

The impact of post-anthesis nitrogen and water availability on yield formation of winter wheat

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ABSTRACT

The effects of irrigation regimes (full irrigation and water-withholding at anthesis) and post-anthesis nitrogen supplies (LN: 0, MN: 20 and HN: 40 kg N/ha) on grain yield and its components in winter wheat were studied, with attention to biomass gain by assimilation and its loss by respiration. Fully-irrigated wheat responded to N fertilization with increased grain number (GN) and decreased grain weight (GW) and achieved similar grain yields (5.2 to 5.5 t/ha) at different N supplies. However, drought-stressed wheat responded to N with higher GN without significant changes in GW, and achieved higher grain yields (2.7 vs. 3.3 t/ha) with HN compared to LN. Net assimilation rates during grain filling (NAR_g) increased with increasing post-anthesis N fertilization for drought-stressed wheat (NAR_g: 3.8 and 4.5 g/m/day for LN and HN). Apparent whole-plant respiration (R_A) was not influenced by increased post-anthesis N fertilizer. Thus, in drought-stressed wheat, the total biomass and straw yield at maturity were increased by increasing N supply. These results suggest that high N supply at anthesis satisfied the grains' increased demand for N by increasing post-floral assimilation, and the surplus assimilates not only compensated for the low-N-induced biomass loss by respiration but may also have increased the straw yield.

Keywords: biomass; drought; grain number; grain weight; photosynthesis; respiration

During the grain filling period, water (W) and nitrogen (N) interactions determine the extents to which grain number (GN) and grain weight (GW) contribute to grain yield (GY) (Saint Pierre et al. 2008). There is some evidence to support the idea that N supply at anthesis could increase GY of drought-stressed wheat more by alleviating sink limitations than by increasing source strength (Madani et al. 2010). First, grain growth in non-irrigated wheat varied from sink limitation to some degree of co-limitation (Acreche and Slafer 2009). These cultivars may have required an ample supply of N fertilizer to attain maximum grain set (GS) and GY, (Kichey et al. 2007). Second, it was clearly illustrated that drought-resistant genotypes with greater GS are better able to reallocate stem dry matter to the grains (Ehdaie et al. 2006). Thus, if the SR remobilized to grains was < 1.5 t/ha, then drought-stressed wheat did not respond to N, and if this amount was < 2.5 t/ha, then the GY increase resulting from increased N supply exceeded 25% (Madani et al. 2010).

These evidences suggest that N supply at anthesis could increase sink capacity under all irrigation regimes (Madani et al. 2010). The increased GS resulting from increased N supply would increase the GY if pre- and/or post-floral assimilate levels increased to meet the demand from grains and inhibited the reduction in assimilate per grain and consequently in GW.

In previous work, Spike-halving caused reductions in GY in all W × N treatments, suggesting that the studied cultivar was sink-limited under different W × N conditions. In present work, we studied the effects of various N treatments on the Chamran cultivar under irrigation and drought conditions with attention to biomass gain by assimilation and its loss by respiration. We hypothesised that under drought conditions (GN < 35), high N supply at anthesis may satisfy the increased grains' demands that resulted from N supply. This could be achieved by increasing post-floral assimilation, and the surplus assimilates could not only compensate for the low-N-induced biomass

loss by respiration but could also increase straw yield at maturity.

MATERIAL AND METHODS

This study was conducted under post-anthesis water and nitrogen deficiencies with the bread winter wheat cv. Chamran during the 2007–2008 and 2008–2009 growing seasons. The research site was located in Ahwaz-Iran (latitude: 31°16'N, longitude: 49°36'E, altitude: 151 m a.s.l.). This region has a hot and humid climate, with 35-year mean annual maximum and minimum daily air temperatures of 32.7°C in August and 19.5°C in February, respectively. The precipitation during the first and second wheat growing seasons (November to May) was 329 and 352 mm, respectively (Madani et al. 2010). There was no precipitation during grain filling period (25 April to 30 May) in the experimental seasons. The soil was a montmorillonite clay loam, 0.5 m deep, low in total nitrogen (2007: 3–4 g/kg; 2008: 4–5 g/kg) and very low in organic matter (9–10 g/kg), with a pH of 7.8 and E_c of 0.44 dS/m. The field experiments were laid out in a randomized complete block design with split-plot arrangement, with three replicates. Water regimes (full irrigation and water-withholding at anthesis) were allotted to main plots, and post-anthesis nitrogen supplies (0, 20 and 40 kg N/ha) were allotted to subplots. Prior to anthesis, all the experimental units were irrigated uniformly when the soil water content reached 75% of the available soil water content (SWC), corresponding to the difference between the SWC at field capacity (θ_{FC}) and wilting point (θ_{WP}). After anthesis, well-watered plots were irrigated in this scheduling. In drought-stressed plots water-withholding was applied 7 days before anthesis and continued to 7 days after anthesis till the SWC reached to 25% (FC-WP). After water-withholding period, the routine irrigation was continued in drought-stressed plots. Day-to-day measurement of the soil water content was done using granular matrix sensors according to the method described by Madani et al. (2010). The amount of water needed in each irrigation event to bring soil water content to field capacity (θ_{FC}) was determined using the formula:

$$ETP_{crop} = ETP_{pan} \times K_c$$

Where: ETP_{crop} , ETP_{pan} and K_c are crop evapo-transpiration, Pan evaporation and crop coefficient, respectively.

Diammonium phosphate ((NH_4)₂HPO₄) and urea (CO(NH₂)₂) were top-dressed at maximum

rates of 200 kg and 100 kg/ha, which corresponded to 36 and 46 kg N/ha, respectively. Therefore, the maximum N supply was 82 kg N/ha. In all nitrogen treatments, one quarter of the total N was applied while sowing and one quarter while tillering. At anthesis, the N supplies were 0, 20 and 40 kg N/ha, resulting in N supplies of 41, 61.5 and 82 kg N/ha for N₁, N₂ and N₃, respectively. The N₃ treatment was applied a day before water-withholding to ensure the fertilizer get to rooted soil in water stress treatment. Each experimental plot measured 2 m × 5 m. Within each plot, wheat was sown at a rate of 450 seeds per square metre in four rows, 0.5 m apart, on 25 November 2007 and 5 December 2008. Sowing was done on both sides of hills, following the cropping techniques customarily adopted in the region. Uniformity of sowing depth was achieved by using a hand dibbler to make holes 3–5 cm deep. At physiological maturity (Zadoks stage 90), grain yield and total biomass were measured by harvesting a sample area of 2 m² at the centre of each plot. Dry weights were recorded after the plant material was oven-dried at 70°C for 48 h. Harvest index (HI) was calculated as the ratio of grain yield to above-ground biomass. Straw yield was calculated as the difference of total biomass and grain yield. A random sample of 20 plants was chosen from two middle rows for recording the grain weight. The number of grains per square metre was calculated as the ratio of grain yield (mg/m²) to grain weight (mg). 7 days before anthesis and before applying the N × W treatments and at physiological maturity, the leaf area index (LAI) and total biomass were measured (2008: 4.6 and 452 g/m²; 2009: 4.3 and 419 g/m²) to determine the net assimilation rate (NARg) during the grain growth period. Grain growth period, corresponding to the days between anthesis and physiological maturity, was determined to be 32 and 26 days for well-watered and drought-stressed wheat in 2008 and 34 and 26 days in 2009, respectively. No differences were observed among nitrogen supplies for the grain growth periods. Leaf samples were harvested two weeks after W × N treatments were applied, and chlorophyll concentrations (chl) were measured using a spectrophotometer at two wavelengths (648.2 and 664.9 nm) for maximum absorptions of chlorophyll a and b, respectively (Liu et al. 2010). 14 days after N × W treatments were applied (one week after anthesis), single plants were removed from each experimental unit at the end of the photoperiod. Their respiration was measured with a laboratory technique (Amthor et al. 1991)

based on the gas exchange system described by Bloom et al. (1989) and according to the formula:

$$C_i = C_a + P (R_A/g_c)$$

Where: P – gas exchange cuvette air pressure (Pa); R_A – the measured leaf CO_2 flux area density (i.e., apparent respiration rate on a leaf area basis, mol CO_2 efflux/m²/s) and g_c – leaf CO_2 conductance (mol CO_2 /m²/s) estimated from leaf H_2O conductance.

Statistical analyses were performed using the GLM procedure of SAS/STAT, using the correct error terms to evaluate water and nitrogen main effects and their interactions. Duncan's multiple range test ($P < 0.05$) was applied for mean separations when F values were significant.

RESULTS AND DISCUSSION

During 2008–2009, full irrigation and water-withholding at anthesis exhibited different responses of the main yield components (GN and GW) to increased N availability (Table 1), indicating that available assimilates were allocated to produce either many small seeds or few larger seeds depending on resource availability (Gambín and Borrás 2009). Well-watered wheat responded to N fertilization by increasing GN and decreasing GW (LN: 10 100 grains/m² and 48.5 mg per grain; MN: 14 600 grains/m² and 43.2 mg per grain; HN: 13 400 and 38.0 mg per grain), while drought-stressed wheat responded by increasing GN without significantly changing GW (LN: 7 200 grains and 33.2 mg per grain; MN: 7 300 grains and 37.0 mg per grain; HN: 9 000 grains and 34.4 mg per grain). A similar trend was observed in 2007–2008 (Table 1). As a result, in 2008–2009 and average of both years, well-watered wheat with MN supply achieved greater GY than the lower (LN) and higher (HN) nitrogen-supplied plants (4.9, 6.3 and 5.1 t/ha for LN, MN and HN, respectively). While for drought-stressed wheat, N fertilization of 40 kg N/ha (HN) increased the GY by 16.6% (2008) and 29.2% (2008–2009), showing that high N supply at anthesis satisfied the demand of the larger number of grains (by N) by increasing the post-floral assimilation (Rodrigues et al. 2007, Fuertes-Mendizabal et al. 2010).

Comparing the two irrigation regimes across the two experimental years, the well-watered wheat (WW) had a higher response than drought-stressed wheat (DW) to N fertilization in terms of GN (WW: 11 300 and 14 600 grains for LN and HN; DW: 8 600 and 9 700 grains for LN and HN). Thus, for

non-irrigated wheat, especially with optimum N supply after anthesis, breeders could direct their selection programs to increase GS (Bruckner and Froberg 1991). In addition, comparing the three nitrogen supplies across the two experimental years, well-watered wheat showed a tendency to saturate its response to N fertilization in terms of GN (Table 1). In fact, the crop gave similar GN values in MN and HN treatments (WW: 15 000 and 14 600 grains for MN and HN; DW: 7 900 and 9 700 grains for MN and HN). Well-watered wheat achieved similar GY with LN and HN, due to lower GW (WW: 46.8 and 37.3 mg for LN and HN; DW: 31.7 and 33.8 mg for LN and HN). Albrizio et al. (2010) reported that there was a strict relationship between GN and GY for drought-stressed wheat with a high response to nitrogen (slope of 0.622 for HN vs. 0.465 for LN) related to constant GW under different nitrogen supplies. However, Pandey et al. (2001) showed a quadratic response in GY and GS with increasing N levels in all irrigation regimes.

Averaged across years, the observed reduction in seed weight (46.8 to 37.3 mg) of well-watered wheat with increased nitrogen supply (HN vs. LN) could be related to different responses of GN and NAR_g to nitrogen supply and, consequently, different assimilate levels per established seed (NAR: 6.0 g/m²/day and GN: 11 300 grains for LN; NAR: 6.3 g/m²/day and GN: 14 600 grains for HN). This behaviour was observed in both cropping years (Table 1). In 2007–2008 and averaged across years, increased nitrogen supply increased both the NAR_g and GN in drought-stressed wheat (NAR: 3.8 g/m²/day and GN: 8 600 grains for LN; NAR: 4.5 g/m²/day and GN: 9 700 grains for HN). However, this behaviour was not observed in 2008–2009 (Table 1). Indeed, the different responses of GW and GY to N supply under various irrigation regimes could be explained by the responses of photosynthesis and respiration, and the consequent assimilates available per grain with different N supplies and irrigation regimes.

Well-watered wheat produced more GN than drought-stressed wheat (13 600 vs. 8 800 grain/m²). When the sink is capable, post-anthesis N is incorporated more into grains than leaves (Mi et al. 2010). Thus, Osaki et al. (1995) reported that Chl was increased by decreasing the sink demand for nitrogen. This behaviour was also observed in the present study (Figure 1). While in both years, whole-plant apparent respiration (R_A) increased with increasing post-anthesis N fertilizer (2008: 28.1, 35.2 and 56.1 nmol CO_2 /g DW/S for LN, MN

Table 1. Means for total biomass, grain yield, harvest index, grain weight, number of grains per spike, total grain weight per spike, straw yield at maturity, number of grains per square meter, net assimilation rate during grain filling, whole-plant apparent respiration, flag leaf chlorophyll content and net CO₂ exchange as affected by post-anthesis water and nitrogen interaction in separated and combined analysis of 2007–2008 and 2008–2009 data

	Total biomass (t/ha)			Grain yield (t/ha)		
	2007–2008	2008–2009	combined	2007–2008	2008–2009	combined
W ₁ N ₁	14.3 a (a)	15.9 a (a)	15.1 a (a)	5.6 b (a)	4.9 b (b)	5.2 b (b)
W ₁ N ₂	14.8 a (a)	14.9 a (a)	14.8 a (a)	6.1 b (a)	6.3 a (a)	6.2 a (a)
W ₁ N ₃	12.1 b (ab)	13.4 b (ab)	12.7 b (ab)	5.8 b (a)	5.1 b (b)	5.5 b (b)
W ₂ N ₁	8.5 b (c)	9.6 b (c)	9.1 b (c)	3.0 b (bc)	2.4 b (d)	2.7 b (d)
W ₂ N ₂	8.5 b (c)	9.1 b (c)	8.8 b (c)	2.7 b (c)	2.7 b (cd)	2.7 b (d)
W ₂ N ₃	10.4 a (bc)	11.4 a (bc)	10.9 a (bc)	3.5 a (b)	3.1 a (c)	3.3 a (c)
	Harvest index (%)			Grain weight (mg)		
W ₁ N ₁	39.2 b (ab)	30.8 b (ab)	35.0 b (ab)	45.1 a (a)	48.5 a (a)	46.8 a (a)
W ₁ N ₂	41.2 b (ab)	37.3 a (ab)	39.2 ab (ab)	39.6 b (ab)	43.2 b (ab)	41.4 ab (ab)
W ₁ N ₃	47.9 a (a)	38.1 a (a)	43.0 a (a)	36.6 b (ab)	38.0 c (b)	37.3 b (b)
W ₂ N ₁	35.3 a (ab)	25.0 a (b)	30.1 a (b)	30.2 a (b)	33.2 a (b)	31.7 a (b)
W ₂ N ₂	31.8 a (b)	29.7 a (ab)	30.7 a (b)	31.4 a (b)	37.0 a (b)	34.2 a (b)
W ₂ N ₃	33.7 a (b)	27.2 a (ab)	30.4 a (b)	33.2 a (b)	34.4 a (b)	33.8 a (b)
	Number of grains per spike			Total grain weight per spike (g)		
W ₁ N ₁	36.6 b (b)	32.4 b (ab)	34.5 b (b)	1.7 a (a)	1.6 b (b)	1.6 b (b)
W ₁ N ₂	45.1a (a)	50.9 a (ab)	48.0 a (a)	1.8 a (a)	2.2 a (a)	1.9 a (a)
W ₁ N ₃	48.2 a (a)	41.4 a (a)	44.8 a (a)	1.8 a (a)	1.6 b (b)	1.6 b (b)
W ₂ N ₁	28.2 b (c)	23.8 b (b)	26.0 b (c)	0.9 b (c)	0.8 b (d)	0.8 b (d)
W ₂ N ₂	26.3 b (c)	22.9 b (b)	24.6 b (c)	0.8 b (c)	0.8 b (d)	0.8 b (d)
W ₂ N ₃	32.6 a (bc)	28.0 a (b)	30.3 a (bc)	1.1 a (c)	1.0 a (c)	1.0 a (c)
	Straw yield at maturity (t/ha)			Number of grains per square meter × 10 ³		
W ₁ N ₁	8.7 a (a)	11.0 a (a)	9.9 a (a)	12.4 b (b)	10.1 b (b)	11.3 b (b)
W ₁ N ₂	8.7 a (ab)	10.6 a (ab)	9.6 a (ab)	15.4 a (a)	14.6 a (a)	15.0 a (a)
W ₁ N ₃	6.3 b (bc)	8.3 b (bc)	7.3 b (bc)	15.8 a (a)	13.4 a (a)	14.6 a (a)
W ₂ N ₁	5.5 b (c)	7.2 ab (c)	6.4 b (c)	9.9 a (c)	7.2 b (c)	8.6 b (cd)
W ₂ N ₂	5.8 b (c)	6.4 b (c)	6.0 b (c)	8.6 b (d)	7.3 b (c)	7.9 b (d)
W ₂ N ₃	6.9 a (bc)	8.3 a (bc)	7.6 a (abc)	10.5 a (c)	9.0 a (b)	9.7 a (c)
	Net assimilation rate during grain filling (g/m ² /day)			Whole-plant apparent respiration (nmol CO ₂ /g DW/S)		
W ₁ N ₁	5.8 b (b)	6.2 a (a)	6.0 a (a)	28.1 b (bc)	28.3 b (c)	28.3 c (c)
W ₁ N ₂	6.4 a (a)	6.6 a (a)	6.4 a (a)	35.2 b (b)	38.1 b (bc)	38.0 b (b)
W ₁ N ₃	6.2 ab (ab)	6.4 a (a)	6.3 a (a)	56.1 a (a)	49.0 a (a)	49.2 a (a)
W ₂ N ₁	4.1 b (c)	4.0 a (b)	4.1 b (c)	27.9 a (bc)	35.2 b (bc)	31.7 a (bc)
W ₂ N ₂	3.9 b (c)	3.9 a (b)	3.9 b (c)	21.2 a (c)	31.4 b (c)	28.1 a (c)
W ₂ N ₃	4.4 a (c)	4.3 a (b)	4.3 a (b)	28.2 a (bc)	42.2 a (ab)	35.1 a (bc)
	Chlorophyll content (mg/g DW)			Net CO ₂ exchange (mg CO ₂ /dm ² /h)		
W ₁ N ₁	7.8 a (a)	7.8 a (a)	7.8 a (c)	29 b (b)	37.2 a (a)	33.1 a (a)
W ₁ N ₂	8.1 a (a)	8.2 a (a)	8.1 a (c)	38.4 a (a)	33 a (a)	35.7 a (a)
W ₁ N ₃	8.0 a (a)	8.1 a (a)	8.1 a (c)	31 b (ab)	38.4 a (a)	34.7 a (a)
W ₂ N ₁	4.6 b (c)	4.0 b (c)	4.3 b (a)	24.6 ab (bc)	20.5 b (b)	22.5 b (b)
W ₂ N ₂	5.2 b (b)	4.8 b (c)	5.0 b (a)	19.5 b (c)	23.4 b (b)	21.4 b (b)
W ₂ N ₃	5.6 a (b)	6.2 a (b)	5.9 a (b)	26.4 a (bc)	35.2 a (a)	30.8 a (b)

W₁ – post-anthesis full irrigation; W₂ – water with-holding at anthesis; N₁ – 0 kg/ha N; N₂ – 20 kg/ha N; N₃ – 40 kg/ha N at anthesis. Means within each column of each category followed by different letters are significantly different ($P < 0.05$) according to the Duncan test

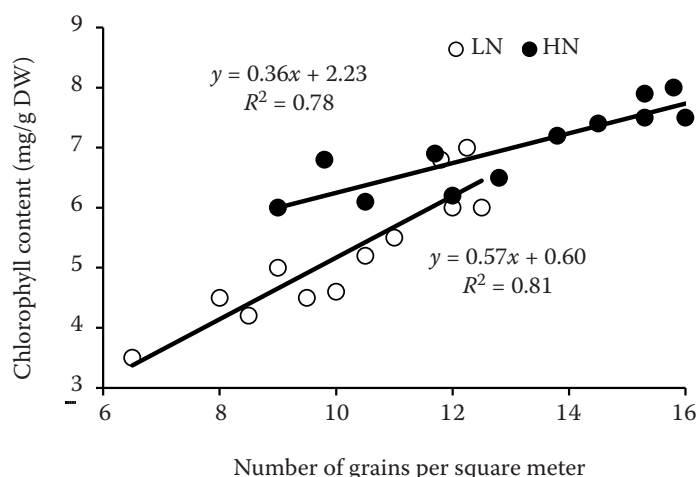


Figure 1. The relationship between number of grains per square meter ($\times 1000$) and chlorophyll content in grain as a function of post-anthesis nitrogen supply. LN – 0 kg/ha; HN – 40 kg/ha

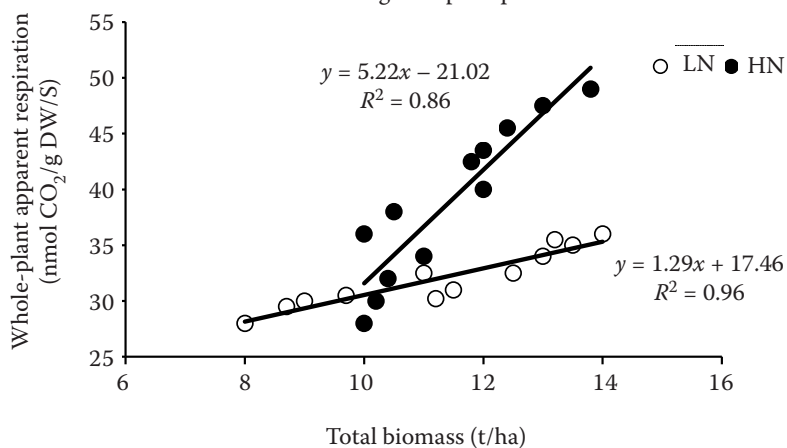


Figure 2. The relationship of total biomass and whole-plant apparent respiration as a function of post-anthesis nitrogen supply. LN – 0 kg/ha; HN – 40 kg/ha

and HN; 2009: 28.3, 38.1 and 49.0 nmol CO₂/g DW/S for LN, MN and HN). Indeed, N-induced carbon loss in terms of R_A after anthesis exceeded assimilation during grain filling in terms of biomass; this could not be compensated for by current assimilation or by SR reallocation to grains when post-anthesis N was applied over a certain rate (Sun et al. 2007). As a result, the shortage of assimilates caused a reduction in available assimilates per grain, and consequently in the GW with increasing N supply (Table 1). Therefore, the strong trade-off between GN and GW resulted in similar yields among different nitrogen supplies (Table 1). In addition, due to large R_A values, the TB (Total biomass) and SR values were decreased by increasing N supplies (Table 1).

Averaged across years, NAR_g, NCO₂ and Chl increased with increasing post-anthesis N fertilizer for drought-stressed wheat (NAR_g: 3.8 and 4.5 g/m²/day for LN and HN; NCO₂: 22.5 and 30.8 mg CO₂/dm²/h for LN and HN; Chl: 4.3 to 5.9 mg/g DW). This trend was observed in both years. The only exception was seen in 2008–2009, when NAR_g was not influenced by nitrogen supply. Averaged across years and in 2007–2008, R_A was not influenced by increasing post-anthesis N fertilizer (Table 1). There was a strict relationship between TB and R_A with a

high response to nitrogen (Figure 2), showing that N-induced respiration was low, due to the small amount of biomass present (Sun et al. 2007). As a result, available assimilates per grain, and consequently, GW remained constant (Table 1). Therefore, greater GN resulted in greater yields with higher nitrogen supplies (Table 1). In addition, in drought-stressed wheat, the surplus assimilates increased the TB and SR (Table 1). The results conclude that the response of GN to N is similar at different irrigation regimes. While, the response of NAR and consequently GW (assimilates per grain) to N is dependent on water availability.

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