content (%), stage effective rooting depths, and furrow irrigation efficiencies, respectively.

Nitrogen dosing and timing patterns. Diammonium phosphate ($(NH_4)_2HPO_4$) and urea ($CO(NH_2)_2$) fertilizers were employed at a maximum rate of 200 kg/ha and 100 kg/ha, which corresponds to 36 kg and 46 kg N/ha, respectively. Therefore, the maximum N supply amounted to 82 kg N/ha. In all nitrogen treatments, one quarter of the total N was applied at sowing and one quarter at tillering. At anthesis, the N supply was 0, 20.5 and 41 kg N/ha, resulting in an N supply of 41, 61.5 and 82 kg N/ha for N_1, N_2 and N_3, respectively.

Source: sink manipulation. Sink manipulations 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) which were done for all plants in each plot and one spike halving, which was performed by cutting the ears in two parts for whole spikes of each experimental unit. The amount of dry matter and N removed was not determined.

Agronomic practices and sampling. A subplot size of 2 × 5 m, having 4 rows 5-meter long was used and sowing was done in both sides of hills on 25 November 2007 and 5 December 2008 at the rate of 450 plants per square meter. Uniformity of sowing depth was achieved by using a hand dibbler to make holes 3–5 cm deep. The spaces between rows were 50 cm wide. Within each plot, an area of 2 m^2 was hand harvested on 5 May each growing season to estimate the grain, biological and straw yield. Dry weights were recorded after the plant material had been oven dried at 70°C for 48 h. At harvest, a random sample of 20 plants was chosen from two middle rows for recording number of grains per spike and 1000-grain weight. Harvest index was calculated as the ratio of grain yield to aboveground biomass. The following formula was used for calculating the amount of stem reserves mobilization to grain:

Table 4. Means for grain yield, total biomass, straw yield, harvest index, number of grains per spike (NGS), 1000-grain weight (TSW) and total grain weight per spike (TGWS) as affected by two-way interactions between all experimental factors in combined analysis of 2007–2008 and 2008–2009 data

Treatments		Grain yield (t/ha)	Total biomass (t/ha)	Straw yield (t/ha)	Harvest index (%)	NGS	TSW (g)	TGWS (g)
W1	N1	3.92[a]	12.26[a]	8.33[a]	32.78[a]	27.83[b]	43.62[a]	1.19[a]
	N2	4.20[a]	11.78[a]	7.57[a]	36.67[a]	32.18[ab]	40.96[ab]	1.27[a]
	N3	4.27[a]	11.90[a]	7.62[a]	36.19[a]	34.16[a]	38.51[b]	1.29[a]
W2	N1	2.25[b]	9.09[a]	6.83[a]	25.75[b]	20.85[b]	33.54[a]	0.68[b]
	N2	2.42[ab]	9.05[a]	6.62[a]	27.41[ab]	22.55[ab]	33.73[a]	0.73[ab]
	N3	2.69[a]	8.93[a]	6.23[a]	31.11[a]	24.74[a]	35.57[a]	0.81[a]
N1	S1	3.96[a]	12.09[a]	8.12[ab]	32.85[a]	30.28[a]	39.25[ab]	1.20[a]
	S2	3.39[ab]	10.16[ab]	6.76[b]	33.13[a]	25.29[b]	40.83[ab]	1.03[ab]
	S3	3.11[b]	9.93[ab]	6.81[b]	32.26[a]	27.03[ab]	34.66[b]	0.94[b]
	S4	2.24[c]	9.75[b]	7.51[ab]	23.12[b]	19.54[c]	35.23[b]	0.68[c]
	S5	2.72[bc]	11.44[ab]	8.72[a]	24.97[b]	19.55[c]	42.93[a]	0.82[bc]
N2	S1	4.48[a]	12.30[a]	7.82[ab]	36.19[a]	36.32[a]	37.78[ab]	1.35[a]
	S2	3.58[ab]	11.95[ab]	8.36[a]	30.15[a]	30.36[ab]	35.57[b]	1.09[ab]
	S3	2.97[b]	9.85[bc]	6.87[abc]	30.54[a]	26.66[bc]	34.06[b]	0.90[b]
	S4	2.77[b]	8.68[c]	5.90[c]	33.49[a]	23.68[bc]	36.80[ab]	0.84[b]
	S5	2.76[b]	9.30[c]	6.53[bc]	29.82[a]	19.83[c]	42.49[a]	0.83[b]
N3	S1	4.38[a]	11.83[a]	7.44[a]	37.28[ab]	37.57[a]	35.57[b]	1.33[a]
	S2	4.30[a]	10.94[ab]	6.64[a]	41.00[a]	37.53[a]	35.09[b]	1.30[a]
	S3	3.01[bc]	9.96[b]	6.94[a]	30.70[bc]	25.45[b]	36.34[a]	0.91[bc]
	S4	2.30[c]	9.42[b]	7.07[a]	25.33[c]	21.74[b]	32.87[b]	0.71[c]
	S5	3.37[b]	12.09[a]	6.53[a]	33.95[b]	24.95[b]	40.34[a]	1.02[b]
W1	S1	5.64[a]	14.56[a]	8.91[a]	39.67[a]	42.48[a]	41.84[ab]	1.71[a]
	S2	4.69[b]	13.49[a]	8.80[a]	35.34[ab]	34.51[b]	43.17[ab]	1.42[b]
	S3	3.78[c]	11.27[b]	7.48[ab]	34.65[ab]	31.60[b]	36.87[c]	1.14[c]
	S4	2.82[d]	9.34[c]	6.52[b]	31.58[b]	22.68[c]	38.77[bc]	0.85[d]
	S5	3.73[c]	11.24[b]	7.50[ab]	34.82[ab]	25.69[c]	44.51[a]	1.13[c]
W2	S1	2.91[a]	9.59[a]	6.68[ab]	31.21[ab]	26.97[a]	33.23[b]	0.88[a]
	S2	2.83[a]	8.54[b]	5.71[b]	34.18[a]	27.61[a]	31.16[b]	0.86[a]
	S3	2.28[b]	8.56[b]	6.27[ab]	27.68[bc]	21.16[b]	33.17[b]	0.69[b]
	S4	2.09[b]	9.22[ab]	7.13[a]	23.05[c]	20.63[b]	31.17[b]	0.63[b]
	S5	2.17[b]	9.19[ab]	7.02[a]	24.34[c]	17.20[c]	39.33[a]	0.65[b]

W1, W2 – post-anthesis moderate irrigation and severe water deficiency, respectively. N1, N2, N3 – 0, 20.5, and 41 kg/ha N at anthesis, respectively. S1, S2, S3, S4, 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 within each column of each category followed by the different letters are significantly different ($P < 0.05$) according to Duncan test. Categories are separated by blank rows

Amount of stem reserves mobilization to grain (t/ha) – maximum stem dry matter after anthesis (t/ha) – stem dry matter at maturity (t/ha).

Statistical analysis. Data were statistically analyzed using analysis of variance technique appropriate for randomized complete block-design with post-anthesis nitrogen supply and source: sink restriction factors split on water regime. Duncan's multiple range test ($P < 0.05$) was applied for mean separation when F values were significant.

RESULTS AND DISCUSSION

Yield under post-anthesis water stress. Grain yield was significantly reduced by 40% due to severe post-anthesis water deficiency (Tables 2 and 4). This value is by 16% higher than the value reported by Palta et al. (1994). Moderate water stress let to a grain yield of 4.13 t/ha and a significantly higher biomass (25%) and harvest index (20%) compared to severe water stress (Table 2 and 3). It indicates that post-anthesis water stress reduced both source strength and sink capacity. The significant correlation between grain yield and aboveground biomass (r = 0.80, P < 0.01) and the low correlation with harvest index (r = 0.38, P < 0.05) under severe soil water stress indicates that the reduction in grain yield due to post-anthesis drought was more related to a reduction in post-anthesis dry matter accumulation (source strength) than its allocation to the grain. A shortage of assimilates due to water stress during grain filling significantly reduced the number of grains per spike from 31.4 to 22.7 and 1000-grain weight from 41.0 to 33.1 g (Tables 2 and 3). Grain yield and number of grains per spike were strongly associated (r = 0.94, P < 0.01), indicating that less allocation of assimilates to the grains and a low harvest index were mainly due to a reduced number of grains per spike, rather than to grain weight reduction. Grain number is usually determined before flowering (Kichey et al. 2007); thus, water stress after anthesis and during grain filling can cause more reduction in grain weight than grain number. However, Nicolas and Turner (1993) demonstrated that across diverse genetic materials, the correlation between rate of reduction in kernel weight by current photosynthesis restriction and rate of reduction by drought stress is significant (r = 0.81, P < 0.01).

Yield and post-anthesis nitrogen supply. More post-anthesis nitrogen supply (N3 vs. N1) significantly increased grain yield by 10% through an enhanced dry matter allocation to grains, resulting in harvest-index and total grain weight per spike higher by 13 and 11%, respectively, without any effect on post-anthesis dry matter production and total biomass (Tables 2 and 3). Higher harvest index and yield at additional N supply (N3) vs. post-anthesis N deficiency (N1) was due to 17% more grains per spike (24.3 vs. 29.5), and a significant reduction by 7% in grain mass (Tables 2 and 3). This is not surprising because grain weight is dependent rather on carbohydrate availability than on N assimilate supply (Demotes-Mainard et al. 1999).

Yield and source: sink manipulation at anthesis. Defoliation (source restriction), reduced dry matter allocation to the grain, as well as dry matter accumulation; therefore, the harvest-index and total aboveground biomass were reduced equally by around 24% after full defoliation (Table 3). Results show that in strong source strength limited wheat, the reduction of harvest index was associated with reduction in current photosynthesis and dry matter accumulation. Ear halving did not increase the straw yield (Table 3). It seems that after sink restriction, because of controlling the effect of sink capacity on source strength (Figure 1), the current photosynthesis was hampered (Madani et al. 2010) and resulted in lower total biomass (Table 3). Therefore, there were no further assimilates in ear halved plants for incorporating to stem or maybe further assimilates incorporated to root instead of stem to increase nitrogen uptake and use efficiency and increase sink capacity through N related mechanisms (Figure 2). Only after removal of all leaves, the individual grain weight decreased by 7% (37.5 to 35.0 g) compared to control plants (Table 3); but the number of grains per spike already reduced after removal of flag leaf leaves by 11% (34.7 to 31.1). This indicates that source restrictions at anthesis exert its effect on grain yield mostly through the number of grains per spike, rather than through individual grain weight (Table 3). A 50% reduction in the number of grains per ear is expected after post-anthesis ear halving; however we found reduction of only 38% (34.7 to 21.4), and an increased grain weight (37.5 to 42 g) of 10% (Table 3). A higher availability of assimilates for spikelets in the half remaining of the ear increased grain set which indicates the

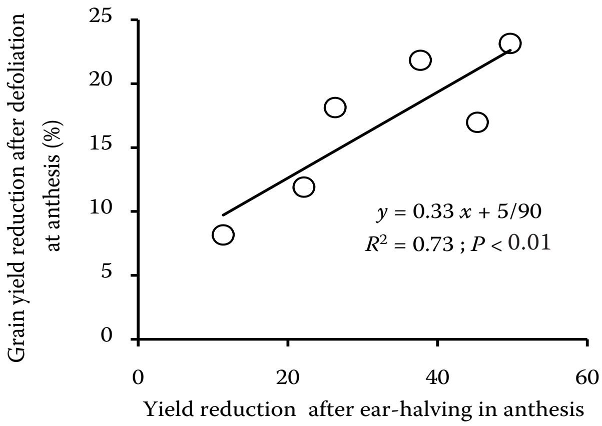


Figure 1. Relationship between grain yield reduction after ear-halving at anthesis and yield reduction after full defoliation at anthesis in combined analysis of 2007–2008 and 2008–2009 data

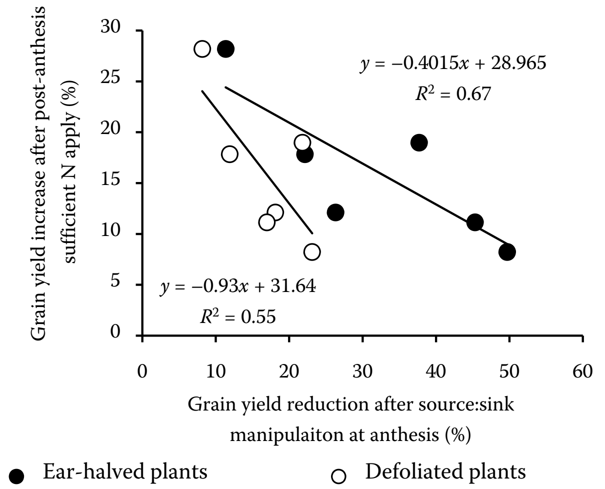


Figure 2. Relationship between grain yield reduction after source: sink manipulation at anthesis and grain yield increase after post-anthesis sufficient N apply (N3 vs. N1) under water stress in combined analysis of 2007–2008 and 2008–2009 data

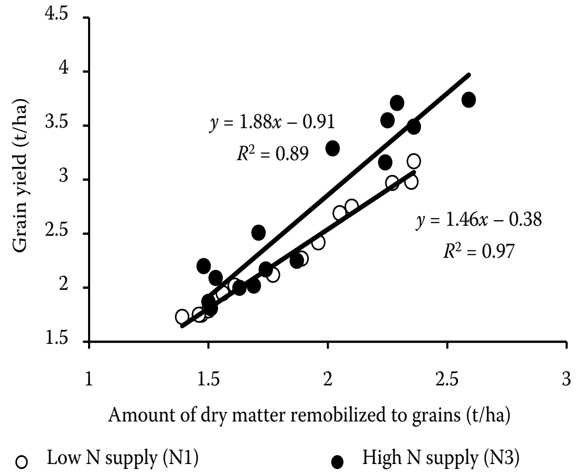
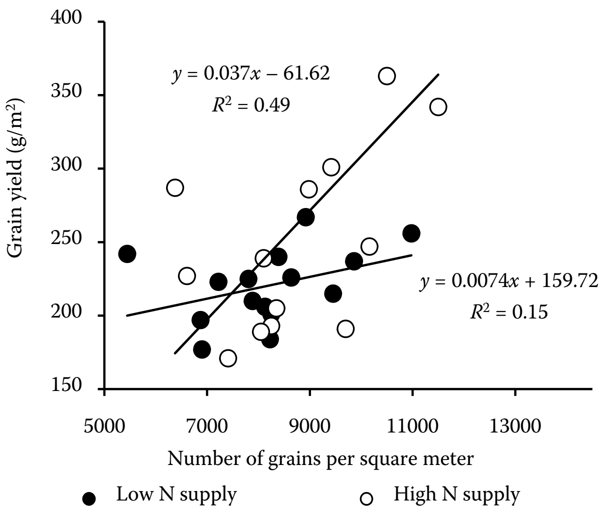


Figure 3. Relationship between dry matter remobilization to grains and grain yield for low (N1) and high (N3) nitrogen supply under water stress in combined analysis of 2007–2008 and 2008–2009 data

potential for further increases in grain weight and grain set if ample assimilates are provided.

Water regime × nitrogen supply. Under different conditions produced by the combination of the fertilization and irrigation levels, grain weight per spike responded significantly to the increase in the source-sink ratio (Tables 2 and 4). Under moderate irrigation, additional N supply (N3 vs. N1) at anthesis significantly reduced 1000 grains weight (43.6 to 38.5 g) and increased number of grains per spike (27.8 to 34.0) which caused the equilibration of the total grain weight per spike and grain yield in all N treatments (Table 4). Under water stress, sufficient N supply (N3 vs. N1) increased grains per spike and grain yield by 15.7 and 16.6%, respectively, without changing grain mass (Table 4). This improved yield was mainly due to an increase of the harvest index from 25.8 to 31.1% (Table 4). It suggests that in wheat subjected to post-anthesis water deficiency, additional N supply at anthesis could increase dry matter allocation to grain i.e. raise sink capacity. This finding is in line with Ercoli et al. (2008). Under water stress, adding N to N-deficient plants increased amount of dry matter remobilized to grains and source strength based on reserves build up during the pre-floral period (Figure 3). Under water stress, nitrogen consumption could raise the correlation coefficient between grain yield and the number of seeds per unit area (r = 0.15 to r = 0.49) and inhibited further decease in sink capacity which resulted in higher grain yield (Figure 4). Thus, we showed that under water stress, increasing nitrogen supply increased both the amount of dry matter remobilized to grains and grain yield (Figure 3 and Table 4). It was reported that a quadratic response in grain yield and kernel number per square meter was observed with increasing N levels in all irrigation regimes (Pandey et al. 2001)

Water regime × source: sink restrictions. Flag leaf removal under severe post-anthesis drought stress had no significant effect on grain yield and grain yield significantly reduced just after more defoliation (Table 4). On the contrary, under moderate irrigation, cutting whether the flag leaf blade or more leaves significantly reduced grain yield (Table 4). These results showed that the source strength was not additionally limited by the defoliation under low soil water contents. It was reported that the number of grains per unit land area was reduced slightly by defoliation, and in most cases not significantly, except when all leaves were removed (Aggarwal et al. 1990). Under both moderate irrigation and water stress conditions, ear halving significantly decreased grain yield by 34 and 25%, respectively (Table 4). This result indicates that sink strength was limited in both water regimes but mostly under high water soil content. Under moderate irrigation, full defoliation significantly decreased the straw yield by 26.82% (from 8.91 to 6.53 t/ha) but ear halving could not increase vegetative biomass (Table 4). It indicates



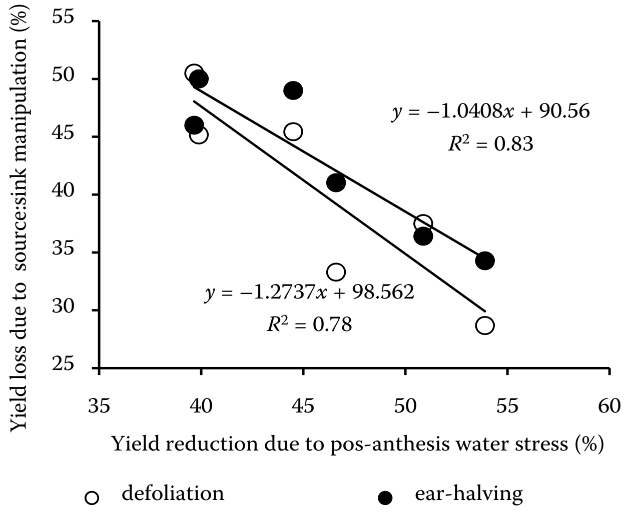
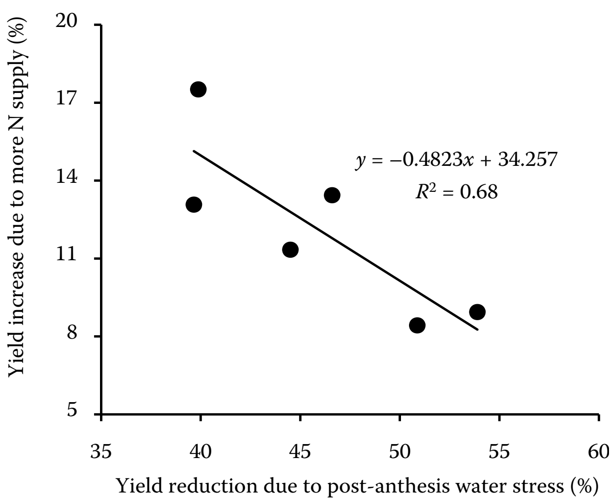


Figure 4. Relationship between number of grains per square meter and grain yield for low and high N supply under water stress in combined analysis of 2007–2008 and 2008–2009 data

Figure 5. Relationship between yield reduction due to post-anthesis water stress and yield loss due to source: sink manipulation in combined analysis of 2007–2008 and 2008–2009 data

that under high water content, source strength was limited and assimilates could not meet the grain demand without support of stem reserves. In ear-halved plants, drought stress significantly decreased grain yield, total above ground biomass and harvest index by 34.22% (3.36 to 2.21 t/ha), 18.23% (11.24 to 9.19 t/ha) and 30.09% (34.82 to 24.34%), respectively (Table 4). This shows that when the sink is restricted, post-anthesis water deficiency increases sink limitation through lower current photosynthesis and dry matter allocation to grains.

N supply × source: sink restrictions. In control plants (S1) and flag leaf removed ones (S2), more N supply at anthesis (N3 vs. N1) could increase grain yield by 9.6% (from 3.96 to 4.38 t/ha) and



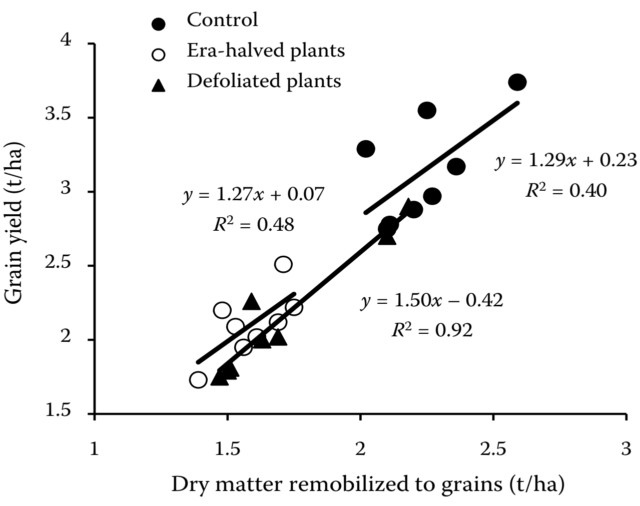


Figure 6. Relationship between yield reduction due to post-anthesis water stress and yield increase due to higher N supply in combined analysis of 2007–2008 and 2008–2009 data

Figure 7. Relationship between dry matter remobilization to grains and grain yield for control, ear-halved and fully defoliated plants under water stress in combined analysis of 2007–2008 and 2008–2009 data

21.2% (from 3.39 to 4.30 t/ha) (Table 4). After ear-halving, late N supply (N3 vs. N1) increased grain yield, harvest index, grain per spike by 19.3% (from 2.72 to 3.37 t/ha), 26.5% (from 25.0 to 34.0%) and 21.5% (from 19.6 to 25.0), respectively (Table 4), but decreased the biomass by 13.4% (from 11.44 to 9.91 t/ha) without any effect on grain mass (Table 4). This suggests that late N increased grain yield of sink-restricted wheat more by dry matter allocation to grains than by increasing current photosynthesis and source strength. Madani et al. (2010) showed that post-anthesis nitrogen supply increases grain yield through an alleviation of sink limitations, rather than increasing source strength. Grain yield loss due to N deficiency was bigger in control plants than in plants with source or sink restrictions (Figure 2), indicating that under low soil water contents, nitrogen-use-efficiency is strongly related to both sink capacity and source strength. Therefore, greater grain set, more current photosynthesis, and reserve reallocation to grains may result to more NUE. Anbessa et al. (2009) reported that reduction in N fertilizer requirements in barley while maintaining yield may be achieved through breeding by targeting increased yield potential in association with higher NUE.

Yield reduction due to water stress (ranging from 40% to 55%) correlates positively to both source strength and sink capacity (Figure 5), indicating that increasing both grain set and photosynthesis capacity would be a constructive method for improving WUE. Wheat plants responded to nitrogen and water simultaneously. Thus, relative yield increase due to more N increased when yield loss due to water stress reduced (Figure 6).

It was reported that dry matter remobilization to grains is strongly and positively related to sink capacity than source strength (Blum 1994). Thus, under low (< 1.5 t/ha) amounts of reserves remobilization, more N supply could not increase grain yield, but when the amount of dry matter remobilized to grain was more than 2.5 t/ha (capable sink), post-anthesis N could increase grain yield by more than 25% (3 to 4 t/ha) (Figure 3). Dordas (2009) showed that dry matter translocation was on average by 22% higher at the fertilized treatments compared with the control, which indicates that fertilization made plants translocate higher amount of dry matter. It seems that higher N supply would increase grain set or inhibit its further reduction due to water stress conditions, as well as increase source strength based on the reserves built up during the pre-floral period. Under water stress, full defoliation reduced the grain yield and reserves reallocation to grains (Figure 7), indicating that little source limitation is based on reserves build up during the pre-floral period and does not depend on current photosynthesis.

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