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Nitrogen Availability Affects the Yield of Winter Wheat Subjected to Water Stress during Grain Filling

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The effects of irrigation regimes (full irrigation and water-withholding at anthesis) and postanthesis nitrogen (N) supplies (LN, 0; MN 20; and HN, 40 kg N ha\(^{-1}\)) 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), whereas drought-stressed wheat responded with greater GN without significant changes in GW. Apparent whole-plant respiration (\(R_a\)) was not influenced by increased postanthesis N fertilizer. Thus, in drought-stressed wheat, the total biomass and stem reserves 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 postfloral assimilation, and the surplus assimilates not only compensated for the low-N-induced biomass loss by respiration but also may have increased the stem reserves.

Keywords Grain number, grain weight, nitrogen availability, water stress, wheat

Introduction

Wheat yields in semi-arid regions are limited not only by inadequate water (W) supply but also by nitrogen (N) shortage late in the cropping season (Karam et al. 2009). During the grain-filling period, W and 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 are some publications on the negative effects of N under drought conditions (Haeberle, Svoboda, and Raimanova 2008); however, 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 nonirrigated wheat varied from sink limitation to some degree of colimitation (Acreche et al. 2009), and to attain maximum grain set (GS) and GY, these cultivars may have required an ample supply of N fertilizer (Kichey et al. 2007). Second, it has been clearly illustrated that drought-resistant genotypes with greater GS are better able to reallocate stem reserves (SR) to the grains (Ehdaie et al. 2006). In addition, the interaction between GS and demand for SR during grain filling seems to depend on the interaction between W and N (Bonnett and Incoll 1992). Thus, if the SR remobilized to grains was <1.5 t ha\(^{-1}\), then drought-stressed wheat did not respond to N, and if this amount
was <2.5 t ha\(^{-1}\), then the GY increase resulting from increased N supply exceeded 25\% (Madani et al. 2010). This evidence indicated that N supply at anthesis increased source strength based on reserves accumulated during the prefloral period by improving the GS (Bancal 2008). Third, N supply at anthesis increased GY of sink-restricted wheat more by efficient relocation of SR to the grain than by increasing the biomass (Madani et al. 2010).

This evidence suggests that N supply at anthesis could increase sink capacity under both irrigation regimes (Madani et al. 2010; Albrizio et al. 2010). The increased GS resulting from increased N supply would increase the GY if pre- and/or postfloral assimilate levels increased to meet the demand from grains and inhibited the reduction in assimilate per grain and consequently in GW.

In previous work, we investigated the effects of water regimes and N supply, as well as various source–sink treatments, on the Chamran cultivar (Madani et al. 2010). That experiment found that spike-halving caused reductions in GY in all W \(\times\) N treatments, and that the reduction in GN due to W and/or N deficiencies could not be compensated for by a greater individual GW. It was also found that sink reduction by thinning 50\% of the spikelets reduced GN per ear by 38.5\% and increased individual GW by 12.0\%, showing the plasticity of wheat GW and GS when sufficient assimilates were available. Finally, it found that W \(\times\) N interaction exerted its effect on GY mostly through GN rather than GW.

All of these results suggested that the studied cultivar was sink-limited under different W \(\times\) N conditions. These findings prompted us to perform a second study to investigate the effects of treatments that could modify the source–sink relationship in the studied cultivar.

Here, we studied the effects of various N treatments on the Chamran cultivar under irrigation and drought conditions. We hypothesized 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 postfloral assimilation, and the surplus assimilates could not only compensate for the low-N-induced biomass loss by respiration but could also increase stem reserves at maturity. We focused on the role of N supply at anthesis in source strengthening based on the net assimilation rate during grain filling and SR reallocation to the grains. Additionally, we investigated biomass gain by assimilation and its loss by respiration, as well as its partitioning between the stem and grains.

**Materials and Methods**

This study was conducted under postanthesis water and N deficiencies with the bread winter wheat Chamran during the 2007–2008 and 2008–2009 growing seasons. The Chamran genotype is tolerant to drought and semitolerant to N-induced lodging, with average actual grain yield, individual grain weight, grain protein content, and plant height of 6.2 t ha\(^{-1}\), 39 mg, 10.4\%, and 95 cm, respectively. This genotype is cultivated mainly in southwestern Iran and is well adapted to the region, which has hot and humid springs. The research site was located in Ahwaz, Iran (latitude 31° 16’ N, longitude 49° 36’ E, altitude 151 m). 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 amounts during the first and second wheat-growing seasons (November to May) were 329 and 352 mm, respectively (Madani et al. 2010). The soil was a montmorillonite clay loam, 0.5 m deep, low in total N (2007, 3–4 g kg\(^{-1}\); 2008, 4–5 g kg\(^{-1}\)) and very low in organic matter (9–10 g kg\(^{-1}\)), with a pH of 7.8 and electrical conductivity (EC) of
0.44 dS m\(^{-1}\). 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 postanthesis N supplies (0, 20, and 40 kg N ha\(^{-1}\)) 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 (\(\theta_{FC}\)) and wilting point (\(\theta_{WP}\)). After anthesis, irrigation was stopped in drought-stressed plots and continued in well-watered 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 (\(\theta_{FC}\)) was determined according to Albrizio et al. (2010), using the formula \(\text{ETP}_{\text{crop}} = \text{ETP}_{\text{pan}} \times K_c\), where \(\text{ETP}_{\text{crop}}\), \(\text{ETP}_{\text{pan}}\), and \(K_c\) are crop evapotranspiration, pan evaporation, and crop coefficient, respectively. Diammonium phosphate [(NH\(_4\)]\(_2\)HPO\(_4\)] and urea [CO(NH\(_2\)]\(_2\)] were applied at maximum rates of 200 kg and 100 kg ha\(^{-1}\), which corresponded to 36 and 46 kg N ha\(^{-1}\), respectively. Therefore, the maximum N supply was 82 kg N ha\(^{-1}\). In all N 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\(^{-1}\), resulting in N supplies of 41, 61.5, and 82 kg N ha\(^{-1}\) for N\(_1\), N\(_2\), and N\(_3\), respectively. Each experimental plot measured 2m \(\times\) 5m. Within each plot, wheat was sown at a rate of 450 seeds per square meter in four rows, 0.5 m apart, on 25 November 2007 and 5 December 2008. Sowing was done on both sides of rows, 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, grain yield, total biomass, and stem reserves were measured by harvesting a sample area of 2 m\(^2\) at the center of each plot. Dry weights were recorded after the plant material had been oven dried at 70 °C for 48 h. Harvest index (HI) was calculated as the ratio of grain yield to aboveground biomass. A random sample of 20 plants was chosen from two middle rows for recording the grain weight. The number of grains per square meter was calculated as the ratio of grain yield (mg m\(^{-2}\)) to grain weight (mg). At anthesis and before applying the N \(\times\) W treatments, the leaf area index (LAI) and total biomass were measured (2008, 4.6 and 452 gr m\(^{-2}\); 2009, 4.3 and 419 gr m\(^{-2}\)) to determine the net assimilation rate (NARg) during the grain growth period. Grain growth periods, corresponding to the days between anthesis and physiological maturity, were 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 N supplies during the grain growth periods. Leaf samples were harvested 2 weeks after W \(\times\) N treatments were applied, and chlorophyll concentrations 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). Two weeks after N \(\times\) W treatments were applied, single plants were removed from each experimental unit at the end of the photoperiod. Their respiration was measured with a laboratory technique (Amthor, Koch, and Bloom 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 is gas exchange cuvette air pressure (Pa), \(R_A\) is the measured leaf CO\(_2\) flux area density [i.e., apparent respiration rate on a leaf area basis, mol carbon dioxide (CO\(_2\)) efflux m\(^{-2}\) S\(^{-1}\)], and \(g_c\) is leaf CO\(_2\) conductance (mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) estimated from leaf H\(_2\)O conductance. Statistical analyses were performed using the GLM procedure of SAS/STAT, using the correct error terms to evaluate water and N 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

Total biomass (TB), grain yield (GY), and stem reserves at maturity (SR) were considerably less in 2008 than in 2009 (Table 1), probably due to the lower initial soil N level (3–4 vs. 4–5 g kg\(^{-1}\)) and lower rainfall (329 vs. 352 mm from November to May) in the 2008 experiment. The values of LAI and TB at anthesis and the spike numbers per square meter were found to be 4.3, 419 gr m\(^{-2}\), and 300 in 2008 and 4.6, 452 gr m\(^{-2}\), and 320 in 2009. The net assimilation rate during grain filling (NARg) and whole-plant apparent respiration at 2 weeks after anthesis (RA) values for both growing seasons were similar (Table 1), showing that the differences in TB, GY, and SR between the growing seasons could have been due to the differences in soil and climate properties at the vegetative stage, before the application of postanthesis N doses and irrigation regimes.

During 2008–2009, the two irrigation regimes 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 (Gambin and Borras 2009). Well-watered wheat responded to N fertilization by increasing GN and decreasing GW (LN, 10,100 grains m\(^{-2}\) and 48.5 mg per grain; MN, 14,600 grains m\(^{-2}\) and 43.2 mg per grain; HN, 13,400 and 38.0 mg per grain), whereas 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).

Indeed, in 2008–2009, well-watered wheat with MN achieved greater total grain weight per spike (TGWS) than wheat with lower (LN) and higher (HN) N supplies (2.2 g per spike for MN vs. 1.6 g per spike for LN and HN), showing the different responses of number of grains per spike (NGS) and GW to N supply (NGS: 32.4 and GW: 48.5 mg for LN; NGS: 50.9 and GW: 43.2 mg for MN; NGS: 41.4 and GW: 38.0 mg for HN). In 2007–2008, additional N supply (HN vs. LN) at anthesis significantly reduced GW (48.5 to 38.5 mg) and increased NGS (32.4 to 41.4), which caused the equilibration of the TGWS in all N treatments (Table 1). This showed that the ample assimilate supply for filling of the larger number of grains (by supplying N) is provided by the increased post- or prefloral photosynthesis or postfloral assimilates, and/or SR that were able to be reallocated to the grains (prefloral assimilates) were decreased by N-induced respiration (Sun et al. 2007). A similar trend was observed in the average of both years (Table 1). As a result, in 2008–2009 and the average of both years, well-watered wheat with MN supply achieved greater GY than the lower (LN) and higher (HN) N-supplied plants (4.9, 6.3, and 5.1 t h\(^{-1}\) for LN, MN, and HN, respectively). However, in 2007–2008, N fertilization had no significant effect on GY (Table 1). On average, across the years, the drought-stressed wheat with HN supply achieved greater TGWS than the MN and LN N supplies (1.0 g per spike for HN vs. 0.8 g per spike for LN and MN), by increasing NGS without significantly changing the GW (NGS, 26.0 and 30.3 for LN and HN, respectively). As a result, for drought-stressed wheat, N fertilization of 40 kg N ha\(^{-1}\) (HN) increased the GY by 16.6% (2008) and 29.2% (2008–2009), showing that sufficient assimilate to filling the larger number of grains (by supplying N) is provided by increasing the source strength, based on the post- or/and prefloral photosynthesis rates resulting from more N supply (Fuertes-Mendizabal et al. 2010). However, in drought-stressed wheat, fertilization with 20 kg N ha\(^{-1}\) (MN) had no significant effect on GY in either year (Table 1).
Table 1
Means for total biomass, grain yield, harvest index, grain weight, number of grains per spike, total grain weight per spike, stem reserves 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 analyses of 2007–2008 and 2008–2009 data

| Parameter                  | 2007–2008 | 2008–2009 | Combined | 2007–2008 | 2008–2009 | Combined |
|----------------------------|-----------|-----------|----------|-----------|-----------|----------|
| Total biomass (t ha⁻¹)     |           |           |          |           |           |          |
| W₁N₁                       | 14.3 a (a)| 15.9 a (a)| 15.1 a (a)| 5.6 b (a) | 4.9 b (b) | 5.2 b (b) |
| W₁N₂                       | 14.8 a (a)| 16.9 a (a)| 15.8 a (a)| 6.1 b (a) | 6.3 a (a) | 6.2 a (a) |
| W₁N₃                       | 12.1 b (ab)| 13.4 b (ab)| 12.7 b (ab)| 5.8 b (a) | 5.1 b (b) | 5.5 b (b) |
| W₂N₁                       | 8.5 b (c) | 9.6 b (c) | 9.1 b (c) | 3.0 b (bc)| 2.4 b (d) | 2.7 b (d) |
| W₂N₂                       | 8.5 b (c) | 9.1 b (c) | 8.8 b (c) | 2.7 b (c) | 2.7 b (cd)| 2.7 b (d) |
| W₂N₃                       | 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 (%)          |           |           |          |           |           |          |
| W₁N₁                       | 39.2 b (ab)| 30.8 b (ab)| 35.0 b (ab)| 45.1 a (a)| 48.5 a (a)| 46.8 a (a)|
| W₁N₂                       | 41.2 b (ab)| 37.3 a (ab)| 39.2 ab (ab)| 39.6 b (ab)| 43.2 b (ab)| 41.4 ab (ab)|
| W₁N₃                       | 47.9 a (a) | 38.1 a (a) | 43.0 a (a) | 36.6 b (ab)| 38.0 c (b)| 37.3 b (b) |
| W₂N₁                       | 35.3 a (ab)| 25.0 a (b) | 30.1 a (b) | 30.2 a (b) | 33.2 a (b) | 31.7 a (b) |
| W₂N₂                       | 31.8 a (b) | 29.7 a (ab) | 30.7 a (b) | 31.4 a (b) | 37.0 a (b) | 34.2 a (b) |
| W₂N₃                       | 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 |           |           |          |           |           |          |
| W₁N₁                       | 36.6 b (b) | 32.4 b (ab)| 34.5 b (b) | 1.7 a (a) | 1.6 b (b) | 1.6 b (b) |
| W₁N₂                       | 45.1 a (a) | 50.9 a (ab)| 48.0 a (a) | 1.8 a (a) | 2.2 a (a) | 1.9 a (a) |
| W₁N₃                       | 48.2 a (a) | 41.4 a (a) | 44.8 a (a) | 1.8 a (a) | 1.6 b (b) | 1.6 b (b) |
| W₂N₁                       | 28.2 b (c) | 23.8 b (b) | 26.0 b (c) | 0.9 b (c) | 0.8 b (d) | 0.8 b (d) |
| W₂N₂                       | 26.3 b (c) | 22.9 b (b) | 24.6 b (c) | 0.8 b (c) | 0.8 b (d) | 0.8 b (d) |
| W₂N₃                       | 32.6 a (bc)| 28.0 a (b) | 30.3 a (bc)| 1.1 a (c) | 1.0 a (c) | 1.0 a (c) |

(Continued)
| Parameter                          | 2007–2008 | 2008–2009 | Combined | 2007–2008 | 2008–2009 | Combined |
|-----------------------------------|-----------|-----------|----------|-----------|-----------|----------|
| Stem reserves at maturity (t h⁻¹) |           |           |          |           |           |          |
| W₁N₁                             | 8.7 a (a) | 11.0 a (a) | 9.9 a (a) | 12.4 b (b) | 10.1 b (b) | 11.3 b (b) |
| W₁N₂                             | 8.7 a (ab)| 10.6 a (ab)| 9.6 a (ab)| 15.4 a (a) | 14.6 a (a) | 15.0 a (a) |
| W₁N₃                             | 6.3 b (bc)| 8.3 b (bc)| 7.3 b (bc)| 15.8 a (a) | 13.4 a (a) | 14.6 a (a) |
| W₂N₁                             | 5.5 b (c) | 7.2 ab (c) | 6.4 b (c) | 9.9 a (c)  | 7.2 b (c)  | 8.6 b (cd)|
| W₂N₂                             | 5.8 b (c) | 6.4 b (c)  | 6.0 b (c) | 8.6 b (d)  | 7.3 b (c)  | 7.9 b (d)  |
| W₂N₃                             | 6.9 a (bc)| 8.3 a (bc)| 7.6 a (abc)|10.5 a (c) | 9.0 a (b)  | 9.7 a (c)  |
| Number of grains per square meter × 10³ |           |           |          |           |           |          |
| W₁N₁                             |           |           | 9.9 a (a) | 12.4 b (b) | 10.1 b (b) | 11.3 b (b) |
| W₁N₂                             |           |           | 9.6 a (ab)| 15.4 a (a) | 14.6 a (a) | 15.0 a (a) |
| W₁N₃                             |           |           | 7.3 b (bc)| 15.8 a (a) | 13.4 a (a) | 14.6 a (a) |
| W₂N₁                             |           |           | 6.4 b (c) | 9.9 a (c)  | 7.2 b (c)  | 8.6 b (cd)|
| W₂N₂                             |           |           | 6.0 b (c) | 8.6 b (d)  | 7.3 b (c)  | 7.9 b (d)  |
| W₂N₃                             |           |           | 7.6 a (abc)|10.5 a (c) | 9.0 a (b)  | 9.7 a (c)  |
| Whole-plant apparent respiration (nmol CO₂ g⁻¹ DW S⁻¹) |           |           |          |           |           |          |
| W₁N₁                             |           |           | 6.0 a (a) | 28.1 b (bc)| 28.3 b (c)| 28.3 c (c)|
| W₁N₂                             |           |           | 6.4 a (a) | 35.2 b (b) | 38.1 a (a) | 38.0 b (b)|
| W₁N₃                             |           |           | 6.3 a (a) | 56.1 a (a) | 49.0 a (a) | 49.2 a (a)|
| W₂N₁                             |           |           | 3.8 b (c) | 27.9 a (bc)| 35.2 b (bc)| 31.7 a (bc)|
| W₂N₂                             |           |           | 3.7 b (c) | 21.2 a (c) | 31.4 b (bc)| 28.1 a (c)|
| W₂N₃                             |           |           | 4.5 a (b) | 28.2 a (bc)| 42.2 a (ab)| 35.1 a (bc)|
| Chlorophyll content (mg g⁻¹ DW)   |           |           |          |           |           |          |
| W₁N₁                             |           |           | 6.0 a (a) | 29 b (b)   | 37.2 a (a) | 33.1 a (a)|
| W₁N₂                             |           |           | 6.4 a (a) | 38.4 a (a) | 33 a (a)   | 35.7 a (a)|
| W₁N₃                             |           |           | 6.3 a (a) | 31 b (ab)  | 38.4 a (a) | 34.7 a (a)|
| W₂N₁                             |           |           | 3.8 b (c) | 24.6 ab (bc)|20.5 b (b)| 22.5 b (b)|
| W₂N₂                             |           |           | 3.7 b (c) | 19.5 b (c) | 23.4 b (b) | 21.4 b (b)|
| W₂N₃                             |           |           | 4.5 a (b) | 26.4 a (bc)| 35.2 a (a) | 30.8 a (b)|
| Net CO₂ exchange (mg CO₂ dm⁻² h⁻¹) |           |           |          |           |           |          |
| W₁N₁                             |           |           | 6.0 a (a) | 29 b (b)   | 37.2 a (a) | 33.1 a (a)|
| W₁N₂                             |           |           | 6.4 a (a) | 38.4 a (a) | 33 a (a)   | 35.7 a (a)|
| W₁N₃                             |           |           | 6.3 a (a) | 31 b (ab)  | 38.4 a (a) | 34.7 a (a)|
| W₂N₁                             |           |           | 3.8 b (c) | 24.6 ab (bc)|20.5 b (b)| 22.5 b (b)|
| W₂N₂                             |           |           | 3.7 b (c) | 19.5 b (c) | 23.4 b (b) | 21.4 b (b)|
| W₂N₃                             |           |           | 4.5 a (b) | 26.4 a (bc)| 35.2 a (a) | 30.8 a (b)|

Notes. W₁ and W₂, postanthesis fully irrigation and water-holding at anthesis, respectively. N1, N2, and N3 denote 0, 20, and 40 kg ha⁻¹ N at anthesis, respectively. Means within each column of each category followed by the different letters are significantly different (P < 0.05) according to Duncan's test.
Comparing the two irrigation regimes across the two experimental years, the well-watered wheat (WW) had a greater 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 nonirrigated wheat, especially with optimum N supply after anthesis, breeders could direct their selection programs to increase GS (Bruckner and Frohberg 1991). In addition, comparing the three N supplies across the two experimental years, WW 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 N (slope of 0.622 for HN vs. 0.465 for LN) related to constant GW under different N supplies, indicating that the supply of assimilates for grain growth (source strength), along with the reserves accumulated in the vegetative organs prior to anthesis, is enough to meet the demand of developing grains (Rodrigues et al. 2007). A quadratic response in GY and GS was observed with increasing N levels in all irrigation regimes (Pandey, Maranville, and Admou 2001).

Averaged across years, the observed reduction in seed weight (46.8 to 37.3 mg) of WW with increased N supply (HN vs. LN) could be related to different responses of GN and NARg to N supply and, consequently, different assimilate levels per established seed (NAR, 6.0 g m⁻² day⁻¹ and GN, 11,300 grains for LN; NAR, 6.3 g m⁻² day⁻¹ and GN, 14,600 grains for HN). This behavior was observed in both cropping years (Table 1). In 2007–2008 and averaged across years, increased N supply increased both the NARg and GN in drought-stressed wheat (NAR, 3.8 g m⁻² day⁻¹ and GN, 8,600 grains for LN; NAR, 4.5 g m⁻² day⁻¹ and GN, 9,700 grains for HN). However, this behavior 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.

In both years, WW with LN and HN achieved similar NARg values, net CO₂ exchange rates (NCO₂), and chlorophyll contents (Chl) of flag leaves 2 weeks after anthesis. The only exception was observed in 2007–2008, when NARg was influenced by 40 kg N h⁻¹ fertilizer (11.9 to 12.7 g⁻¹ m⁻² day⁻¹). Well-watered wheat produced more GN than drought-stressed wheat (13,600 vs. 8,800 grain m⁻²). When the sink is capable, postanthesis N is incorporated more into grains than leaves (Mi et al. 2010). Thus, the response of Chl to N supply was small in higher GN (Osaki, Iyoda, and Tadano 1995). This behavior also was observed in the present study (Figure 1). In both years, whole-plant apparent respiration (RAR) increased with increasing postanthesis N fertilizer (2008, 28.1, 35.2, and 56.1 nmol CO₂ g⁻¹ DW S⁻¹ for LN, MN, and HN; 2009, 28.3, 38.1, and 49.0 nmol CO₂ g⁻¹ DW S⁻¹ for LN, MN, and HN). Indeed, N-induced carbon loss in terms of RAR 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 postanthesis 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 N supplies (Table 1). In addition, due to large RAR values, the TB and SR values were decreased by increasing N supplies (Table 1).
Averaged across years, NARg, NCO₂, and Chl increased with increasing postanthesis N fertilizer for drought-stressed wheat (NARg, 3.8 and 4.5 g⁻¹ m⁻² day⁻¹ for LN and HN; NCO₂, 22.5 and 30.8 mg CO₂ dm⁻² h⁻¹ for LN and HN; Chl, 8.6 to 11.3 mg g⁻¹ DW). This trend was observed in both years. The only exception was seen in 2008–2009, when NARg was not influenced by N supply. Drought-stressed wheat had lower GN than well-watered wheat (Table 1). When the sink is not capable, some of the N absorbed postanthesis may be incorporated into the leaves instead of the grains (Mi et al. 2010). Osaki et al. (1995) reported that Chl was increased by decreasing the sink demand for N. Averaged across years and in 2007–2008, Rₐ was not influenced by increasing postanthesis N fertilizer (Table 1). In 2008–2009, N fertilization of 20 kg N ha⁻¹ (MN) did not increase the RA, and RA increased only after 40 kg h⁻¹ (HN) N application (35.2, 31.4, and 42.2 nmol CO₂ g⁻¹ DW S⁻¹ for LN, MN, and HN, respectively). Thus, the correlation of TB with Rₐ as a function of N indicated that for drought-stressed wheat, N-induced respiration was low, due to the small amount of biomass present (Sun et al. 2007). Therefore, greater GN resulted in greater yields with higher N supplies (Table 1). In drought-stressed wheat, the surplus assimilates increased the TB and SR (Table 1). Thus, in both years, different responses of TB and SR to N were observed in WW and drought-stressed wheat (Table 1). In drought-stressed wheat, increasing the N supply at anthesis from 0 (LN) to 40 (HN) kg N⁻¹ ha⁻¹ stimulated the production of an additional TB by 22.3% (2008) and 21.8% and 28.7% (2009) and SR by 25.4 (2008) and 15.3% (2009). In well-watered wheat, increasing the N supply at anthesis from 0 (LN) to 40 (HN) kg N⁻¹ ha⁻¹ decreased TB by 15.4% (2008) and 15.7% (2009) and SR by 27.5% (2008) and 25.5% (2009).

In addition, in both years, WW with HN achieved greater HI than did wheat with lower N supplies (2008, 39.2 and 47.9 for LN and HN; 2009, 30.8 and 38.1 for LN and HN). Indeed, the increase in HI with N fertilizer is due to N-induced respiratory loss of stem reserves, not to more efficient reallocation of stem reserves to the grains, increasing the GY by supplying N. Fuertes-Mendizabal et al. (2010) reported that SR contribution to grain filling was independent of N supply. In this study, in drought-stressed wheat in both years, N fertilization had no significant effect on HI (Table 1), indicating that under
Figure 2. Relationship of total biomass and whole-plant apparent respiration as a function of postanthesis nitrogen supply (LN, 0 kg ha\(^{-1}\); HN, 40 kg ha\(^{-1}\)).

drought conditions (grains <35), high N supply at anthesis satisfied the demand of the larger number of grains (by N) by increasing the postfloral assimilation, and the surplus assimilates not only compensated for the low-N-induced biomass loss by respiration but also increased the stem reserves at maturity. The results suggest that when the sink was limiting the grain filling, postanthesis N supply not only increased the GN of drought-stressed wheat but also increased assimilate per grain and decreased GW.

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