Field Crops Research 117 (2010) 245–257

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Sowing date and nitrogen fertilisation effects on dry matter and nitrogen dynamics for durum wheat: An experimental and simulation study

Roberto Ferrise[a], Andrea Triossi[a], Pierre Stratonovitch[b,c], Marco Bindi[a], Pierre Martre[b,c,*]

[a] *Department of Agronomy and Land Management, University of Florence, Florence, Italy*
[b] *INRA, UMR 1095 Genetic, Diversity and Ecophysiology of Cereals, 234 Avenue du Brezet, F-63 100 Clermont-Ferrand, France*
[c] *University Blaise Pascal, UMR 1095 Genetic, Diversity and Ecophysiology of Cereals, Clermont-Ferrand, France*

ARTICLE INFO

Article history:
Received 9 November 2009
Received in revised form 15 March 2010
Accepted 16 March 2010

Keywords:
Crop simulation model
Dry matter accumulation
Nitrogen accumulation
Nitrogen nutrition
Sowing date
T. turgidum L. subsp. *durum* (Desf.) Husn.

ABSTRACT

The effects of sowing date and nitrogen (N) fertilisation on the dynamics of dry matter (DM) and N accumulation during grain filling and on final grain yield and protein concentration for durum wheat were studied in two field experiments. In addition, the ability of the wheat simulation model *SiriusQuality*1 to simulate grain yield and protein concentration for durum wheat was evaluated. The model simulated the anthesis date and the grain filling duration with a root mean square error of 1.7 and 2.2 days, respectively. The model simulated reasonably well the changes in the dynamics of leaf, stem and grain DM and N in response to sowing date and N fertilisation. Harvest grain yield and protein concentration were simulated with a root mean square error of 0.045 kg DM m^{-2} and 1.25%, respectively. The longer vegetative period with autumn sowing compared with winter sowing resulted in higher crop DM and N at anthesis, which was associated with higher final grain yield. Independently of the sowing date or N fertilisation, post-anthesis DM accumulation contributed 70% to final grain yield. Post-anthesis N accumulation contributed between 25% and 40% to final grain N yield depending on the sowing date and N fertilisation. The efficiency of vegetative DM and N remobilisation was not modified by the sowing date or N fertilisation, averaging 21% and 74%, respectively. Sowing date had larger effects on grain DM yield than on grain N yield and grain protein concentration was significantly higher for the late sowing date than for the normal sowing date. N treatments did not affect crop phenology, but N fertilisation allowed the crops accumulating more DM and N during the vegetative period. In addition, high-N crops, because of their larger canopy, accumulated more DM and N during grain filling than low-N crops, resulting in higher grain yield and protein concentration at harvest. Both grain number per unit ground area and grain yield were closely correlated with crop DM and N at anthesis. Single grain DM was not modified by N availability. Averaged across N treatments, single grain DM varied from 44.2 to 57.3 mg DM grain^{-1}. These variations were almost entirely accounted for by the mean daily maximum temperature calculated for the 15 days prior to anthesis, suggesting that the temperature during the period of active cell division in the ovary is a major determinant of the final size of durum wheat grains.

1. Introduction

Durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn.) is cultivated over more than 13 million hectares world wide and Italy is the main European producer with 3.5 million tons per year. The protein concentration of durum wheat is the main determinant of its end-use value. Its cultivation involves large land areas with intensive nitrogen (N) fertilisation to achieve high yields and protein concentrations. N use efficiency of cereals (i.e. grain yield per unit of available soil and fertiliser N) is still very low, around 33 kg DM kg^{-1} N for most cereals (Raun and Johnson, 1999). In order to optimize the use of chemical N fertiliser by the crop and minimize N volatilisation and the risk of surface and ground water pollution, it is necessary to get a better understanding of the effects of crop management practices on crop dry matter (DM) and N accumulation.

Sowing date is one of the most important management factor affecting cereal production and quality (McLeod et al., 1992). In a given region, the optimum sowing date depends mainly upon the timing of rainfall (Jackson et al., 2000). In most cases, delaying sowing beyond the optimum period reduces wheat yields (Anderson and Smith, 1990; Bassu et al., 2009). Differences in DM and N contents at anthesis in response to sowing date were related to differences in the number of days from sowing to anthesis (Ehdaie and

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[*] Corresponding author at: INRA, UMR 1095 Genetic, Diversity and Ecophysiology of Cereals, 234 Avenue du Brezet, F-63 100 Clermont-Ferrand, France. Tel.: +33 473 624 351; fax: +33 473 624 457.
E-mail address: pierre.martre@clermont.inra.fr (P. Martre).

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doi:10.1016/j.fcr.2010.03.010

Waines, 2001), which for winter bread wheat (*Triticum aestivum* L.) results in large differences in N accumulation (Widdowson et al., 1987). As a consequence, delaying sowing date can cause significant differences of environmental conditions during grain filling, usually causing grains to grow with increasing temperatures and diminishing moisture conditions (Panozzo and Eagles, 1999; Subedi et al., 2007). For durum wheat, post-anthesis DM assimilation accounts for 50–80% of grain DM yield, depending on N and water supplies (Ercoli et al., 2008), the genotype (Arduini et al., 2006; Masoni et al., 2007) and the sowing density (Arduini et al., 2006). By changing the relative duration of the pre-anthesis period and the environmental conditions during the grain filling period, sowing date may significantly modify the contribution of the post-anthesis DM and N accumulation to grain DM and N yields, respectively, as well as the efficiency of vegetative DM and N remobilisation.

N is the major nutrient influencing grain yield and protein concentration (Gauer et al., 1992; Ehdaie and Waines, 2001). Prior to anthesis, N supply affects crop growth and photosynthetic capacity. In winter wheat, N application has large effects on leaf area expansion and duration (Langer and Liew, 1973); which have been associated frequently with grain yield (Slafer and Savin, 1994). The supply of assimilate to grain originates both from current assimilation and from remobilisation of assimilates stored temporarily in vegetative parts during the vegetative period (Austin et al., 1980; Gebbing and Schnyder, 1999; Santiveri et al., 2004). Remobilisation of N accumulated prior to anthesis has been suggested to be the major determinant of mature grain N content (Austin et al., 1977; Cox et al., 1985). However, the contribution of post-anthesis N uptake to mature grain N content may vary between 10% and 70% depending on soil N and water availability and temperature during the grain filling period (Palta and Fillery, 1995; Martre et al., 2006; Mi et al., 2000) and on the genotype (Kichey et al., 2007).

The contribution of post-anthesis DM and N accumulation to grain DM and N yields and the efficiency of vegetative DM and N remobilisation to grains have often been quantified from crop growth analysis (e.g. Cox et al., 1985; Arduini et al., 2006; Ercoli et al., 2008). This method of quantification of N remobilisation and post-anthesis accumulation has been shown to give similar results compared with calculations based on ^{15}N-labelling experiments, although the ^{15}N-labelling method gives lower coefficient of variation (Kichey et al., 2007). As for DM remobilisation and post-anthesis accumulation, several authors have found that the growth analysis method significantly overestimates the contribution of DM remobilisation to grain yield compared with ^{13}C- or ^{14}C-labelling experiments, mostly because the growth analysis method does not take into account the loss of DM due to respiration (e.g. Gebbing and Schnyder, 1999). However, labelling experiments are expensive and difficult to carry out in the field. For this reason very few studies have quantified post-anthesis N and DM remobilisation and accumulation using labelling experiments. In the present study the growth analysis approach has been used to quantify the contribution of post-anthesis DM and N remobilisation and accumulation to grain DM and N yields and the efficiency of vegetative DM and N remobilisation.

Although several studies have documented the effects of sowing date and N nutrition on winter cereal yield and protein concentration, in particular for winter bread wheat, studies on durum wheat are very limited. The aim of this work was to examine the effect of sowing date and N fertilisation on the dynamics of DM and N accumulation during the grain filling period for durum wheat. In addition, the aim was to evaluate the ability of the wheat simulation model *SiriusQuality*1 (Martre et al., 2006) to simulate grain yield and protein concentration for durum wheat in response to sowing dates and N treatments. Few of the existing wheat simulation models have been evaluated for durum wheat. Published studies show either poor (Donatelli et al., 1997) or reasonably accurate (Pala et al., 1996; Pecetti and Hollington, 1997; Bassu et al., 2009) simulation of grain yield responses to N fertilisation or sowing date, but no study has evaluated the ability of wheat simulation models to simulate grain protein concentration for durum wheat.

2. Materials and methods

2.1. Plant material and growing conditions

The durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn.) cultivar Creso was grown in two rain-fed field experiments carried out at the University of Florence, Italy (11°13′E, 43°46′N; 42 m elevation) during the 2002–2003 and 2004–2005 growing seasons (referred below as 2003 and 2005), respectively. In 2003, the experiment was in a field where the previous crop was a 3-year lucerne stand, the soil was a sandy loam (7.0% clay, 39.9% silt) to 1.5 m. The top soil (0–40 cm layer) had an apparent bulk density of 1.59 Mg m^{-3} and contained 4.5 Mg N ha^{-1} of organic N with a C-to-N ratio of 12.1 and a pH of 6.9. In 2005, the experiment was in a field where the previous crop was a sunflower. The soil was a clay loam (36.1% clay, 30.7% silt) to 1.2 m. The top soil had an apparent bulk density of 1.30 Mg m^{-3} and contained 6.12 Mg N ha^{-1} of organic N with a C-to-N ratio of 13.3 and a pH of 8.5.

Seeds were sown at a density of 150 seeds m^{-2} on 11 December 2002 and 05 November 2004 (normal sowing, treatments termed 03SD1 and 05SD1, respectively), and 27 January 2003 and 18 January 2005 (late sowing, 03SD2 and 05SD2, respectively) using a 12-row planter with 0.22-m row spacing. Four N treatments were applied with a total of 0, 6, 12 and 18 g N m^{-2} (treatments termed N0, N6, N12 and N18, respectively); one-third of which was applied as ammonium sulphate at growth stage (GS) 15/22 (5th leaf emerged at 50%, 2 tillers visible) and the remaining two third as ammonium nitrate at GS 31 (first stem node detectable). The plots were arranged in a randomized complete block split-plot design with three blocks, where the main plots corresponded to the sowing dates. The sub-plots were 3 m × 2 m. The gaps between the sub-plots were sown as the experimental sub-plots.

2.2. Phenophase, plant sampling and total N concentration determination

Within each sub-plot, 20 plants were randomly tagged and their phenological development monitored. The occurrence of a phenophase was set when it was reached by the 50% of the monitored plants. In both years GS 10 (first leaf through coleoptile), GS 31, GS 39 (male meiosis), GS 59 (heading) and GS 65 (anthesis) were determined as described in Tottman (1987) by daily inspection in the field. In 2005, GS 11 (first leaf emerged at 50%) to 16 (6th leaf emerged at 50%) were also determined and the phyllochron were estimated as the slope of decimal leaf number against thermal time accumulated since emergence (all $r^2 > 0.995$, $P < 0.001$, *d.f.* = 5). The final leaf number was estimated from the date of GS 39 and the calculated phyllochron for leaf 1–6.

In 2005, two samplings were carried out at GS 15/22 and 31 one day before N fertilisers were applied. Two adjacent 0.5-m long rows were sampled within each plot. The whole samples were oven dried at 80 °C for 48 h and their DM and N concentrations were determined.

After anthesis, 16 whole main shoots were randomly sampled from each sub-plot every 5–7 days starting at GS 71 (kernel watery ripe; in 2003) or at GS 65 (in 2005). In the laboratory, leaves, stems, and spikes were separated; spikes were hand threshed and grains were counted. For each plant component, DM was determined after oven drying at 80 °C for 48 h. Grain DM was determined on sub-samples (ca. one-third of the whole sample weight), the remaining

Table 1
*SiriusQuality*1 genotypic parameters used for the durum wheat cultivar Creso.

Parameter	Description	Unit	Value	Reference
TTSOMEM	Thermal time from sowing to emergence	°Cdays	185	Martre et al. (2006)
GFD	Grain filling duration	°Cdays	750	Triboi et al. (2003)
P	Phyllochron	°Cdays	87	Giunta et al. (2001)
PhyllFFLanth	Number of phyllochron between flag leaf ligule appearance and anthesis	Phyllochron	3	Giunta et al. (2001)
SLDL	Daylenght response	leaf h^{-1}	1.15	Giunta et al. (2001)
L_{min}	Minimum possible leaf number	Leaf	7	Brooking et al. (1995)
AreaPLL	Maximum potential surface area of the penultimate leaf	cm^2 $leaf^{-1}$	25	Alvaro et al. (2008) Fois et al. (2009)
K_L	Light extinction coefficient	m^2 soil m^{-2} leaf	0.45	Moreau et al., unpublished data
LUE	Maximum potential light use efficiency	g DM MJ^{-1}	3.4	Fischer (1993)

grains were freeze-dried and stored in vacuum seal bags until N concentration determination.

All samples were milled using a rotor mill (Cyclomill, PBI, UK) and their total N concentration was determined with the Dumas method (AOAC method n° 7.024) using a FlashEA 1112 NC Analyser (Thermo Electron Corp., Waltham, MA, USA). Grain protein concentration was calculated from the concentration of total N by multiplying by a conversion factor of 5.62 (Mossé et al., 1985).

2.3. Calculation of the efficiency of DM and N remobilisation, of the contributions of DM and N accumulated during the grain filling period to final grain DM and N yields, and of the rate and duration of grain DM and N accumulation

The efficiency of DM and N remobilisation and the contribution of DM and N accumulated during the grain filling period to final grain DM and N yields, were calculated using the growth analysis approach (Cox et al., 1985) modified as described below. The quantity of vegetative DM and N remobilised during the grain filling period was calculated as the differences between maximum (post-anthesis) and final DM and N of vegetative organs (leaves, stems, and chaffs), respectively. The efficiency of DM and N remobilisation was then calculated as the quantity of DM and N remobilised during the grain filling period divided by the maximum vegetative DM and N, respectively. The quantity of DM and N accumulated during the grain filling period was calculated as the differences between final grain DM and N yields and the quantity of vegetative DM and N remobilised during the grain filling period, respectively. The contributions of DM and N accumulated during the grain filling period to final grain DM and N yields were then calculated as the quantity of DM and N accumulated during the grain filling period divided by the final grain DM and N yields, respectively.

To determine the rate and duration of accumulation of grain DM and N, single grain DM and N contents versus thermal time after anthesis were fitted with a three-parameter logistic function equation:

$$Q(t) = \frac{Q_{max}}{1 + 0.05\ \exp(-4r(t - t_{95})/Q_{max})} \qquad (1)$$

where Q is the quantity of DM or N, t is accumulated thermal time after anthesis, and Q_{max} is the final value of Q approached as $t \to \infty$, r is the maximum rate of accumulation defined as the derivative of the point of inflexion, and t_{95} is the duration of accumulation defined as the duration, from anthesis, in which 95% of Q_{max} is accumulated.

2.4. Parameterisation of the wheat simulation model SiriusQuality1

The dynamics of crop N and DM and soil N and water were simulated for the different experimental treatments using the wheat simulation model *SiriusQuality*1 v1.5, which consists of submodels that describe on a daily time step crop phenology (Jamieson et al., 1998a), canopy development (Lawless et al., 2005), crop evapotranspiration and soil N and water balances (Addiscott and Whitmore, 1991; Jamieson et al., 1998b), crop biomass and N accumulation and partitioning (Martre et al., 2006), including responses to shortages in the supply of soil water and N.

Soil input parameters were estimated as the following: the volumetric soil water contents at field capacity and permanent wilting point were defined as the volumetric soil water contents at a soil water potential of −0.033 MPa and −1.50 MPa, respectively, and were calculated from the soil textural analysis and apparent bulk density using Campbell's pedotransfer function (Campbell, 1985). The calculated soil available water content was 150 and 199 mm for the 2003 and 2005 experiments, respectively. Saturated soil volumetric moisture content was calculated from the soil apparent bulk density considering a density of soil particles of 2.65 $Mg\,m^{-3}$. The soil water percolation coefficient was calculated from the clay content (Addiscott and Whitmore, 1991) and was set at 1.0 and 0.7 for the 2003 and 2005 soils, respectively.

The soil N mineralisation constant was calculated using the 03SD1 N0 and 05SD1 N0 treatments from the observed crop N at anthesis and the soil organic and inorganic N contents in the 0–40 cm layer at sowing by minimizing the following function:

$$\sum K_0 \times N_0 \times F(T_a) - \left(\frac{N_{crop}^{anth}}{0.5}\right) - N_i \qquad (2)$$

where K_0 (d^{-1}) is the mineralisation constant, N_0 ($g\,N\,m^{-2}$) is the soil organic N in the 0–40 cm layer, F (dimensionless) is the soil temperature function for N mineralisation used in *SiriusQuality*1 (Jamieson et al., 1995), T_a (°C) is the mean daily air temperature, N_{crop}^{anth} ($g\,N\,m^{-2}$) is the crop N content at anthesis, N_i ($g\,N\,m^{-2}$) is the soil inorganic N in the 0–40 cm layer at sowing, and 0.5 (dimensionless) is the soil N utilisation coefficient. Minimizing Eq. (2) gave values of K_0 of 7.61×10^{-5} and $4.15 \times 10^{-5}\,d^{-1}$ for the 2003 and 2005 soils, respectively.

The six genotypic parameters required in *SiriusQuality*1 were estimated from data reported in the literature (Table 1). The phyllochron and the flag leaf ligule to anthesis duration were estimated for the cultivar Creso by Giunta et al. (2001). Creso is a spring cultivar (it has no cold requirement), but it is very photoperiod sensitive (Motzo and Giunta, 2007). In *SiriusQuality*1 the final leaf number (FLN) for spring cultivars is calculated from the daylength of the day the last leaf primordium (DL) occurs:

$$\text{FLN} = \min(L_{min}, L_{min} + \text{SLDL} \times (D_{sat} - \text{DL})) \qquad (3)$$

where D_{sat} (h) is the saturating daylength at which the minimum possible FLN (L_{min}) occurs and SLDL (leaves h^{-1}) is the rate of increase of FLN per hour of daylength less than D_{sat}. D_{sat} is a generic parameter set at 15.0 h (Brooking et al., 1995). L_{min} and SLDL are genotypic parameters. L_{min} was fixed at 7.0 (Brooking et al., 1995) and SLDL was estimated using Eq. (3) and the daylength at single ridge and final leaf number reported by Giunta et al. (2001) for Creso. In *SiriusQuality*1 differences in canopy growth between cultivars are described by the surface area of the penultimate

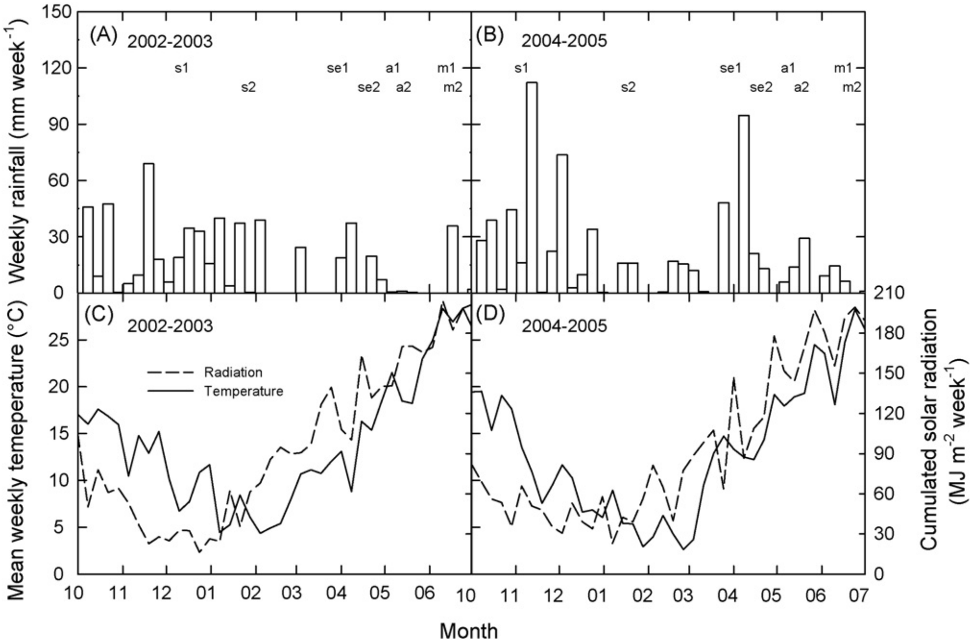

Fig. 1. Cumulated weekly rainfall (A and B) and mean weekly temperature and cumulated solar radiation (C and D) for the 2002–2003 (A and C) and 2004–2005 (B and D) growing seasons at Florence, Italy. The letters indicate sowing (s), beginning of stem extension (se), anthesis (a), and crop maturity (m) dates for each sowing date and the number after the letters indicates the sowing treatment (1 for the November/December sowings, and 2 for the January sowings).

leaf. This parameter was estimated from the flag leaf surface area reported by Alvaro et al. (2008) and Fois et al. (2009) for the cultivar Creso, considering a ratio of surface area between the flag leaf and the penultimate leaf of 0.8 (default value in *SiriusQuality*1). The remaining genotypic parameters were derived from other cultivars (Table 1).

2.5. Statistical analysis

All statistical analyses were done using SPSS for Windows 17.0.0 (SPSS Inc., Chicago, IL, USA). Split Plot ANOVA ($\alpha = 0.05$) was performed to analyze the dry mass and nitrogen data. The main effect of each factor and their interactions were tested using the appropriate standard error terms following Cochran and Cox (1964). Percentage values were analyzed on Bliss angular transformed data (Landi, 1977). Differences between N fertilisation treatments were identified with a *post hoc* Duncan test. Simulated and observed values of grain DM and N yields and protein concentration were compared by least square linear regression of simulated versus observed values and root mean square error (RMSE). RMSE is the standard deviation of mean of the squared deviations around the 1:1 line in a plot of model simulation against measured values. To gain further insight into model performance, the mean square error was partitioned into three components (Gauch et al., 2003): non-unity slope (rotation around the 1:1 line), square bias (translation), and lack of correlation (scattering).

3. Results

3.1. Weather conditions

The two seasons differed greatly in the amount and distribution of rainfall (Fig. 1A and B). In 2003, between sowing and anthesis the crops received a total amount of 250 and 159 mm of rain for 03SD1 and 03SD2, respectively; while in 2005, for the corresponding sowing dates the crop received 530 mm and 304 mm. From anthesis to the end of grain filling, rainfalls were only 25 and 8 mm for 03SD1 and 03SD2, respectively, and 69 and 30 mm for 05SD1 and 05SD2, respectively.

Mean daily temperatures during the growing season were on average 1 °C higher in 2003 than in 2005 (Fig. 1C and D). In 2003, temperatures were on average 1.6 °C warmer for 03SD2 than for 03SD1, while in 2005, temperatures during the vegetative and reproductive growth periods were 1.1 °C and 1.5 °C higher for 05SD2 than for 05SD1. Cumulated global solar radiations during the pre-anthesis period were similar for the two growing seasons, averaging 1790 and 1307 MJ m^{-2} for SD1 and SD2, respectively. The cumulated global solar radiation from anthesis to the end of grain filling ranged from 782 MJ m^{-2} for 03SD2 to 927 MJ m^{-2} for 05SD1.

3.2. Phenology

No differences in phenology were observed among the N treatments (data not shown). The crop growth cycle (from emergence to the end of grain filling) was 54 and 111 days shorter for SD2 compared with SD1 in 2003 and 2005, respectively. This difference was mainly due to a shortening of the pre-anthesis period for the late sowing date. On average, the late sowing date delayed the anthesis date by 8 days and reduced the duration of grain filling by 4 days (Table 2). *SiriusQuality*1 simulated well the effect of sowing date on the timing of anthesis (Table 2). The anthesis date and the duration of grain filling were simulated with a RMSE of 1.7 and 2.2 days, respectively.

The phyllochron and the final leaf number were determined in 2005. The phyllochron was significantly higher for 05SD1 than for 05SD2 (149 °Cdays vs 85 °Cdays), while the final leaf number was similar for both sowing dates, averaging 9.8 leaves (Table 2). The final leaf number was accurately simulated for 05SD2, but it was overestimated by 3 leaves for 05SD1. In 2003, the simulated final leave number was also higher for 03SD1 than for 03SD2 (Table 2).

3.3. Dry mass dynamics and partitioning

There was no significant sowing date by N interaction for the dynamics of vegetative or grain DM. At GS 15/22 and 31 crop DM

Table 2
Observed and simulated anthesis date, duration of grain filling, and final leaf number for crops of durum wheat grown in Florence, Italy, during the 2002–2003 (2003) and 2004–2005 (2005) growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). The numbers in parenthesis are the differences in days between observed and simulated anthesis date and grain filling duration. The observed duration of grain filling was estimated using a three-parameter logistic function.

Year	Sowing treatment	Anthesis date		Grain filling duration (day)		Final leaf number	
		Observed	Simulated	Observed	Simulated	Observed	Simulated
2003	SD1	07 May	6 May (−1)	35	36 (+1)	–	11.1
	SD2	14 May	13 May (−1)	30	34 (+4)	–	9.8
2005	SD1	09 May	06 May (−3)	38	37 (−1)	9.7	12.7
	SD2	18 May	18 May (0)	34	35 (+1)	9.8	9.7
	RMSE (days)	1.7		2.2		2.1	

was 143% and 287% higher for SD1 compared with SD2, but the differences among N treatments were not statistically significant (data not shown). At anthesis, leaf, stem (including the true stem, the sheaths of the culm leaves and the chaffs) DM increased with N fertilisation up to 12 g N m^{-2} and as illustrated in Fig. 2 for the N0 and N18 treatments the differences among N treatments were conserved during grain filling. Anthesis leaf and stem DM were on average 22% and 15% higher for SD1 than for SD2. Stems DM increased by 21% and 32% during the first 14 days after anthesis for SD1 and SD2, respectively; afterwards, years it decreased until the end of grain filling. For SD1, leaf DM showed a continuous decrease from anthesis to the end of grain filling, while for SD2, it started decreasing only 13 days after anthesis.

*SiriusQuality*1 reproduced reasonably well the patterns of leaf and stem DM during the growing season and it was also able to reproduce the effects of N treatments and of sowing dates on leaf and stem DM (Fig. 2). A closer look at the results shows that the model underestimated leaf DM for N0 in both years and for both sowing dates (Fig. 2A and B). For SD2, the model underestimated stem DM for all N treatments (Fig. 2C and D). In 2003 simulated stem DM started to decrease 3–19 days earlier than observed stem DM (Fig. 2C).

The dynamics of single grain DM followed the typical S-shaped curve and were well fitted by the three-parameter logistic function (all $r^2 > 0.98$, $P < 0.001$). As illustrated in Fig. 3 for 2005, N fertilisation did not affect the kinetics of grain DM. The duration in thermal time of grain filling was not affected by the sowing date, averaging 763 ± 11 °Cdays. However, the maximum rate of grain DM accumulation per unit of thermal time was 8% higher for 05SD2 compared with 05SD1, resulting in 14% larger grain DM at harvest for 05SD2 compared with 05SD1. In contrast, in 2003, single grain DM was 5% higher for 03SD1 than for 03SD2 (46.7 ± 0.5 vs 44.2 ± 0.5 mg DM grain^{-1}), which was mostly due to a higher duration of grain filling for SD1 (764 ± 19 vs 688 ± 26 °Cdays). The differences in sin-

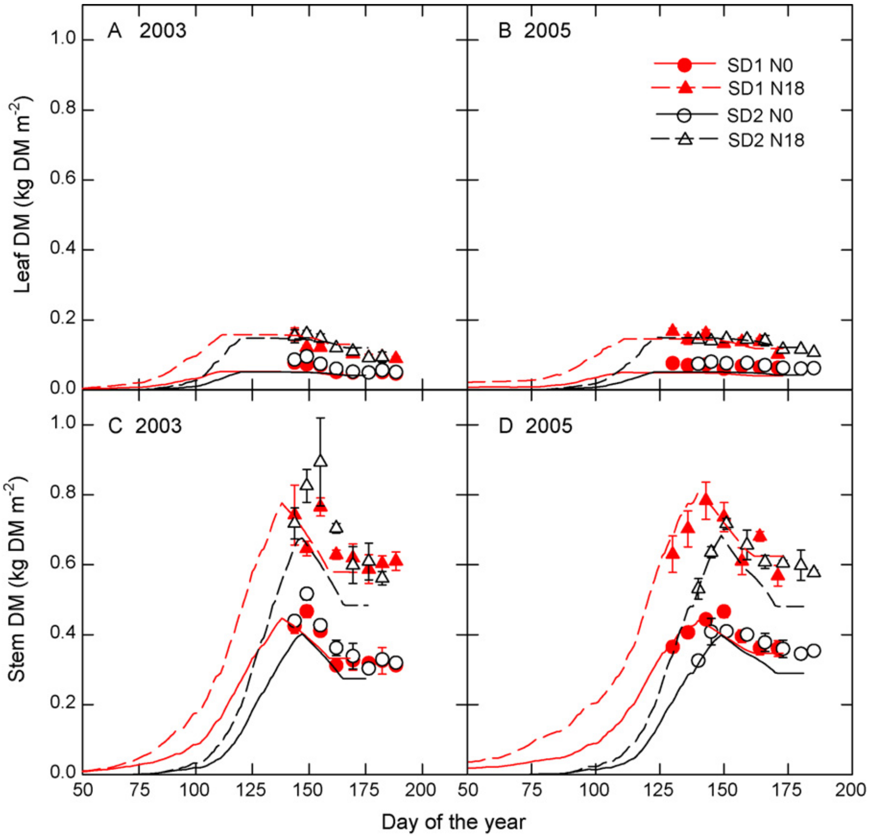

Fig. 2. Observed (symbols) and simulated (lines) leaf (A and B) and stem (C and D) DM per unit ground area versus the day of the year for crops of durum wheat grown in Florence, Italy, during the 2002–2003 (A and C) and 2004–2005 (B and D) growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). Data are presented for the lowest (N0) and highest (N18) rates of N fertilisation. The stem includes the true stem, the sheaths of the culm leaves and the chaffs.Observed data are average ± 1 s.e. for $n = 3$ independent replicates.

gle grain DM due to the year or the sowing date were observed as early as 14 days after anthesis—i.e., at 260–290 °Cdays after anthesis, which correspond to the end of the period of active cell division in the endosperm (Singh and Jenner, 1982; Nicolas et al., 1984). However, no significant correlation was observed between the mean daily temperature ($r < 0.53$; $P = 0.48$), the mean daily maximum temperature ($r < 0.41$; $P = 0.58$), or the number of days with maximum daily temperature above 30 °C ($r < 0.64$; $P = 0.36$) or 35 °C ($r = 0$) calculated for the 15 days after anthesis and single grain DM. Interestingly, the variations of single grain DM in response to the year and the sowing date were almost entirely accounted for by the mean daily maximum temperature calculated for the 15 days prior to anthesis ($r = -0.998$; $P = 0.002$; Fig. 3 inset).

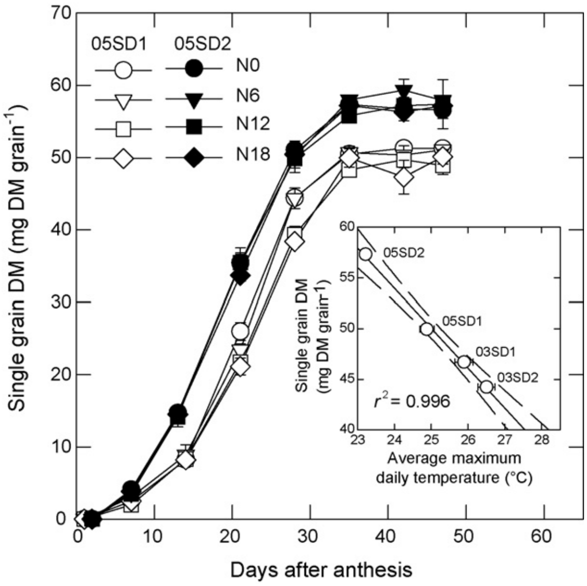

Fig. 3. Single grain DM versus the number of days after anthesis for crops of durum wheat grown in Florence, Italy, during the 2004–2005 growing season. The crops were sown on 5 October (05SD1, open symbols) or on 18 January (05SD2, closed symbols) and received 0 (N0), 6 (N6), 12 (N12), or 18 (N18) g N m^{-2}. Inset, final single grain DM versus mean daily maximum temperature calculated for the 15 days prior to anthesis. Solid line, linear regression ($y = -3.85 \pm 0.18x \pm 148.83 \pm 4.59$, $r^2 = 0.996$, $P < 0.001$); dashed lines, 95% confidence intervals. Data are average ± 1 s.e. for $n = 3$ independent replicates.

3.4. Nitrogen dynamics and partitioning

Similarly to crop DM, at GS 15/22 and 31 crop N was 133% and 267% higher for SD1 compared with SD2, but the differences among N treatments were not statistically significant (data not shown). At anthesis, leaf and stem N contents increased with the rate of N fertilisation (Fig. 4). For a given N treatment, leaf and stem N contents were higher for SD1 than for SD2. Leaf N content was fairly constant during the 14 days after anthesis (Fig. 4B), whereas during that period stem N content increased by 8% and 19% for N0 and N18, respectively (Fig. 4D). For both sowing dates stem and leaf N contents started to decrease 14 days (i.e. ca. 300 °Cdays) after anthesis. Between 14 days after anthesis and the end of grain filling, the N concentration of each organ decreased with a constant relative rate (data not shown) and the leaves and the stem contributed equally to grain N.

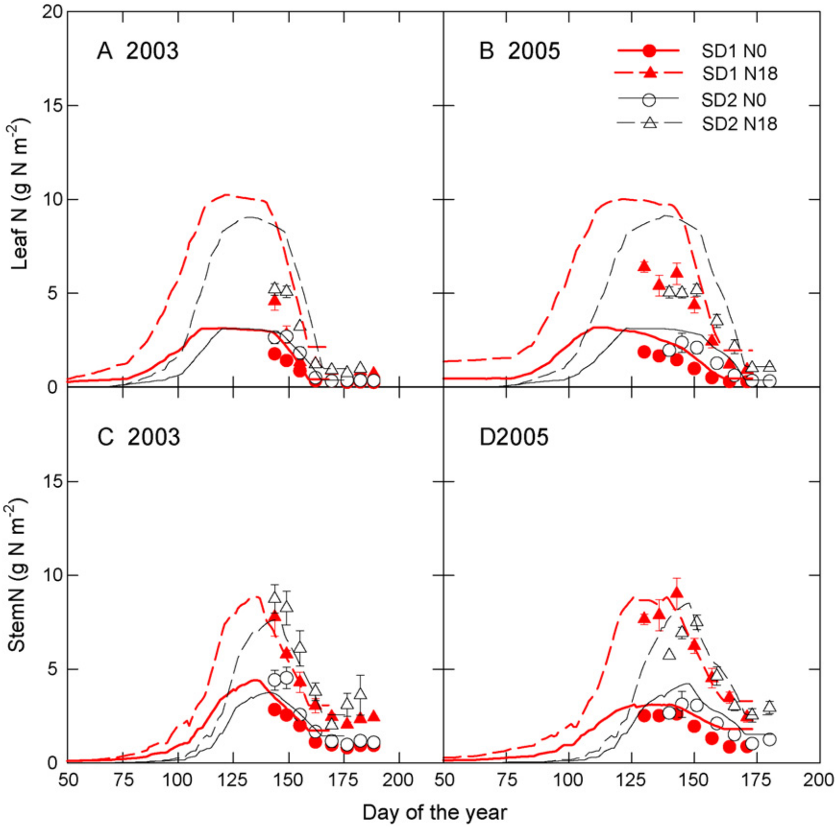

Fig. 4. Observed (symbols) and simulated (lines) leaf (A and B) and stem (C and D) N contents per unit ground area versus the day of the year for crops of durum wheat grown in Florence, Italy, during the 2002–2003 (A and C) and 2004–2005 (B and D) growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). Data are presented for the lowest (N0) and highest (N18) rates of N fertilisation. The stem includes the true stem, the sheaths of the culm leaves and the chaffs. Observed data are average ± 1 s.e. for $n = 3$ independent replicates.

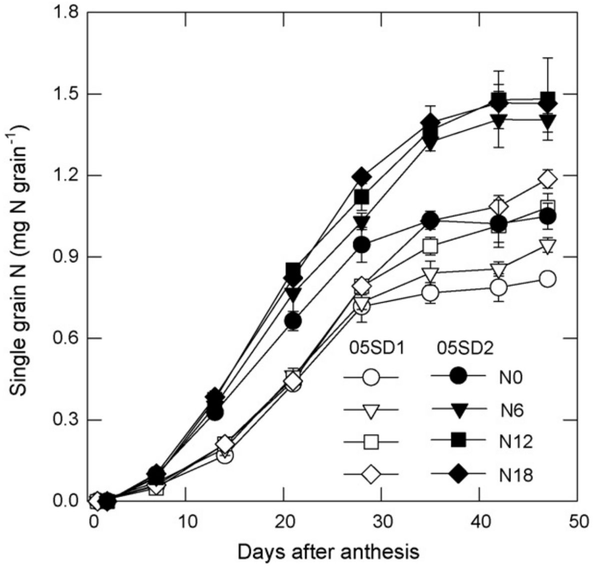

Fig. 5. Single grain N content versus the number of days after anthesis for crops of durum wheat grown in Florence, Italy, during the 2004–2005 growing season. The crops were sown on 5th October (05SD1, open symbols) or on 18 January (05SD2, closed symbols) and received 0 (N0), 6 (N6), 12 (N12), or 18 (N18) g N m^{-2}. Data are average ± 1 s.e. for $n = 3$ independent replicates.

Under high-N availability, *SiriusQuality*1 significantly overestimated leaf N content at anthesis (Fig. 4A and B). Under low N, the model simulated much closely the pattern of leaf N content. The model simulated well the rate of decrease of leaf N content during the linear grain filling period, but simulated leaf N content started to decrease about 7 days latter than observed. The time course of stem N was well simulated by the model under all experimental conditions.

Both the sowing date and the rate of N fertilisation had significant effects on the rate and duration of single grain N accumulation and the sowing date by N interaction was significant for the rate but not for the duration of grain N accumulation (Fig. 5). The maximum rate of grain N accumulation increased in response to N fertilisation by 12% and 30% for 05SD1 and 05SD2, respectively. Similarly, the duration of grain N accumulation increased, in response to N fertilisation by 25% (from 740 ± 42 °Cdays to 924 ± 32 °Cdays) and 9% (from 753 ± 49 °Cdays to 824 ± 32 °Cdays) for 05SD1 and 05SD2, respectively. On average, the maximum rate of grain N accumulation was 35% higher for 05SD2 compared with 05SD1, but the duration of grain N accumulation was not modified by the sowing date. Final grain N content increased in response to N fertilisation by 41%, and, for a given N treatment, it was in average 39% higher for 05SD2 than for 05SD1. Similar results for the kinetics of grain N were observed in 2003 (data not shown).

3.5. *Yield components*

The number of spike per unit ground area was not significantly different among the sowing dates and years, but it increased from 176 ± 30 spikes m^{-2} for the N0 treatments to 297 ± 30 spikes m^{-2} for the N18 treatments. Significant sowing date by N fertilisation interactions was observed for the number of grain per spike and per unit ground area. The number of grain per spike increased in response to N fertilisation by 29% and 10% for the normal and late sowing, respectively (Fig. 6A). With the exception of the lowest N treatment, the number of grain per spike was higher for SD1 than for SD2 and the differences increased 3.5-folds in response to N fertilisation. Similar effects of sowing date and N treatments were observed for the number of grain per unit ground area, but in contrast with the number of grain per spike, the number of grain per unit ground area was more sensitive to N supply than to sowing date (Fig. 6B).

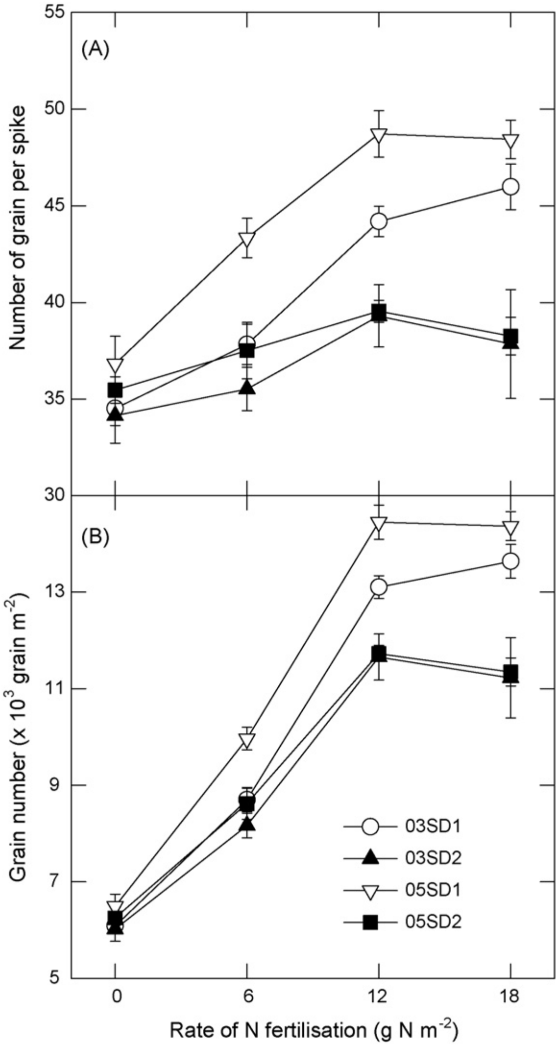

Fig. 6. Grain number per spike (A) and per unit ground area (B) versus the rate of N fertilisation for crops of durum wheat grown in Florence, Italy, during the 2002–2003 and 2004–2005 growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). Data are average ± 1 s.e. for $n = 3$ independent replicates.

As a consequence, the observed variations in the number of grain per unit ground area in response to changes in sowing date were mainly due to differences in the number of grain per spike; while N fertilisation increased both the number of spike per unit ground area and the number of grain per spike. Although the causes (tillering or spike fertility) of the observed variations of grain number per unit ground area in response to sowing date and N fertilisation were not the same, there was a unique linear relationship between grain number per unit ground area and crop DM at anthesis (Fig. 7A). The number of grain per unit of ground area was also strongly correlated with crop N content at anthesis (Fig. 7B).

3.6. *Observed grain DM and N yields and grain protein concentration and contributions of post-anthesis DM and N accumulation to grain DM and N yields*

Variations of grain DM yield resulted from year by N treatment and sowing date by N treatment interactions. When considering all experimental conditions, grain DM yields ranged from 0.26 to

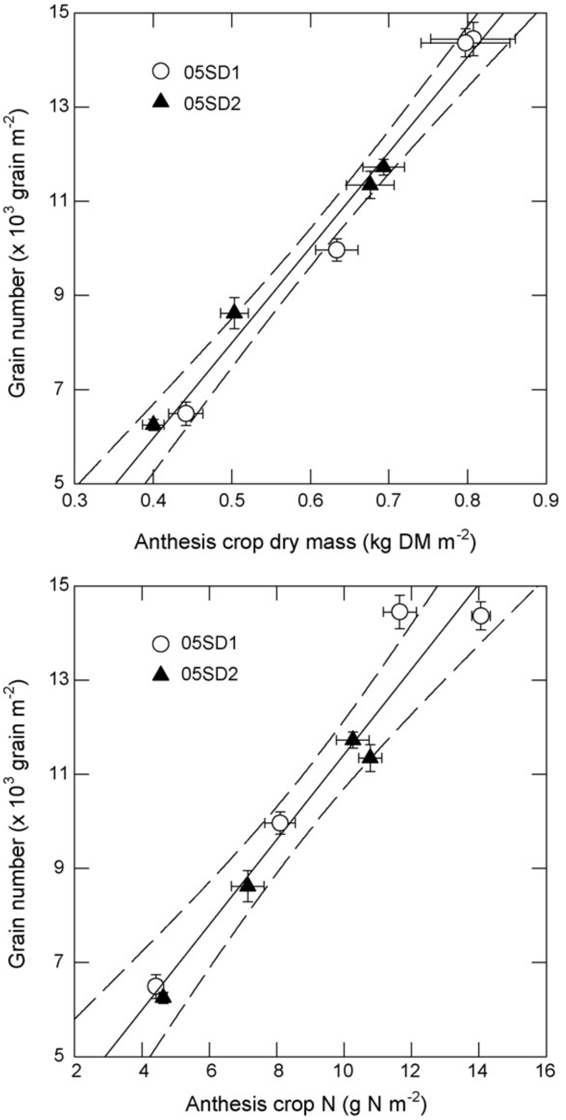

Fig. 7. Grain number per unit ground area versus anthesis crop DM (A) and anthesis crop N (B) for crops of durum wheat grown in Florence, Italy, during the 2004–2005 growing season. Solid lines, linear regressions (A, $y = 2.02 \pm 0.11x - 21301 \pm 719$, $r^2 = 0.98$, $P < 0.001$; B, $y = 90.4 \pm 8.7x \pm 2375 \pm 821$, $r^2 = 0.97$, $P < 0.001$); dashed lines, 95% confidence intervals. Data are average ± 1 s.e. for $n = 3$ independent replicates.

0.71 kg DM m^{-2} (Fig. 8A). Grain yield was closely correlated with both grain number per unit ground area ($r = 0.93$; $P < 0.001$; for 2003 and 2005) and crop DM at anthesis ($r = 0.96$; $P < 0.001$; for 2005). In 2005, the quantities of vegetative DM remobilised and assimilated during grain filling increased by 90% and 100%, respectively, with N fertilisation, but were not modified by the sowing date (data not shown). During grain filling, 21% of the vegetative DM was remobilised, independently of N supply or sowing date (Fig. 8B), which contributed 30% of grain yield (Fig. 8C).

On average, grain N yield was 74%, 161%, and 165% higher for N6, N12, and N18 compared with N0 (Fig. 9A). The quantity of vegetative N remobilised during grain filling increased in response to N fertilisation by 256% and 105% for 05SD1 and 05SD2, respectively (data not shown). However, the efficiency of vegetative N remobilisation during grain filling was not modified by N fertilisation, but it was 4% higher for 05SD1 than for 05SD2, averaging 74% (Fig. 9B). Both sowing dates and N treatments affected post-anthesis N uptake, but sowing date by N interaction was not significant. The quantity of N accumulated during grain filling increased in response to N fertilisation by 90% and 280% for 05SD1 and 05SD2, respectively. The contribution of post-anthesis N to final grain N yield was higher for 05SD2 than for 05SD1 (40% vs 25%; Fig. 9C). Surprisingly, the contribution of post-anthesis N to final grain N yield was not statistically different among sowing dates or N treatments.

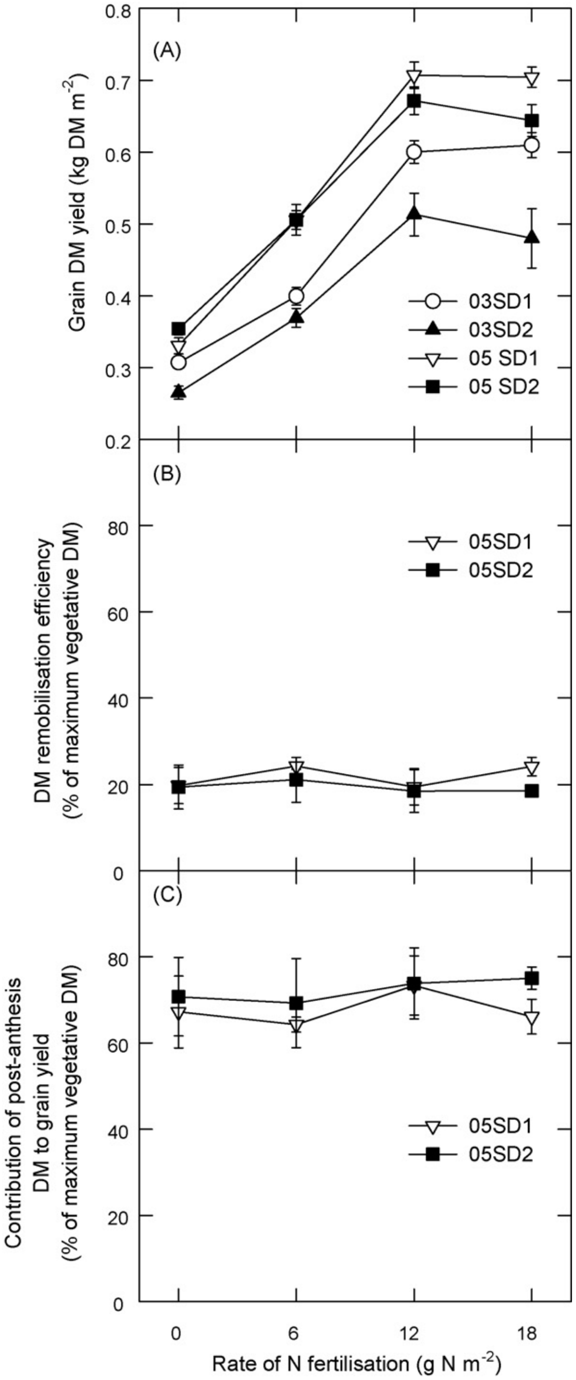

Fig. 8. Grain DM yield (A), DM remobilisation efficiency (B), and contribution of post-anthesis DM to grain DM yield versus the rate of N fertilisation for crops of durum wheat grown in Florence, Italy, during the 2002–2003 and 2004–2005 growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). Data are average ± 1 s.e. for $n = 3$ independent replicates.

There was a significant interaction between year, sowing date and N treatment for grain protein concentration (Fig. 10). Within N treatments, grain protein concentration was not correlated with grain yield (all $r < 0.141$). Averaged over N treatments, grain protein concentration was 5.3% and 19.7% higher for the late than for the normal sowing in 2003 and 2005, respectively. In 2003, grain

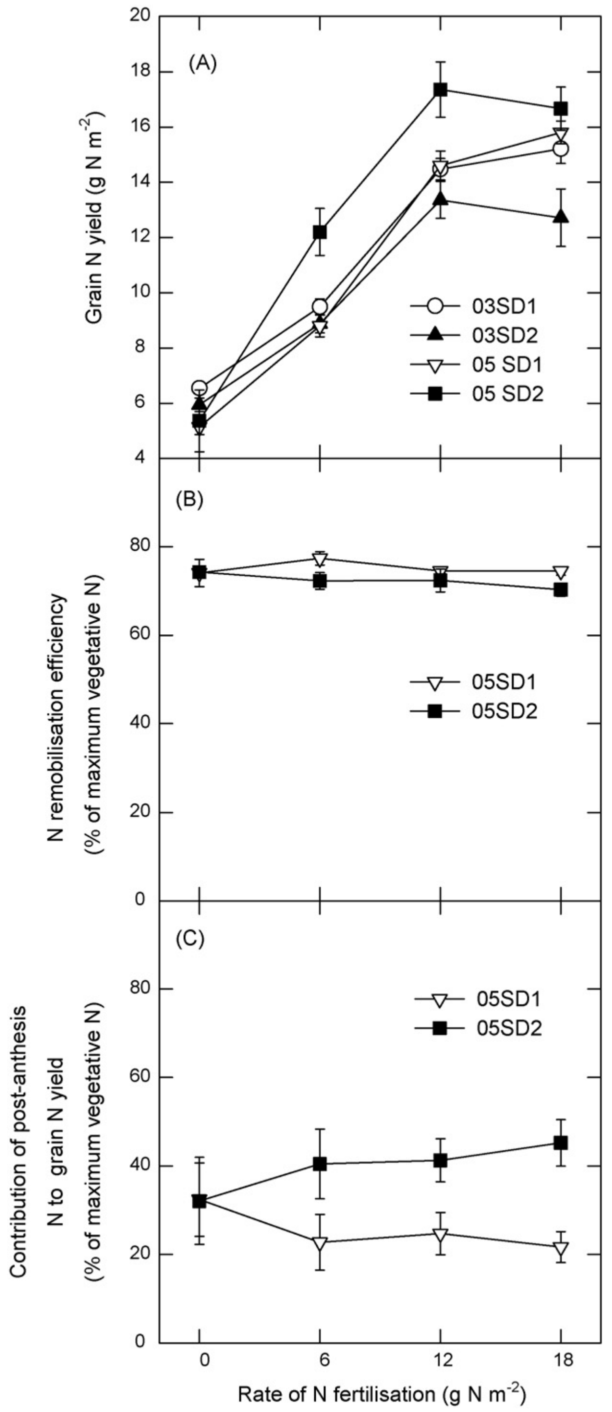

Fig. 9. Grain N yield (A), N remobilisation efficiency (B), and contribution of post-anthesis N to grain N yield versus the rate of N fertilisation for crops of durum wheat grown in Florence, Italy, during the 2002–2003 and 2004–2005 growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). Data are average ± 1 s.e. for $n = 3$ independent replicates.

protein concentration increased in response to N fertilisation by 17%, 31% and 35% for N6, N12 and N18, respectively. In 2005, the response of grain protein concentration to N fertilisation was only half of that observed in 2003.

3.7. Simulated grain DM and N yields and grain protein concentration

*SiriusQuality*1 simulated well the rate and duration of grain N and DM accumulation in response to N fertilisation and sowing date (Fig. 11). Observed variations of final grain DM yield were reasonably well simulated (Fig. 12A; $r = 0.97$; $P < 0.001$), with a RMSE of 0.045 kg DM m^{-2}. Grain N yield was also well simulated (Fig. 12B; $r = 0.98$; $P < 0.001$; RMSE = 0.81 g N m^{-2}). Observed variations of grain protein concentration were simulated with a RMSE of 1.26% (Fig. 12C; $r = 0.77$; $P < 0.001$). The RMSE for grain N yield and protein concentration were essentially due to a lack of correlation, the RMSE for grain yield was equally due to a lack of correlation and a nonentity slope.

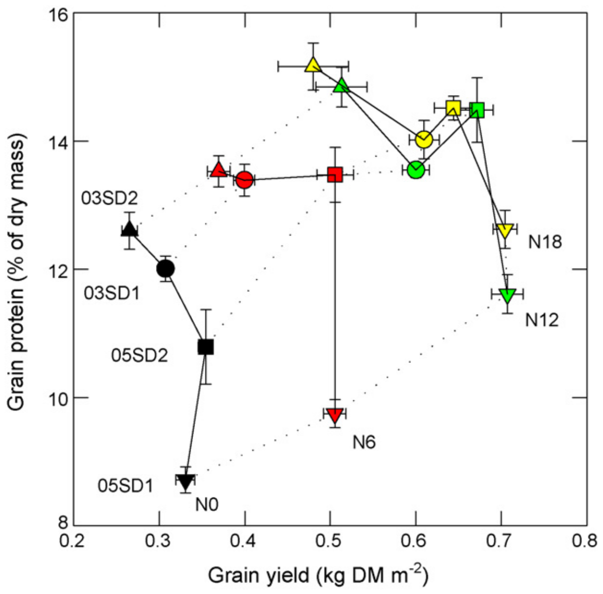

Fig. 10. Grain protein concentration versus grain yield for crops of durum wheat grown in Florence, Italy, during the 2002–2003 and 2004–2005 growing seasons. The crops received 0 (black symbols), 6 (red symbols), 12 (green symbols), or 18 (yellow symbols) g N m^{-2}. The crops were sown in October/November (SD1; 2002–2003, circles; 2004–2005, triangle down) or in January (SD2; 2002–2003, triangle up; 2004–2005, square). Data are average ± 1 s.e. for $n = 3$ independent replicates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

4. Discussion

The response of durum wheat to N fertilisation and sowing date was studied in two field experiments. The longer vegetative period with autumn sowing compared with winter sowing increased crop DM and N at anthesis, resulting in higher grain DM and N yields at maturity. Sowing date had larger effects on grain DM yield than on grain N yield; therefore grain protein concentration was significantly higher for the late sowing date than for the normal sowing date. N fertilisation did not affect crop phenology, but it allowed the crops to accumulate more DM and N during the vegetative period. In addition, high-N crops, because of their larger canopy, accumulated more DM and N during grain filling than low-N crops, resulting in higher grain yield and protein concentration at harvest. However, the efficiency of vegetative crop DM and N remobilisation was modified neither by N fertilisation nor by sowing date. Both the grain number per unit ground area and grain yield were closely correlated with crop DM and N at anthesis. The observed variations of single grain DM in response to the year and sowing date were explained by the mean daily maximum temperature calculated for the 15 days prior to anthesis. The capacity of the wheat simulation model *SiriusQuality*1 to simulate grain yield and protein concentration and DM and N dynamics within the plant was successfully evaluated.

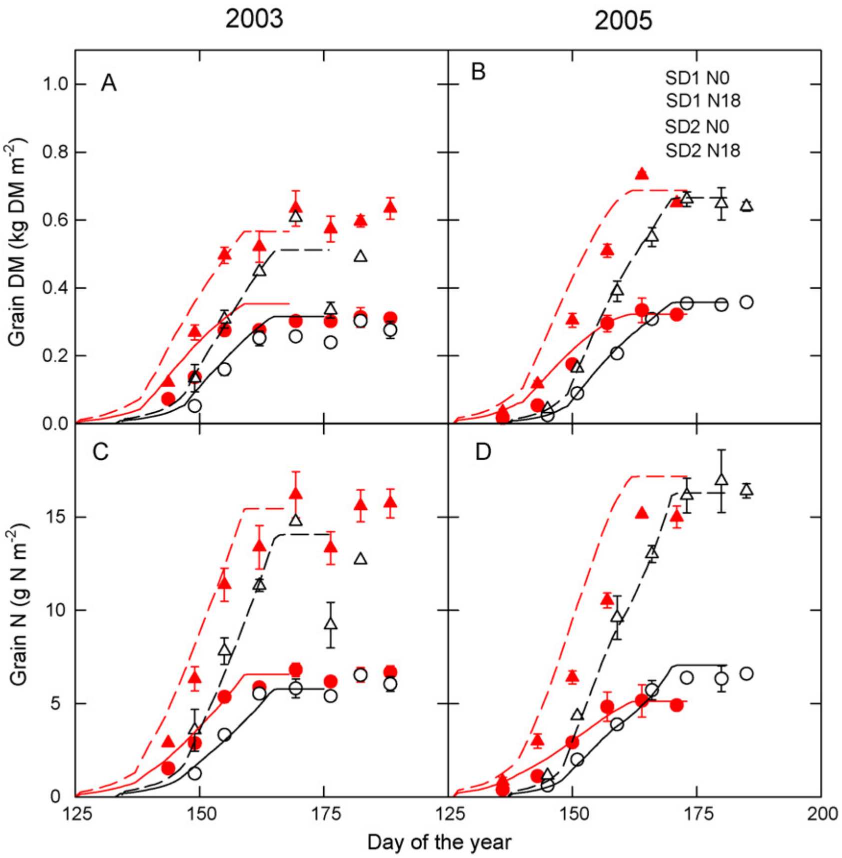

Fig. 11. Observed (symbols) and simulated (lines) grain DM (A and B) and N (C and D) contents per unit ground area versus the number of days after anthesis for crops of durum wheat grown in Florence, Italy, during the 2002–2003 (A and C) and 2004–2005 (B and D) growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). Data are presented for the lowest (N0) and highest (N18) rates of N fertilisation. Observed data are average ± 1 s.e. for $n = 3$ independent replicates.

4.1. Simulation of crop development and DM and N dynamics

A prerequisite for an accurate simulation of crop DM and N accumulation is to reproduce the observed phenology, in particular the anthesis date (Bassu et al., 2009). In *SiriusQuality*1 the anthesis date is calculated from the leaf appearance rate and final leaf number, which allows linking crop phenology with canopy development (Jamieson et al., 1998a; Lawless et al., 2005). Using a unique and independent set of parameter values, the anthesis date was simulated for both years and both sowing dates with a RMSE of only 1.7 days. The accurate simulation of anthesis date resulted from a compensation between the phyllochron and final leaf number.

The phyllochron determined in the field in 2005 for leaf 1–6 was 149 and 85 °Cdays (based on air temperature) for 05SD1 and 05SD2, respectively. The variations of phyllochron with sowing data observed in this study are comparable, but slightly lower, than that previously reported for the cultivar Creso and other durum (Giunta et al., 2001; Motzo and Giunta, 2007) and bread (Jamieson et al., 2008) wheat cultivars. In *SiriusQuality*1 the phyllochron is adjusted for the sowing date. Specifically, the phyllochron is decreased from the value specified by the user by 0.3 °Cdays per day between day of the year 1 and 90, and is lowest between day of the year 90 and 200. In this study the phyllochron was specified at 87 °Cdays. The sowing date adjustment function gave a phyllochron ranging from 83 °Cdays for 03SD2 to 90 °Cdays for 03SD1 and 05SD1. Therefore, as previously reported (Jamieson et al., 2008), the adjustment of phyllochron for sowing date in *SiriusQuality*1 accounts for only a small part the observed variations of the phyllochron with the sowing date. For comparison, the phyllochron calculated using the relationship between daylength 73 days after sowing and phyllochron implemented in the wheat simulation model APSIM by Bassu et al. (2009) for the cultivar Creso is 146 and 111 °Cdays for 05SD1 and 05SD2, respectively.

The observed final leaf number was independent of sowing date. This contrast both with the simulated results presented here and with previously reported experimental results showing differences of 2 to 3 leaves in response to a similar change in sowing dates for spring wheat (e.g. Giunta et al., 2001; Jamieson et al., 2008). In this study the higher simulated leaf number for early sowings compensated for the higher observed phyllochron. Therefore, it would be interesting to assess if *SiriusQuality*1 would be able to simulate the anthesis date for conditions where the final leaf number varies with sowing date.

The timing of the beginning of stem extension was simulated accurately because of compensations between the simulated number of small leaves produced before floral initiation and the simulated number of culm leaves. Therefore, the overestimation of final leaf number had only a small effect on simulated crop DM and N dynamics. The observed thermal time between the appearance of the flag leaf ligule and anthesis was only 150 °Cdays for SD1 compared with 260 °C for SD1. In *SiriusQuality*1 this phenophase is constant (parameter PhyllFLLanth), which in this study also compensated for the underestimation of phyllochron for the early sowing dates.

In *SiriusQuality*1 each process is modelled with a consistent level of detail. The interactive feed-back mechanisms between processes describing direct and indirect effects of environmental and crop management conditions reduce the empiricism compared to other crop simulation models using many corrections and allocation factors (Martre et al., 2006). For example, in *SirisQuality*1 the effect

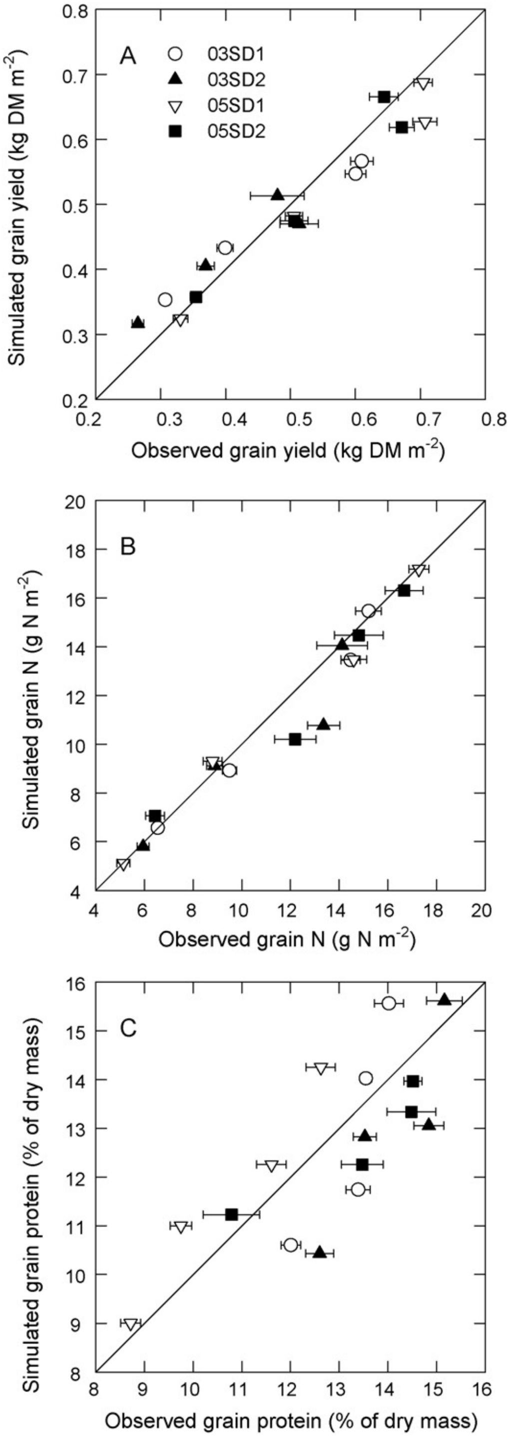

Fig. 12. Observed versus simulated grain DM (A) and N (B) yields, and grain protein concentration (C) for crops of durum wheat grown in Florence, Italy, during the 2002–2003 and 2004–2005 growing seasons. The crops were sown in October/November (normal sowing, SD1) or in January (late sowing, SD2). Observed data are average ± 1 s.e. for $n = 3$ independent replicates. Solid lines, $y = x$.

of N shortage is to reduce first stem nitrogen concentration and then leaf expansion to maintain specific leaf nitrogen concentration. One advantage of this approach is that it reduces the number of parameters and the need to define stress factors, compared with the demand-driven approaches based on nitrogen dilution. This approach also provides more plasticity in the response of the crop to nitrogen availability. Overall, the model shows a high level of adaptability (plasticity) to crop growth conditions, comparable to that observed for real crops. *SiriusQuality*1 simulated reasonably well the responses of leaf, stem, and grain N and DM to N fertilisation and sowing date, but the model overestimated leaf N content at anthesis for high-N crops. This had only slight effects on the dynamics of cop DM, because under high-N conditions biomass production is not limited by N. For high-N crops, the overestimation of leaf N represented up to 22% of observed final grain N, but it did not resulted in an overestimation of simulated grain N because it was compensated by an underestimation of 10% of leaf N remobilisation efficiency. In *SiriusQuality*1 the remobilisation of vegetative N and DM during the grain filling period is calculated so that vegetative tissues reach a fixed concentration of structural N and DM at the end of the grain filling period (Martre et al., 2006). More realistic dynamics of leaf N might be simulated if the rate of vegetative N remobilisation was calculated assuming that the rate of transfer of vegetative N to grains follows a first order kinetics, as observed for bread wheat by Bertheloot et al. (2008) and for durum wheat in this study. The response of grain yield and protein concentration to N fertilisation and sowing date were accurately simulated with a relative RMSE of 9% and 10%, respectively.

4.2. Relationship between anthesis crop DM and N, grain number per unit ground area and grain yield

In agreement with many studies on bread wheat (e.g. Fischer, 1993; Sayre et al., 1997; Gonzalez et al., 2003), we found a close correlation between grain yield and grain number per unit ground area. But grain number per unit ground area was also closely correlated to crop DM and N at anthesis. Similarly, several authors found a close correlation between grain number per unit ground area and spike DM and N at anthesis for bread wheat (e.g. Abbate et al., 1995; Demotes-Mainard et al., 1999). The relationships between grain number per unit ground area and crop DM and N at anthesis may indicate that differences in grain yield due to sowing date and N fertilisation were primarily the consequences of crop growth prior to anthesis, which determines both the number of grain per unit ground area and the capacity of the crop to accumulate DM and N during the grain filling period. As discussed by Sinclair and Jamieson (2006), under most conditions, the close correlation between grain yield and grain number per unit ground area reflects the fact that these two variables are determined by the capacity of the canopy to capture DM and N resources around anthesis, but it does not mean that this correlation is causal (functional). The later point is reinforced by the fact that simulated grain yield and grain number per unit ground area were closely correlated ($r = 0.93$; $P < 0.001$), although in *SiriusQuality*1 the simulation of grain yield is mostly independent of grain number per unit ground area (see below).

In *SiriusQuality*1, the accumulation of structural/metabolic grain DM (i.e. total grain DM minus starch content) is determined by the temperature and by the number of grain per unit ground area and is therefore sink limited. The number of grain per unit ground area is calculated from the ear DM at anthesis, assuming a fixed number of grains per g of ear DM (Weir et al., 1984; Martre et al., 2006). Ear DM is calculated by allocating 50% of the biomass assimilated by the crop during the 2.25 phyllochron preceding anthesis to the ear (Jamieson et al., 1998b). In contrast with structural/metabolic grain DM, in *SiriusQuality*1 the accumulation of storage grain DM (i.e. starch) is entirely source driven (i.e. it is independent of grain number per unit ground area; Martre et al., 2006). In this study, structural/metabolic grain DM accounted for only 13–18% of total grain yield, depending on the experimental conditions. Therefore, variations of structural grain DM, and hence grain number per unit ground area, cannot explain the variations of simulated grain yield (from 0.29 to 0.77 g DM m^{-2}). Instead, most of the variations of simulated grain yield were determined by the size of the pool of remobilisable vegetative DM and by post-anthesis DM accumulation. As for real crops, simulated grain yield was correlated with simulated crop DM ($r = 0.60$; $P < 0.001$) and N ($r = 0.89$; $P < 0.001$) at anthesis. Interestingly the highest correlation was found between grain yield and leaf area index at anthesis ($r = 0.92$; $P < 0.001$). These correlations are emergent properties of the model indicating that the model was able to capture (quantitatively) the complex interactions between canopy development and DM and N assimilation and allocation.

All together these results suggest that in this study the variations of grain yield were mostly source driven. However, the close relationship found between single grain DM and mean daily maximum temperature calculated for the 15 days prior to anthesis (see below) may indicate that in these experiments grain yield was sink rather than source limited.

4.3. Efficiency of dry mass and N remobilisation and contribution of post-anthesis DM and N accumulation to grain DM and N yields

N accumulated by the crop during the grain filling period contributed 25–40% to final grain N yield. During the initial phase of grain growth, the stem and the leaves continued to accumulate N. In good agreement with a recent study on bread wheat (Bertheloot et al., 2008), the N content of all organs started to decrease at the same time and with a rate that was proportional to their N concentration. Leaves and stem contributed equally to grain N, but most of the N temporarily stored in the vegetative tissues after anthesis was stored in the stem. The saturation effect observed for N12 and N18 most likely reflected the limited capacity of the plant to store N. Root N-uptake is down-regulated when cell storage capacity is filled, causing the N in excess to remain in the soil until new DM is formed (Clarkson, 1986). As a consequence, in our study DM and N contents at anthesis were well correlated ($r = 0.96$; $P < 0.001$). Simulated crop DM and N at anthesis were also correlated ($r = 0.84$; $P > 0.001$), which is an emergent property of the model.

The contribution of post-anthesis DM and N to grain DM and N yields, respectively, and the efficiency of vegetative DM and N remobilisation found in the present study were comparable to values previously reported for durum wheat (e.g. Arduini et al., 2006; Ercoli et al., 2008; Masoni et al., 2007) and bread wheat (e.g. Cox et al., 1985; Kichey et al., 2007; Ehdaie et al., 2006). The analysis of DM and N remobilisation showed that even though the total quantity of vegetative DM and N remobilised was higher for early sowing and at increasing N availability, the efficiency DM and N remobilisation were not modified by sowing date or N treatment. In contrast, Ercoli et al. (2008) found that the efficiency of DM and N remobilisation for durum wheat plants grown in pots increases slightly with N availability and decreases in response to post-anthesis water deficit.

The contribution of post-anthesis DM accumulation to final grain DM yield was not modified by the sowing date or N fertilisation. However, the contribution of post-anthesis N accumulation to final grain N yield was two times higher for SD2 compared with SD1. The higher rate of N accumulation observed in SD2 might in part be attributed to higher post-anthesis N assimilation for SD2 compared with SD1.

4.4. Single grain DM and N contents

Single grain DM is a major component of grain yield, but it also largely contributes to grain milling quality (Evers and Millar, 2002). Here, single grain DM showed large variations in response to sowing date and year (from 44.2 to 57.3 mg DM grain^{-1}); while neither N availability nor grain number affected single grain DM. These results agree well with results reported for bread wheat (e.g. Triboi et al., 2003). Single grain N accumulation was affected by both the sowing date and N fertilisation. The former had an effect on the rate of grain N accumulation, while the latter increased both the duration and the maximum rate of grain N accumulation. Fischer (1993) showed that for bread wheat high amounts of N in the crop at anthesis allow leaf area to be sustained for longer, which increases solar radiation interception and DM accumulation. However, here we found a longer duration of grain N accumulation with N fertilisation, but the duration of grain DM accumulation was not modified by the N treatment.

The final single grain DM of several species, including bread wheat (Calderini and Reynolds, 2000; Calderini et al., 1999a), barley (Scott et al., 1983), and sorghum (Yang et al., 2009), was found to be positively related ($r > 0.95$) with the size and DM of the maternally derived ovary wall from which the pericarp develops. In wheat, rapid expansion of floret carpels, which will form the ovary wall, occurs between booting and anthesis and this period has been shown to be very critical in the determination of single grain DM for bread wheat (Calderini et al., 1999a,b, 2001). In good agreement with these results, in this study the variations of single grain DM were almost entirely accounted for by the mean daily maximum temperature calculated for the 15 days prior to anthesis. This result suggests that the temperature during the period of active cell division in the ovary is a major determinant of the rate of grain filling and of single grain DM for durum wheat. Several studies have shown that the phase of endosperm division is the most sensitive phase of grain development after anthesis to water deficit (Nicolas et al., 1984) or temperature (e.g. Jones et al., 1984; Tashiro and Wardlaw, 1990; Commuri and Jones, 2001).

Acknowledgements

This work was supported by a Galileo French/Italian bilateral project (grant no. 08418ZJ), and by the French National Research Agency (grant no. ANR–06–GPLA–016–003). The authors thank Dr. Vincent Allard and three anonymous reviewers for their comments on an earlier version of the manuscript.

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