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Post-Anthesis Dry Matter and Nitrogen Dynamics in Durum Wheat as Affected by Nitrogen and Temperature during Grain Filling

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Durum wheat (*Triticum turgidum* L. var. *durum* Desf.) is commonly grown in Mediterranean conditions, where temperature stress during grain filling can limit productivity. This research was performed to evaluate the effect of temperature during grain filling on dry matter and nitrogen dynamics in two Italian durum wheat varieties, Appio and Creso, grown with different nitrogen availabilities. The experiment compared two different temperature regimens, one within the normal range occurring during grain filling in Central Italy, the other within the normal range occurring in the southern regions of Italy (20/15 °C and 28/23 °C day/night, respectively). Plants were grown in pots outdoor until anthesis and afterward were placed in growth chambers. Results showed that nitrogen fertilization and post-anthesis temperature affected growth, accumulation and partitioning of dry matter and N in durum wheat which, in turn, modified grain yield and N content. Grain yield was better expressed at 20/15 °C, while grain protein concentration was favoured under the 28/23 °C temperature regime. Higher temperature promoted remobilization of dry matter and restrained current photosynthesis, but reduced grain yield, indicating that the loss of photosynthesis could not compensate for the gain from increased remobilization. Grain N content, on the contrary, was promoted under the higher temperature regime, as high temperature reduced N remobilization but did not inhibit root water and nitrogen uptake, given that no water shortage occur.

Keywords: accumulation, nitrogen, remobilization, temperature

Introduction

Wheat is grown around the world under a wide range of environmental conditions, where climatic factors influence plant growth, which in turn affects yield and grain characteristics related to grain quality (Dupont and Altenbach 2003). In the southern regions of Italy, where temperatures following anthesis often exceed 30 °C, wheat yields average 2.5–3 t ha^{-1}, compared with over 5 t ha^{-1} in cooler regions of central and northern Italy (ISTAT 2009). Grain quality is generally higher at higher temperatures as a consequence of an increase of grain N concentration (Borghi et al. 1997; Novaro et al. 1997).

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Much of the work carried out for analysing the effect of temperature on remobilization of assimilates during grain filling in wheat has been concentrated on bread wheat, whereas research on durum wheat is less abundant. However, bread and durum wheat respond differently to environmental conditions, especially in areas where temperature and drought stress can constrain yield potential during grain filling (Edhaie and Waines 2001; Moragues et al. 2006). Assimilates for grain growth during grain filling come from current photosynthesis and from reserve carbohydrates accumulated before anthesis in vegetative plant part and remobilized into grain during grain filling. Under optimum temperature conditions, photosynthesis provides the greatest part of grain yield of durum wheat, accounting for up to 90% of the carbohydrates in grain while remobilization accounts for only 10–30% (Arduini et al. 2006; Alvaro et al. 2008). For N the reverse is true, as remobilization of pre-anthesis stored N is the primary source of N for durum wheat grain, accounting for 66–82% of grain N content (Papakosta and Gagianas 1991; Edhaie and Waines 2001).

Hot and dry conditions occurring during grain filling reduce photosynthesis rate, limiting the contribution of current assimilates to grain filling (Hafsi et al. 2007; Alvaro et al. 2008; Pampana et al. 2007). In these conditions, remobilization of pre-anthesis reserves becomes particularly important (Tahir and Nakata 2005; Ercoli et al. 2008).

This research was conducted to evaluate the effect of temperature during grain filling on dry matter and nitrogen dynamics in two Italian durum wheat varieties grown with different nitrogen availabilities. Our experiment compared two different temperature regimens, one within the normal range occurring during grain filling in Central Italy, the other within the normal range occurring in the southern regions of Italy. Irrigation was supplied as needed to avoid the confounding effects of water deficit.

Materials and Methods

Full description of the site and detailed procedures in the field experiments have been reported in a previous paper (Ercoli et al. 2009). Briefly, durum wheat varieties Appio and Creso were grown with three N rates (0, 241.4 and 362.1 mg N pot^{-1} calculated on a per surface base and corresponding to 0, 120 and 180 kg N ha^{-1}) and at two regimes of day/night air temperature during grain filling (20/15 °C and 28/23 °C). The three N rates were chosen as: 0 is the unfertilized control, 120 kg N is the rate recommended by the current environmental legislation in Italy, and 180 is the optimal rate for the expected yield. Plants were grown outdoor in pots of 7 L volume containing 7 kg soil until anthesis (stage 60 of the scale of Zadoks et al. 1974). Fertilizers were applied before seeding and were uniformly distributed throughout the volume of soil. Nitrogen was applied as urea. At anthesis plants were placed in two growth chambers per temperature regime. Growing conditions were 14/10 h day/night photoperiod regime at 20/15 °C and 28/23 °C. Photosynthetic photon flux density at the top of the plant canopy was 400 µmol m^{-2} s^{-1}. Relative humidity was kept at 65 ± 5%. Pots were watered regularly to avoid water limitation. The experiment was set up in a split-plot design. Whole plot treatments (temperature regimes) were randomly assigned to the four growth chambers. The experimental unit was one pot, a total of 36 pots in each chamber were used, comprising the factorial combination of two varieties and three N rates. Each combination was replicated three times to ensure a greater accuracy of sampling.

At anthesis and physiological maturity (stage 90) plants were cut at ground level and separated into leaves, culms and spikes at anthesis, and into leaves, culms, chaff and grain at physiological maturity. All plant parts were oven dried at 65 °C to constant weight for dry weight determination. Mean kernel weight, number of kernels per spike, and harvest index (HI) were measured at maturity. Plant samples were analyzed for nitrogen concentration (microKjeldahl) and N contents were calculated by multiplying the N concentration by dry weight.

The following parameters were calculated, following Ercoli et al. (2006), as:

– post-anthesis dry matter (DMA) and N accumulation (NA) = dry matter or N content of the whole plant at physiological maturity – dry matter or N content of the whole plant at anthesis;
– dry matter remobilization (DMR) and N remobilization (NR) = dry matter or N content of vegetative organs or at anthesis – dry matter or N content of vegetative organs at physiological maturity;
– dry matter and nitrogen remobilization efficiency = (DMR or NR / dry matter or N content of the whole plant at anthesis) × 100;
– contribution of dry matter or nitrogen remobilization to grain = (DMR or NR / grain yield or grain N content at physiological maturity) × 100.

For the estimate of DMR and NR it was assumed that all of the dry matter and N lost from vegetative plant parts was remobilized to the developing grain, since losses of dry matter due to plant respiration and losses of N due to volatilization were not determined.

Data were statistically treated by ANOVA, performed separately for each harvest. At anthesis the effects of variety (V), N rate (N), and their interactions were tested and at maturity the effects of variety (V), N rate (N), air temperature regime (T) and their interactions were tested. Significantly different means were separated at the 0.05 probability level by the least significant difference test (Steel et al. 1997).

Results

Plant growth and N uptake at anthesis

At anthesis, only nitrogen fertilization and variety effects were tested, since the temperature regimes were imposed during grain filling. The dry weight and the N concentration and content of all plant parts of both varieties increased with the increase of N rate (Table 1). Creso had lower values of culms, leaves and spikes than Appio at N0 but displayed higher increases owing to N fertilization. Compared to N0, the highest N rate increased dry matter of the aerial plant part by about 3-fold (+258%) in Creso and by 136% in Appio. Thus, at N180 dry weight of plants of cv. Creso were 15% greater than Appio. Corresponding increases of N rate increased N concentration of aerial plant part by 4.6 g kg^{-1} in Appio and 3.2 g kg^{-1} in Creso (absolute value). N content of the aerial plant part was by over 3-fold higher (+331%) in N180 compared to N0 in Appio, and by over 4-fold higher (+466%) in Creso (Table 1). Maybe owing to the increase of both dry weight and N concentration in all plant parts.

Table 1. Dry weight and N concentration and content of culms, leaves, spikes and whole plant at anthesis as affected by N rate

N rate	Culms		Leaves		Spikes	
(kg ha^{-1})	Appio	Creso	Appio	Creso	Appio	Creso
			Dry weight (mg plant^{-1})			
0	771.4 a	542.9 a	228.6 a	214.3 a	114.3 a	85.7 a
120	1628.6 b	1614.3 b	400.0 b	457.1 b	328.6 b	271.4 b
180	1757.1 c	2028.6 c	485.7 c	600.0 c	385.7 c	385.7 c
			N concentration (g kg^{-1})			
0	3.8 a	3.9 a	9.4 a	7.4 a	9.3 a	10.6 a
120	4.6 b	4.5 b	14.9 b	11.7 b	10.5 b	11.2 a
180	7.0 c	5.2 c	18.2 c	17.4 c	13.9 c	13.3 b
			N content (mg plant^{-1})			
0	2.9 a	2.1 a	2.1 a	1.6 a	1.1 a	0.9 a
120	7.5 b	7.3 b	6.0 b	5.3 b	3.5 b	3.0 b
180	12.3 c	10.5 c	8.8 c	10.4 c	5.4 c	5.1 c

Within treatments variety and N rate, numbers followed by the same letter are not significantly different at $P \leq 0.05$.

Post-anthesis responses to temperature

Grain yield and yield components

Grain yield was affected by the interaction of variety, N rate and temperature regime (Fig. 1A). The increase of N rate increased grain yield of Appio and Creso at both temperatures, but increases were higher at the lower one. Thus, at N0 grain yield of both varieties did not differ in response to temperature, while at N180 it was 31% lower at 28/23 °C, compared to 20/15 °C. Moreover, with all N rates, grain yield of the two varieties was similar at 28/23 °C, while at 20/15 °C grain yield of Appio was 16% higher than Creso.

Dry weight of the vegetative plant part (leaves, culms and chaff) was also affected by the interaction of N rate and temperature regime and increased with the increase of N rate, with the increases that were higher at 20/15 °C than at 28/23 °C (Fig. 1B).

Accumulation and remobilization of dry matter

Dry matter accumulation during grain filling was affected by the interaction of variety, N rate and temperature regime (Fig. 2A). At 28/23 °C accumulation of both varieties was practically unaffected by N rate, averaging 45 mg plant^{-1}, while at 20/15 °C accumulation increased with the increase of N rate. At this temperature regime, Appio displayed higher values than Creso with all N rates and with N180 accumulation of dry matter was by 83% higher.

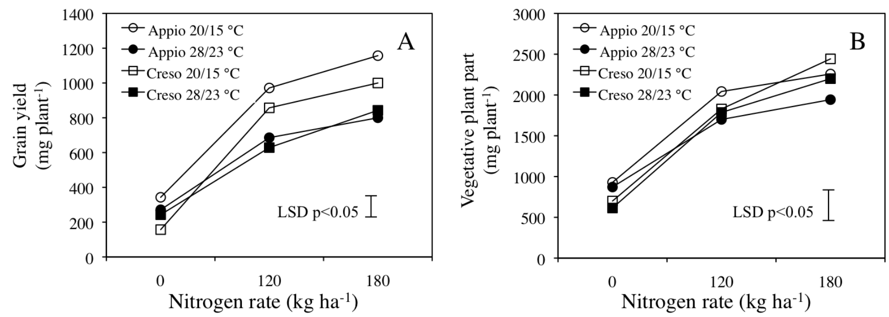

Figure 1. Grain yield (A) and dry weight of vegetative plat part (B) of Appio and Creso at physiological maturity as affected by temperature regime and N rate. In these and in the following figures, vertical bars indicate standard error

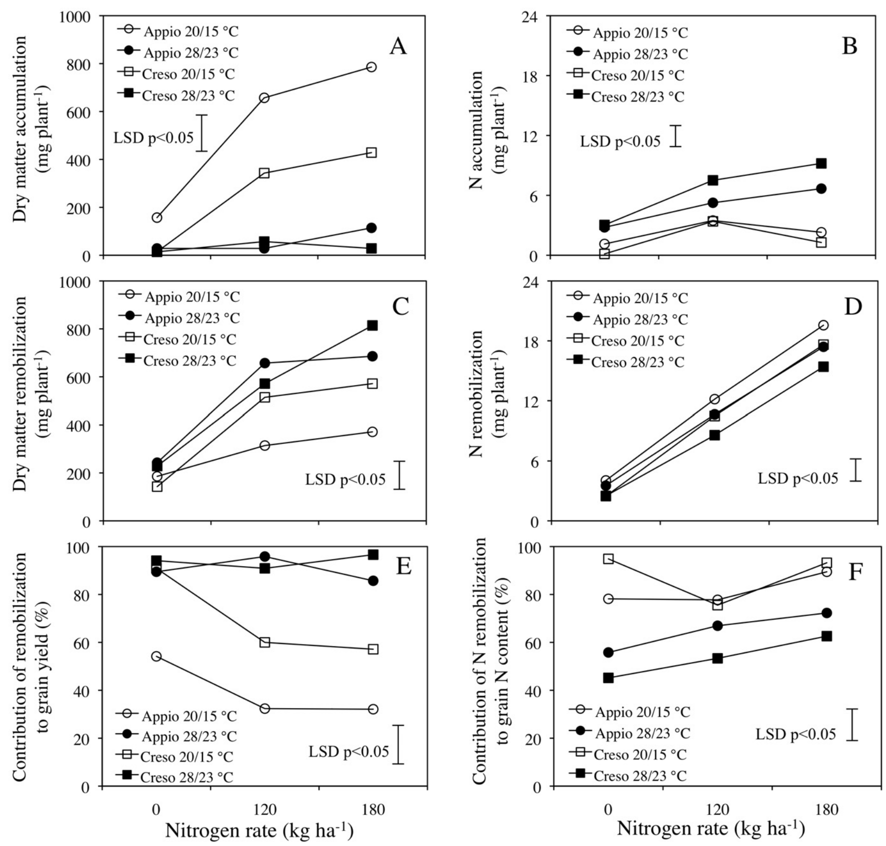

Figure 2. Post-anthesis dry matter (A) and nitrogen (B) accumulation, dry matter (C) and nitrogen (D) remobilization and contribution of dry matter (E) and nitrogen (F) remobilization to grain yield and nitrogen content of Appio and Creso as affected by temperature regime and N rate

Dry matter remobilization during grain filling increased with the increase of N rate, but the increases were greater at 28/23 °C compared to 20/15 °C (Fig. 2C). Differences between varieties were consistent at 20/15 °C at all N rates and at 28/23 °C only with N180. As a consequence, remobilization in unfertilized plants of both varieties was low and unaffected temperature regime, while in plants fertilized with N180 remobilization was consistent, exceeding 370 mg plant^{-1} at 20/15 °C and 680 and mg plant^{-1} at 28/23 °C. Moreover, remobilization was higher in Appio than in Creso.

As a result of the different patterns of accumulation and remobilization of dry matter during grain filling, grain yield relied almost totally on remobilization under the 28/23 °C regime, while at 20/15° C the contribution of remobilization was lower and decreased with the increase of N rate. Moreover, at the 20/15 °C temperature regime, for Appio the relative incidence of remobilization on grain yield was lower than for Creso at all N rates (Fig. 2E).

Remobilization efficiency was not affected by N rate and did not differ between varieties, but increased with the increase of temperature. On average, it was 17% at 20/15 °C and 25.7% at 28/23 °C (results not shown).

In all treatments, the mass of remobilized dry matter was higher than the mass of accumulated dry matter during grain filling, with the exception of Appio at 20/15 °C. For both varieties and at all N rates, the proportion increased with the higher temperature.

Nitrogen uptake

At maturity, N concentration in grain was affected by the interaction between temperature and N rate, but did not differ between varieties. Averaged over varieties, N concentration in grain increased with the increase of temperature and N rate, but values were higher at 28/23 °C. As a consequence, plants exposed to 28/23 °C had 29% higher N concentration in grain, compared to 20/15 °C (Fig. 3A). Nitrogen concentration in vegetative plant parts of both varieties was affected by the interaction of N rate and temperature. The increase of temperature and N rate increased N concentration but the effect of N fertilizer was significant with both 120 and 180 kg N ha^{-1} at 28/23 °C, while at 20/15 °C only with the higher N rate. At all temperatures and N rates, Creso had higher values than Appio (Fig. 3B).

Following the patterns of grain dry weight and N concentration, N content of grain differed between varieties and was affected by temperature regime, while N fertilization did not significantly affect values. At 28/23 °C, grain N content was similar for both varieties (15.4 mg plant^{-1} on average) and was higher compared to 20/15 °C, while at 20/15 °C N content was by 21% higher in Appio than in Creso (Fig. 3C). Nitrogen content of the vegetative plant part was significantly increased by the increase of both temperature and N rate and the effect was greater in Creso with the higher N rate. Consequently, at N0 vegetative N content did not vary among treatments, averaging 2.2 mg plant^{-1}, while at N180 values ranged from 6.9 mg plant^{-1} of Appio at 20/15 °C to 10.7 mg plant^{-1} of Creso at 28/23 °C (Fig. 3D).

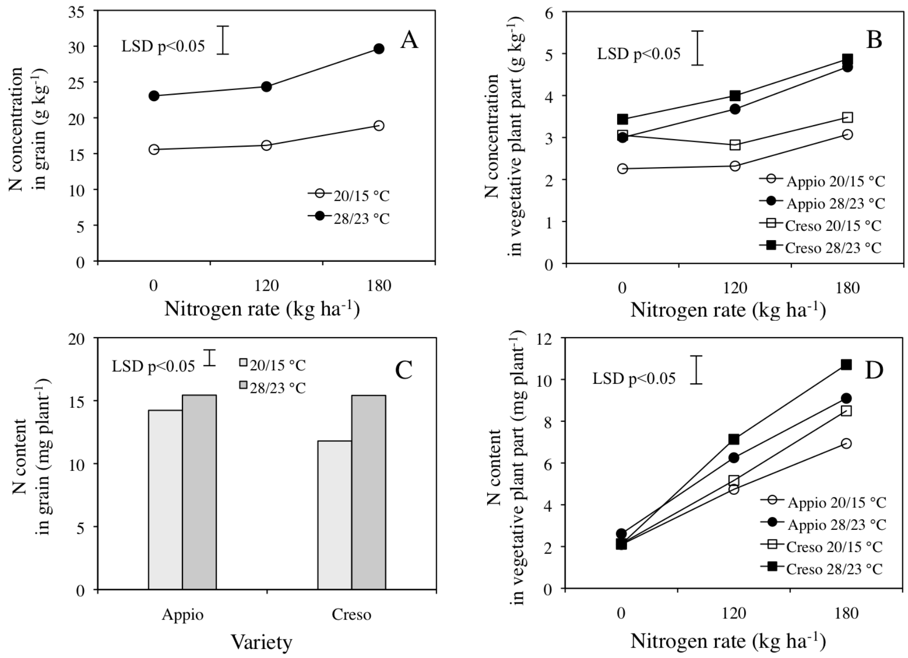

Figure 3. Nitrogen concentration in grain at physiological maturity as affected by temperature regime and N rate (A), nitrogen concentration in vegetative plant part of Appio and Creso as affected by temperature regime and N rate (B), nitrogen content in grain of Appio and Creso as affected by temperature regime (C), and nitrogen content in vegetative plant part of Appio and Creso (D) as affected by temperature regime and N rate

Accumulation and remobilization of nitrogen

Nitrogen accumulation during grain filling of both varieties was significantly influenced by the interaction of N rate and temperature regime. At 20/15°C accumulated nitrogen of both varieties was lower than that at 28/23 °C, and was practically unaffected by N rate. Conversely, at 20/15 °C accumulated N was increased by the increase of N rate and the response of Creso was higher than that of Appio (Fig. 2B).

The amount of post-anthesis remobilized N was also significantly affected by the interaction of variety, temperature regime and N rate. In unfertilized plants, N remobilization was not modified by temperature regime, while in fertilized plants it was increased by N rate and the response to N fertilizer was greater at 20/15 °C than at 28/23 °C (Fig. 2D).

Following the pattern of both accumulated and remobilized N, the contribution of remobilized N to grain N content was higher at 20/15 °C (78–95%) compared to 28/23 °C (45–67%). In both varieties, there were no significant differences in the contribution of remobilization in response to N fertilization at 20/15 °C, while at 28/23 °C the increase of N rate slightly increased values, and Appio showed higher values than Creso (Fig. 2F).

Nitrogen remobilization efficiency was not affected by N rate and did not differ between varieties, but slightly decreased with the increase of temperature. On average, it was 67% at 20/15 °C and 59% at 28/23 °C (results not shown).

Similarly to what observed about dry matter, the remobilization of nitrogen was higher than post-anthesis accumulation in all treatments. For both varieties and at all N rates, the proportion decreased with the higher temperature.

Discussion

Results in literature on bread wheat indicated that temperature above the optimum during grain filling reduced wheat grain yield, as a consequence of the lower rate of dry matter accumulation in kernels and of the duration of grain development (Guedira and Paulsen 2002). The optimum temperature for kernel growth during grain filling is about 15–20 °C in many cultivars and there is a decrease in kernel weight of 1–5% for each 1 °C above this base (Wardlaw and Moncur 1995; Gibson and Paulsen 1999). These findings agree with the results obtained in our research, where the increase of temperature from 20/15 to 28/23 °C reduced grain yield of durum wheat by 3.5% for each 1 °C rise in temperature. In a previous paper, we found that temperature affected grain yield by the reduction of both the duration of all stages of grain development and the rate of accumulation of dry matter in kernels (Ercoli et al. 2009). Conversely, high temperature increased grain N content, since the shortening of the duration of all stages of grain development was compensated for by an increase of the rate of N accumulation in grain. The increase in grain protein content due to the effect of high temperatures is in agreement with other studies on bread and durum wheat (Ciaffi et al. 1996; Labuschagne et al. 2009). Following Triboi and Triboi-Blondel (2002), a compensation phenomenon between the rate of N accumulation and the duration of the process is likely to occur, inexistent at the accumulation level of dry matter. The depositions of starch and proteins in wheat grain are regarded as independent events, which are controlled by separate mechanisms, and the deposition of starch is more sensitive to heat stress than the deposition of proteins (Jenner et al. 1991; Barneix 2007).

Overall, current assimilation and remobilization of dry matter were inversely related: the higher was the former the lower was the latter. At 20/15 °C accumulation of dry matter was similar to remobilization, while at 28/23 °C remobilization was prevailing on accumulation, so that the main source of grain dry matter was remobilization. For N the reverse was true, as at 20/15 °C the prevailing source of N in grain came from current assimilation and at 28/23 °C N accumulation was similar to N remobilization. At the low temperature regime, the slow senescence that is needed for a steady state of photosynthesis might deter mobilization of reserve carbohydrates for export to grain (Blum 1998), while at the high temperature the high water availability in soil does not prevent N uptake. The mechanisms that drive the rate of carbohydrate and protein accumulation in grain, preventing dry matter remobilization from vegetative tissues when photosynthesis rate is high or N remobilization when nitrate supply in soil is abundant, are far from clear (Barneix 2007).

Nitrogen rate increased remobilization of dry matter and N during grain filling and this effect depended exclusively on pre-anthesis growth and N uptake, as remobilization efficiency of both dry matter and N were not modified by N fertilization. This result was consistent with the findings of Papakosta and Gagianas (1991) and Dordas (2009), who showed that application of N fertilizer increased N remobilization but did not affect N remobilization efficiency in both bread and durum wheat.

Varieties differed in their response to temperature. Grain yield of Appio was higher than Creso at 20/15 °C, owing to higher current assimilation during grain filling, while at 28/23 °C grain yield did not vary between varieties and was lower, owing to the negative effect of temperature on assimilation. Thus, the different sensitivity to temperature of the two varieties is probably a consequence of the reliance of assimilates for grain filling on different sources. In Appio kernel filling relies mainly on assimilation, which is more sensitive to temperature.

In conclusion, we have shown that nitrogen fertilization and post-anthesis temperature affected growth, accumulation and partitioning of dry matter and N in durum wheat which, in turn, modified grain yield and N content. Grain yield was better expressed at 20/15 °C, while grain protein concentration was favoured under the 28/23 °C temperature regime. Higher temperature promoted remobilization of dry matter and restrained current photosynthesis, but reduced grain yield, indicating that the loss of photosynthesis could not compensate for the gain from increased remobilization. Grain N content, on the contrary, was promoted under the higher temperature regime, as high temperature reduced N remobilization but did not inhibit root water and nitrogen uptake, given that no water shortage occur.

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