

# Remobilization of Dry Matter, Nitrogen and Phosphorus in Durum Wheat as Affected by Genotype and Environment

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Received: 16 June 2006. Accepted: 21 December 2006

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## Abstract

Field studies were carried out to determine dry matter (DM), nitrogen (N) and phosphorus (P) assimilation until anthesis and DM, N and P remobilization during grain filling in wheat. Twentyfive durum wheat (*Triticum durum* L.) varieties were grown in Tuscany at Grosseto and at Arezzo. At Grosseto 76% of DM was assimilated during pre-anthesis while at Arezzo the amount was 81%. At Grosseto 44% and at Arezzo 35% of N was accumulated until anthesis, while 33% of P was stored until anthesis in both localities. Cultivar differences in DM and N remobilization were positively related to pre-anthesis dry matter and N content at anthesis ( $r > 0.74$ ). Environmental constraints on carbon, N and P availability in the plant are crucial factors in determining grain yield and N and P content in grain, affecting both accumulation and remobilization. In the low rainfall site of Grosseto, most of the grain yield originated from dry matter accumulation, while in the wetter environment of Arezzo remobilization and accumulation contributed equally to grain yield. Conversely, at Grosseto grain N content relied most on remobilization and at Arezzo remobilization and accumulation contributed equally. Finally, at Grosseto and at Arezzo accumulation of P was the main source of grain P content.

*Key-words:* assimilation, dry matter, durum wheat, nitrogen, phosphorus, remobilization.

## 1. Introduction

During vegetative and early reproductive growth of wheat, assimilated carbon and nitrogen are accumulated temporarily in the stems and leaves as carbohydrate or protein reserve. Much of these reserves can be remobilised and transported to the developing grain, representing a significant contribution to the final grain yield.

Stem reserve carbohydrates may attain high levels of more than 40% of total stem dry weight and principally consist of a range of fructosyl-oligosaccharides (fructan) together with sucrose and hexose (Yang et al., 2004). These reserve carbohydrates are designed as water soluble carbohydrates (WSC) to distinguish them from the structural carbohydrates present in cell

walls. In durum wheat, pre-anthesis reserves contribute from 10% up to more than half of the grain yield depending on environmental conditions, genotype and cultural practices (Van Sanford and MacKown, 1987; Kobata et al., 1992; Blum, 1998; Van Herwaarden et al., 1998; Gebbin et al., 1999; Yang et al., 2001). During the latter part of grain filling, vegetative plant parts can lose up to 50% of their dry matter and the disappearance of WSC accounts for 90-100% of this weight loss (Bonnett and Incoll, 1993; Gent, 1994; Gebbin et al., 1999).

In durum wheat, during grain filling, nitrogen relocation to the grains exceeds nitrogen uptake, and account for 50% to 92% of the nitrogen accumulated in the grains at maturity (Cox et al., 1985a, 1985b and 1986; Papakosta

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and Garianas, 1991; Ehdaie and Waines, 1996; Przulj and Momcilovic, 2001a and 2001b).

Phosphorus is the other main nutrient of crop production, in fact although the total amount of P in the lithosphere is abundant, crop productivity is often limited by P availability. Phosphorus is a relatively mobile element in plants moving easily among organs. In wheat the grain at maturity becomes the major sink of P, accounting for up to 90% of the total P content of the aerial plant part, with 20-90% of this being retranslocated from other tissues (Batten and Wardlaw, 1987). Most P uptake occurs by anthesis and remobilization can account for 56-63% of grain P content at maturity (Masoni et al., 2007).

There are three components involved in remobilization of stored C, N and P to grain yield in wheat: i) the ability to store assimilates in the vegetative plant parts until anthesis; ii) the sink strength of the spike, which is mainly dependent on the number of grains per spike, and iii) the efficiency with which the stored reserves are remobilized and translocated to grain (Marshall and Wardlaw, 1973; Fageria and Baligar, 1999; Prystupa et al., 2004). This study examined the relative contribution of dry matter, nitrogen and phosphorus accumulated and remobilized during grain filling to grain yield of durum wheat. We utilized 25 commercial varieties growing in two contrasting rainfed environments in Tuscany (Italy).

## 2. Materials and methods

Field experiments were carried out in 1996-1997 comparing 25 durum wheat (*Triticum durum* Desf.) varieties in two localities of Tuscany. Localities were Grosseto (42° 48' N, 11° 2' E; 2 m a.s.l.) and Arezzo (43° 18' N, 11° 49' E; 240 m a.s.l.) and were 140 km apart. Varieties were:

Ares, Bronte, Ceedur, Ciccio, Cirillo, Colosseo, Creso, Duilio, Durfort, Exeldur, Gemme, Gianni, Grazia, Iride, Italo, Ixos, Lloyd, Neodur, Ofanto, Parsifal, Rusticano, San Carlo, Simeto, Solex, Svevo.

In both localities the climate is hot mediterranean. At Grosseto mean annual maximum and minimum daily air temperatures are 20.7 °C and 9.6 °C, respectively, and total annual rainfalls are 602 mm, with 401 mm received during the period of durum wheat cultivation, that is from November through June. At Arezzo mean annual maximum and minimum daily air temperature are 19.8 °C and 8.7 °C, respectively, and total annual rainfall is 755 mm, with 499 mm received from November through June.

At Grosseto the soil was loamy and at Arezzo it was clay-loam. Chemical and physical properties of soils are reported in Table 1.

Each experiment consisted in a randomized block with three replications with plots of 10 m<sup>2</sup>. All plots were managed using practices similar to those used by producers in the surrounding areas of the two localities. At both sites the preceding crop was sunflower. Soil was ploughed at 40 cm depth in November; final seedbed preparation was carried out just prior to sowing by harrowing twice with a disc harrow and with a rotating harrow. Sowing was carried out at both sites on 5<sup>th</sup> December 1996 by means of a plot drill. Sowing density was 450 viable seeds m<sup>-2</sup>. Phosphorus was applied before ploughing at rate of 120 kg ha<sup>-1</sup> of P<sub>2</sub>O<sub>5</sub> at Arezzo and 92 kg ha<sup>-1</sup> at Grosseto. Nitrogen was applied before seeding at rates of 36 kg ha<sup>-1</sup> of N at both localities and at the end of tillering, at rate of 144 kg ha<sup>-1</sup> of N at Arezzo and 104 kg ha<sup>-1</sup> at Grosseto. At both localities fertilizers used were triple super-phosphate, di-ammonium phosphate ad ammonium nitrate and weed control was performed at the stage of 4<sup>th</sup>-5<sup>th</sup> leaf un-

Table 1. Chemical and physical properties of soils in the two localities.

Soil property		Grosseto	Arezzo
Sand (2 mm > Ø > 0.05 mm)	%	47.0	39.2
Silt (0.05 mm > Ø > 0.002 mm)	%	38.2	26.0
Clay (Ø < 0.002 mm)	%	21.8	34.8
pH		7.5	7.6
Organic matter (Walkley and Black method)	%	0.9	1.5
Total N (Kjeldahl method)	g kg <sup>-1</sup>	0.6	0.8
Available P (Olsen method)	mg kg <sup>-1</sup>	26.3	28.9
Exchangeable K (method with BaCl <sub>2</sub> )	mg kg <sup>-1</sup>	170.0	136.7

folded by distributing a commercial graminicide.

To determine remobilization during grain filling, plants were harvested at anthesis and at physiological maturity. Anthesis occurred on 22-26 April at Grosseto and on 2-5 May at Arezzo. Physiological maturity occurred on 20-25 June at Grosseto and on 3-8 July at Arezzo.

At anthesis and at physiological maturity, plants from four adjacent rows of 1 m length were manually cut at ground level. Plants were separated into culms, spikes and leaves at anthesis, and into culms, leaves, chaff and grain at maturity. For dry weight determination, samples from all plant parts were oven dried at 65 °C to constant weight. At maturity, mean kernel dry weight was also measured and the number of kernels per unit area and harvest index (HI) were calculated. Samples of each plant part were analyzed for nitrogen (microKjeldahl method) and phosphorus (ammonium-molybdophosphoric blue color method) concentrations; N and P contents were calculated by multiplying N or P concentration by dry weight.

Post-anthesis dry matter and N and P accumulation were calculated as the difference between dry weight or N or P content of the aerial plant part at physiological maturity and at anthesis.

The dry matter and N and P remobilization during grain filling (DMR, NR and PR) were calculated following Cox et al. (1986) and Papakosta and Garianas (1991), as:

- DMR = dry wt. of the aerial plant part at anthesis - (dry wt. of leaves + culms + chaff at maturity);
- NR = N content of the aerial plant part at anthesis - (N content of leaves + culms + chaff at maturity);
- PR = P content of the aerial plant part at anthesis - (P content of leaves + culms + chaff at maturity).

For these estimates, it was assumed that all of the dry matter and N and P lost from vegetative plant parts were remobilized to the developing grain, since losses of dry matter due to plant respiration and losses of N due to volatilization during grain filling were not determined.

The dry matter, N and P remobilization efficiency (DMRE, NRE and PRE) were calculated as:

- DMRE = (DMR / dry wt. of the aerial plant part at anthesis) × 100;
- NRE = (NR / N content of the aerial plant part at anthesis) × 100;

- PRE = (PR / P content of the aerial plant part at anthesis) × 100.

The contribution of dry matter, N and P remobilized to grain (CDMRG, CNRG and CPRG) were calculated as:

- CDMRG = (DMR / dry wt. of grain at maturity) × 100;
- CNRG = (NR / N content of grain at maturity) × 100;
- CPRG = (PR / P content of grain at maturity) × 100.

Data were statistically treated by ANOVA, in order to test the main effects of location and variety and their interactions. Separate statistical analyses were conducted for dry matter and N and P accumulation and remobilization for each harvest. Duncan's multiple range test was used to separate the means when the ANOVA F-test indicated a significant effect of the treatment (Steel and Torrie, 1997).

### 3. Results

During the 1996-1997 growing season temperature was close to the long-term average in both locations (Fig. 1). Rainfall during the growing

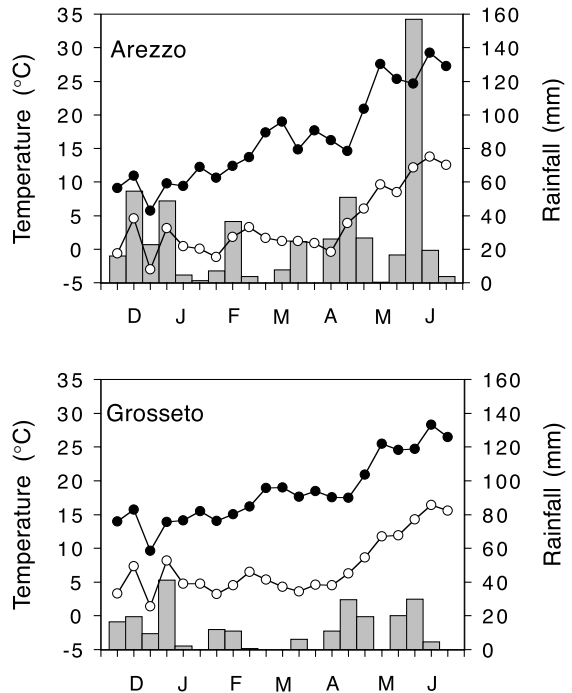


Figure 1. Rainfalls and temperatures in the 1996-1997 durum wheat growing season at the two localities. Total rainfall was 232.6 mm at Grosseto and 527.6 at Arezzo.

Table 2. Dry matter of vegetative plant part at anthesis and maturity and grain yield in the 25 wheat varieties at the two localities (Locality x Variety interaction).

Variety	Vegetative Plant Part				Grain Yield	
	Anthesis		Maturity		Grosseto	Arezzo
	Grosseto	Arezzo	Grosseto	Arezzo		
	Dry matter q ha <sup>-1</sup>					
Ares	79.0	101.2	66.5	77.8	38.0	49.0
Bronte	75.3	103.8	62.7	79.4	40.4	51.1
Ceedur	76.0	108.8	65.6	83.3	38.9	53.7
Ciccio	85.1	115.9	71.8	92.7	35.5	44.6
Cirillo	84.9	113.5	73.7	86.4	34.1	54.0
Colosseo	76.1	113.3	65.1	87.3	40.9	55.6
Creso	80.3	112.1	66.7	86.9	40.8	52.3
Duilio	84.8	114.2	69.3	90.4	42.9	48.8
Durfort	76.7	112.1	64.2	88.7	37.9	46.2
Exeldur	81.2	102.7	67.5	81.0	34.6	44.8
Gianni	91.8	116.3	77.8	90.1	42.8	51.2
Giemme	82.1	104.1	70.1	80.7	41.0	46.7
Grazia	90.1	120.5	78.0	96.3	41.6	54.0
Iride	77.7	103.6	69.1	82.7	32.3	48.0
Italo	73.9	103.8	63.6	79.1	38.9	50.4
Ixos	79.4	113.2	67.6	87.5	33.0	54.4
Lloyd	79.3	115.0	67.0	88.3	38.4	56.4
Neodur	80.7	118.9	70.6	95.4	37.9	48.6
Ofanto	76.3	108.9	65.4	87.6	32.3	45.0
Parsifal	82.7	110.2	70.7	88.4	35.2	48.2
Rusticano	83.8	110.8	70.2	87.2	37.2	50.7
San Carlo	93.5	121.9	79.0	99.9	38.9	50.9
Simeto	80.9	104.2	67.0	79.4	38.1	51.2
Solex	78.2	107.0	67.2	84.3	39.9	48.8
Svevo	74.1	114.0	62.7	87.6	41.8	56.7
LSD <sub>P ≤ 0.05</sub>	7.6		6.4		3.9	

season and grain filling period was lower than the long-term average at Grosseto and higher at Arezzo. During the seeding-anthesis period rainfall was 158.6 mm at Grosseto and 304.2 mm at Arezzo and during grain filling was 77.5 mm at Grosseto and 223.4 mm at Arezzo. Minimum temperature was always higher at Grosseto than at Arezzo with a range of difference in decadic mean between 5 °C in winter and 3 °C in spring. Maximum temperature was higher at Grosseto than at Arezzo in winter while was the same in spring.

### 3.1 Dry matter

Dry matter of vegetative plant part at anthesis and at maturity differed between localities and among varieties (Tab. 2). At Arezzo all varieties had higher vegetative dry weight, both at anthesis and at maturity, and grain yield and number of kernels per unit area than at Grosseto. Moreover, at Arezzo most of the varieties had also higher number of spikes per unit area.

At anthesis, the highest vegetative dry weight was recorded for cv. San Carlo in both localities, while the lowest was recorded for cv. Italo at Grosseto and for cv. Ares at Arezzo. At maturity cv. San Carlo had the highest vegetative dry weight in both localities, and the lowest was recorded for cv. Bronte and Svevo at Grosseto and for cv. Ares at Arezzo.

At Arezzo grain yield ranged from 44.6 q ha<sup>-1</sup> of cv. Ciccio to 56.7 q ha<sup>-1</sup> of cv. Svevo while at Grosseto it ranged from 32.3 q ha<sup>-1</sup> of cv. Iride and Ofanto to 42.9 q ha<sup>-1</sup> of cv. Duilio. The lowest difference between the two locations was observed for cv. Giemme and Duilio (less than 6 q ha<sup>-1</sup>) and the highest for cv. Ixos (over 21 q ha<sup>-1</sup>).

The number of kernels per square meter ranged at Arezzo from 11,500 of cv. Giemme to 17,900 of cv. Ceedur and at Grosseto from 8,400 of cv. Colosseo to 12,300 of cv. Exeldur. The lowest difference between the two locations was observed for cv. Ciccio (less than 500 ker-

Table 3. Harvest Index, Mean Kernel Weight and Number of Spikes and Number of Kernels in the 25 wheat varieties at the two localities (Locality x Variety interaction).

Variety	Harvest Index		Mean Kernel Weight		Number of Spikes		Number of Kernels	
	Grosseto	Arezzo	Grosseto	Arezzo	Grosseto	Arezzo	Grosseto	Arezzo
	%		mg kernel <sup>-1</sup>		n m <sup>-2</sup>		n m <sup>-2</sup> x 10 <sup>3</sup>	
Ares	36.4	38.6	39.4	34.3	580.6	737.0	9.7	14.3
Bronte	39.2	39.2	39.3	39.6	564.8	644.4	10.3	12.9
Ceedur	37.2	39.2	27.7	30.1	707.4	970.4	14.1	17.9
Ciccio	33.1	32.5	32.1	38.6	737.0	844.4	11.1	11.6
Cirillo	31.6	38.5	33.3	34.8	481.5	700.0	10.3	15.5
Colosseo	38.6	38.9	48.7	37.6	629.6	725.9	8.4	14.8
Creso	38.0	37.6	43.8	40.9	603.7	696.3	9.3	12.8
Duilio	38.2	35.1	43.0	33.3	666.7	711.1	10.0	14.7
Durfort	37.1	34.2	34.0	32.1	611.1	833.3	11.1	14.4
Exeldur	33.9	35.6	28.1	28.4	713.9	685.2	12.3	15.8
Gianni	35.5	36.2	40.8	34.7	922.2	803.7	10.5	14.8
Giemme	36.9	36.7	42.0	40.7	763.0	588.9	9.8	11.5
Grazia	34.8	35.9	35.5	33.3	651.9	744.4	11.7	16.2
Iride	31.9	36.7	29.8	31.6	422.2	648.1	10.9	15.2
Italo	38.0	38.9	43.4	33.3	663.0	703.7	9.0	15.2
Ixos	32.8	38.3	41.8	33.9	433.3	622.2	7.9	16.0
Lloyd	36.4	39.0	35.3	38.5	613.0	603.7	10.9	14.6
Neodur	34.9	33.8	36.3	34.8	550.0	574.1	10.5	14.0
Ofanto	33.1	33.9	33.7	36.1	500.0	577.8	9.6	12.5
Parsifal	33.2	35.3	41.4	35.7	618.5	648.1	8.5	13.5
Rusticano	34.6	36.8	37.4	33.0	537.0	688.9	9.9	15.4
San Carlo	33.0	33.8	37.8	40.2	588.9	774.1	10.3	12.7
Simeto	36.3	39.2	40.5	39.5	651.9	607.4	9.4	13.0
Solex	37.3	36.7	35.1	36.8	550.0	581.5	11.3	13.2
Svevo	40.0	39.3	39.8	36.5	718.5	733.3	10.5	15.5
LSD <sub>P ≤ 0.05</sub>	3.6		3.4		55.7		1.0	

nels m<sup>-2</sup>) and the highest for cv. Ixos (more than 8,000 kernels m<sup>-2</sup>).

Twenty of twentyfive varieties showed a higher number of spikes per unit area at Arezzo. The highest values (more than 920 spikes m<sup>-2</sup>) were for cv. Gianni at Grosseto and cv. Ceedur at Arezzo, while the lowest were for cv. Iride at Grosseto (only 422 spikes m<sup>-2</sup>) and cv. Neodur at Arezzo (574 spikes m<sup>-2</sup>).

Mean kernel weight was similar between localities for 16 varieties, was higher at Arezzo for one variety and was higher at Grosseto for eight varieties. The highest difference (about 10 mg) between localities in mean kernel weight was recorded for cv. Colosseo, Italo and Duilio. Harvest Index of all varieties did not vary between localities, with the exception of cv. Cirillo, Iride and Ixos that showed higher values at Arezzo (Tab. 3).

Dry matter assimilation during grain filling was similar between the two localities (Fig. 2) ranging from 20.9 q ha<sup>-1</sup> of cv. Exeldur to 30.4

q ha<sup>-1</sup> of cv. Svevo at Grosseto and from 21.4 q ha<sup>-1</sup> of cv. Ciccio to 30.3 q ha<sup>-1</sup> of cv. Svevo at Arezzo. Fifteen of twenty-five varieties had the same assimilation in the two localities, seven had higher values of dry matter assimilates at Arezzo, and only three had higher value at Grosseto. The highest difference (7.5 q ha<sup>-1</sup>) between localities was detected for cv. Ixos.

Dry matter remobilization was higher at Arezzo than at Grosseto for all the varieties. In the first location dry matter remobilization ranged from 20.9 q ha<sup>-1</sup> of cv. Iride to 27.1 q ha<sup>-1</sup> of cv. Cirillo and in the second one from 8.6 q ha<sup>-1</sup> of cv. Iride to 15.5 q ha<sup>-1</sup> of cv. Duilio. The highest difference (15.9 q ha<sup>-1</sup>) between locations was recorded for cv. Cirillo and the lowest (7.5 q ha<sup>-1</sup>) for cv. San Carlo.

At Arezzo assimilation and remobilization of dry matter were similar, as 21 varieties showed a difference of less than 4 q ha<sup>-1</sup>. On the contrary, at Grosseto for all varieties assimilation was heavily higher than remobilization with a

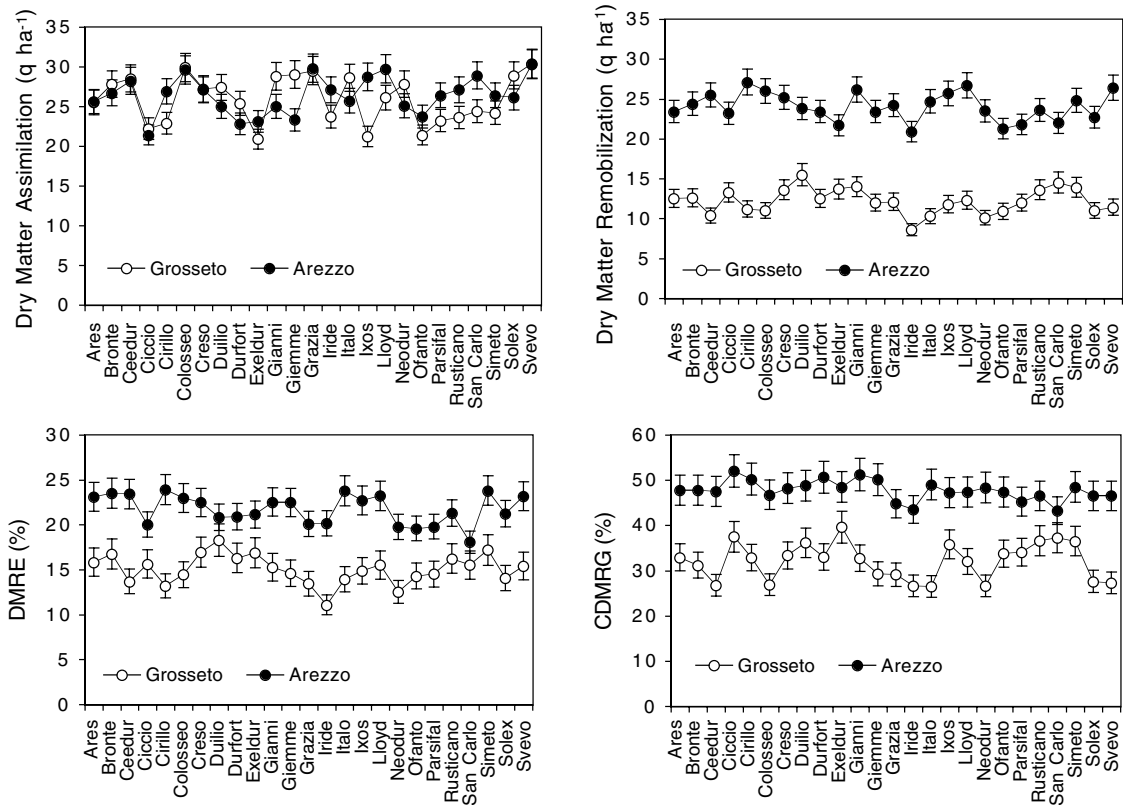


Figure 2. Dry matter remobilization and assimilation, dry matter remobilization efficiency (DMRE) and contribution of dry matter remobilized to grain (CDMRG) in the 25 wheat cultivars at the two localities. Vertical bars indicate standard error. Where not shown, error bar lies within the symbol.

difference that ranged from 7.2 q ha<sup>-1</sup> of cv. Exeldur to 19.0 q ha<sup>-1</sup> of cv. Svevo.

Dry matter remobilization efficiency was always higher at Arezzo. In this locality values ranged from 18.0% of cv. San Carlo to 23.4% of cv. Ceedur while at Grosseto values ranged from 11.1% of cv. Iride to 18.3% of cv. Duilio.

Contribution of dry matter remobilization to grain yield was higher at Arezzo than at Grosseto for all varieties. At Arezzo values ranged from 43.2% of cv. San Carlo to 52.0% of cv. Ciccio while at Grosseto ranged from 26.5% of Italo to 39.6% of Exeldur.

We estimated the relationship between the amount of dry matter remobilization and dry matter of the whole plant at anthesis for the 25 varieties in the two localities. The regression model fitted well the observed values ( $r = 0.94$ ) and dry matter remobilization was positively associated with dry matter accumulated at anthesis (Fig. 5). At the increase of one unit of dry matter assimilated at anthesis the dry matter remobilized increased by 37 kg ha<sup>-1</sup>. Grain yield

was also positively related to dry matter remobilization ( $r = 0.93$ ). At the increase of one unit of dry matter remobilized grain yield increased by 1.1 q ha<sup>-1</sup>.

The higher grain yield recorded at Arezzo can be related to a higher dry matter remobilization. This depends on a higher biomass accumulated at anthesis, to a higher efficiency of remobilization and to a higher sink strength of the spike due to a higher number of kernels per unit area. The difference between localities in the biomass accumulated up to anthesis is likely to depend on the rainfall during the jointing stage that at Arezzo was more than 100 mm and at Grosseto was less than 50 mm. The difference between localities in the efficiency of remobilization can be attributed to the rainfall during grain filling that was 77.5 mm at Grosseto and 223.4 mm at Arezzo.

### 3.2 Nitrogen

Nitrogen concentration of the vegetative plant part at anthesis and maturity and of grain did

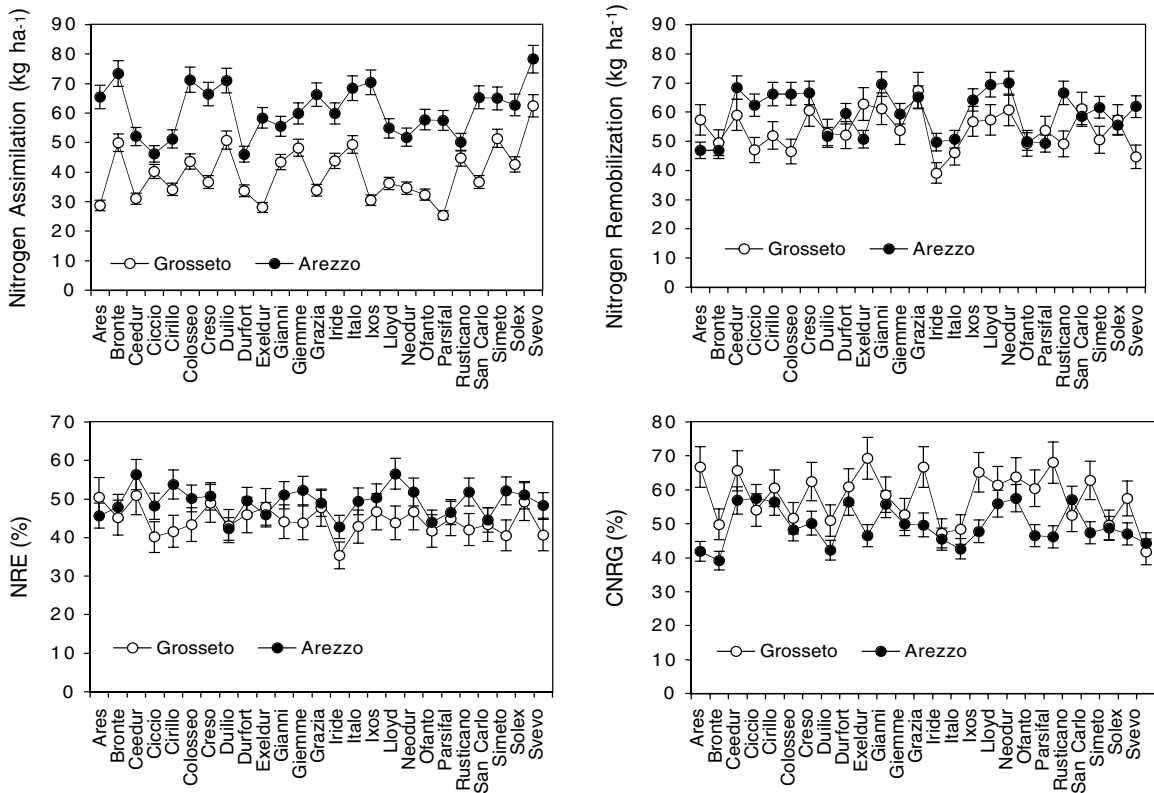


Figure 3. Nitrogen remobilization and assimilation, nitrogen remobilization efficiency (NRE) and contribution of nitrogen remobilized to grain (CNRG) in the 25 wheat cultivars at the two localities. Vertical bars indicate standard error. Where not shown, error bar lies within the symbol.

not significantly differ among the 25 wheat varieties. Mean values of N concentration of vegetative plant part at anthesis and at maturity were lower at Arezzo than at Grosseto (15 vs 11 g kg<sup>-1</sup> and 10 vs 7 g kg<sup>-1</sup> respectively at the two stages). Nitrogen concentration in grain did not differ between localities (about 24 g kg<sup>-1</sup>).

The varieties exhibited great variation in N content of the vegetative plant part at anthesis in the two localities (Tab. 4). At Grosseto values ranged from 107 kg ha<sup>-1</sup> of cv. Colosseo to 141 kg ha<sup>-1</sup> of cv. San Carlo, and at Arezzo ranged from 98 kg ha<sup>-1</sup> of cv. Bronte to 137 kg ha<sup>-1</sup> of cv. Gianni. Between localities the highest difference was recorded for cv. Colosseo (25 kg ha<sup>-1</sup>) and the lowest for cv. Duilio (0.4 kg ha<sup>-1</sup>). At maturity N content of the vegetative plant part was significantly higher at Grosseto for nine varieties and did not differ between localities for the remaining ones. At Grosseto values ranged from 56 kg ha<sup>-1</sup> of cv. Ares to 80 kg ha<sup>-1</sup> of cv. San Carlo and at Arezzo from 51 kg ha<sup>-1</sup>

of cv. Bronte to 73 kg ha<sup>-1</sup> of cv. San Carlo.

Grain N content for all the varieties was higher at Arezzo than at Grosseto. The difference between locations in grain N content was over 30 kg N ha<sup>-1</sup> for six varieties and over 40 kg N ha<sup>-1</sup> for two varieties. At Grosseto the range for grain N content was from 79 kg ha<sup>-1</sup> for cv. Parsifal to 107 kg ha<sup>-1</sup> for cv. Svevo and at Arezzo it range from 105 kg ha<sup>-1</sup> for cv. Durfort to 140 kg ha<sup>-1</sup> for cv. Svevo.

Assimilation of N during grain filling was higher for all the varieties at Arezzo, ranging from 46 kg ha<sup>-1</sup> of cv. Durfort to 78 kg ha<sup>-1</sup> of cv. Svevo, whereas at Grosseto it ranged from 28 kg ha<sup>-1</sup> of cv. Exeldur to 62 kg ha<sup>-1</sup> of cv. Svevo. The highest difference between localities was detected for cv. Ixos (40 kg ha<sup>-1</sup>) and the lowest for cv. Rusticano (only 5 kg ha<sup>-1</sup>).

At Arezzo N remobilization ranged from 47 kg ha<sup>-1</sup> of cv. Ares and Bronte to 70 kg ha<sup>-1</sup> of cv. Neodur, whereas at Grosseto it ranged from 39 kg ha<sup>-1</sup> of cv. Iride to 67 kg ha<sup>-1</sup> of cv. Grazia

Table 4. Nitrogen content of vegetative plant part at anthesis and maturity and of grain in the 25 wheat varieties at the two localities (Locality x Variety interaction).

Variety	Vegetative Plant Part				Grain	
	Anthesis		Maturity		Grosseto	Arezzo
	Grosseto	Arezzo	Grosseto	Arezzo		
	N kg ha <sup>-1</sup>					
Ares	113.6	102.7	56.3	55.8	85.9	112.2
Bronte	109.7	98.0	60.2	51.2	99.4	120.1
Ceedur	115.7	121.3	56.8	53.0	89.9	120.3
Ciccio	117.0	129.6	70.1	67.3	87.0	108.4
Cirillo	124.9	123.2	73.0	57.1	85.9	117.2
Colosseo	107.2	132.2	60.7	66.0	90.0	137.3
Creso	123.9	131.3	63.4	64.8	97.1	132.8
Duilio	122.5	122.1	69.9	70.6	103.4	122.5
Durfort	113.5	119.9	61.5	60.5	85.7	105.3
Exeldur	131.0	110.4	68.3	59.8	90.7	108.9
Gianni	138.8	136.5	77.7	67.0	104.4	124.9
Gemme	122.4	113.8	68.8	54.5	101.7	119.1
Grazia	141.3	133.2	73.9	68.2	101.1	131.2
Iride	110.5	116.5	71.5	66.8	82.7	109.4
Italo	107.4	102.5	61.4	51.9	95.3	118.9
Ixos	121.5	127.4	64.8	63.3	87.1	134.4
Llyod	130.9	122.7	73.7	53.4	93.3	124.1
Neodur	130.2	134.9	69.6	65.0	95.1	121.5
Ofanto	118.1	113.5	68.9	63.6	81.4	107.6
Parsifal	119.4	105.6	65.8	56.5	78.8	106.5
Rusticano	116.9	128.4	67.8	61.9	93.7	116.6
San Carlo	141.3	131.4	80.2	73.0	97.6	123.7
Simeto	124.6	118.3	74.1	56.8	101.7	126.5
Solex	116.5	108.7	59.2	53.3	99.8	118.1
Svevo	109.9	128.1	65.3	66.3	107.0	140.0
LSD <sub>P ≤ 0.05</sub>	12.3		7.4		10.3	

(Fig. 3). Eleven varieties showed higher N remobilization at Arezzo, 12 had the same value in the two localities and only 2 had higher values at Grosseto. The highest difference between localities was for cv. Colosseo (20 kg N ha<sup>-1</sup>).

Eleven of 25 varieties had higher N remobilization efficiency at Arezzo and the remaining 14 were unaffected by location. Nitrogen remobilization efficiency ranged from 42% (cv. Duilio) to 57% (cv. Llyod) at Arezzo and from 40% (cv. Ciccio) to 51% (cv. Ceerdur) at Grosseto.

Contribution of remobilized nitrogen to N content in grain (CNRG) was in the range of 42-58% at Arezzo and 42-69% at Grosseto. Twelve of 25 varieties had higher CNRG at Grosseto and the remaining 13 had values that did not vary according to the locality. The highest difference (25%) between Arezzo and Grosseto was detected for the variety Ares.

At Arezzo N assimilation was higher than N remobilization for 13 varieties, and was lower

for 8 varieties. At Grosseto N assimilation was higher than N remobilization only for cv. Svevo, and was lower for 17 varieties. The variety Svevo was also the sole variety that showed a N assimilation higher than N remobilization in both localities, while for seven varieties the reverse was true.

Similarly to dry matter remobilization and plant dry matter at anthesis, also N remobilization was closely related to N content at anthesis (Fig. 5). The relationship was weaker ( $r = 0.74$ ), so grain N content relays also on N uptake during grain filling. Conversely, grain N content was not related to N remobilization.

### 3.3 Phosphorus

Phosphorus concentration of vegetative plant part at anthesis and maturity and of grain did not significantly differ among the 25 wheat varieties. Mean values of phosphorus concentration of vegetative plant part at anthesis and at maturity were higher at Arezzo than at Gros-



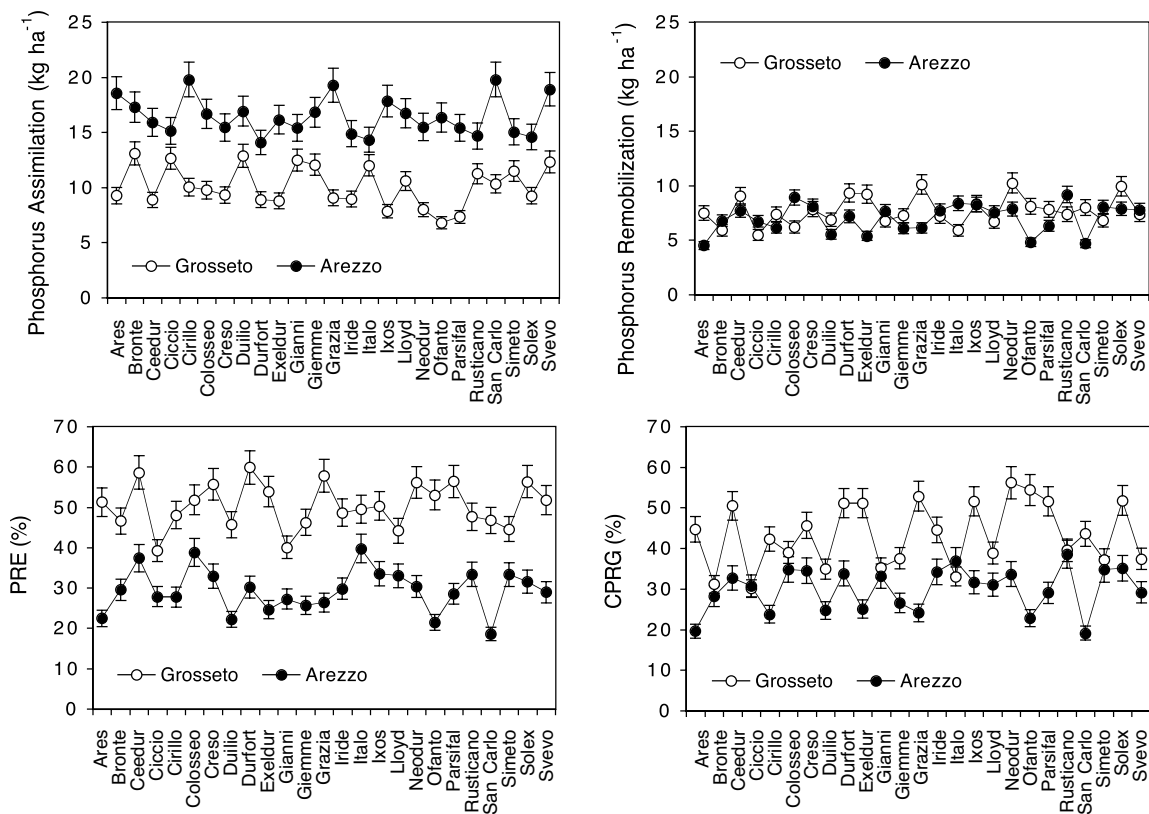


Figure 4. Phosphorus remobilization and assimilation, phosphorus remobilization efficiency (PRE) and contribution of phosphorus remobilized to grain (CPRG) in the 25 wheat cultivars at the two localities. Vertical bars indicate standard error. Where not shown, error bar lies within the symbol.

seto: 2.2 versus 1.9 g kg<sup>-1</sup> and 1.9 g kg<sup>-1</sup> versus 1.1 g kg<sup>-1</sup> respectively at the two stages. Phosphorus concentration in grain did not differ between localities (4.7 g kg<sup>-1</sup>).

Conversely, phosphorus content of the vegetative plant part at anthesis and maturity and of grain was higher at Arezzo than at Grosseito, owing to the higher dry matter of the plant (Tab. 5). At anthesis P content of the vegetative plant part ranged from 20 kg ha<sup>-1</sup> for cv. Ares to 28 kg ha<sup>-1</sup> for cv. Gianni at Arezzo and from 12 kg ha<sup>-1</sup> for cv. Colosseo to 18 kg ha<sup>-1</sup> for cv. Neodur at Grosseito. Variety Svevo showed the highest difference between environments (13 kg ha<sup>-1</sup>), while cv. Exeldur had the lowest one (5 kg ha<sup>-1</sup>). At maturity the differences between environments were unchanged and phosphorus content in vegetative plant part ranged from 6 kg ha<sup>-1</sup> (cv. Colosseo) to 10 kg ha<sup>-1</sup> (cv. Gianni) at Grosseito and from 13 kg ha<sup>-1</sup> (cv. Italo) to 21 kg ha<sup>-1</sup> (cv. San Carlo) at Arezzo. Variety Svevo also at this stage showed the highest difference

in P content between localities (12 kg ha<sup>-1</sup>) and cv. Ceedur and Italo showed the lowest one (7 kg ha<sup>-1</sup>).

Phosphorus content in grain ranged from 15 kg P ha<sup>-1</sup> for cv. Ofanto to 20 kg P ha<sup>-1</sup> for cv. Duilio at Arezzo and from 21 kg P ha<sup>-1</sup> of cv. Ofanto to 27 kg P ha<sup>-1</sup> of cv. Svevo at Grosseito. Variety Ixos showed the highest difference between localities (10 kg P ha<sup>-1</sup>), while cv. Duilio showed the lowest one (3 kg P ha<sup>-1</sup>).

Phosphorus assimilation during grain filling was higher at Arezzo for all the varieties (Fig. 4). Assimilation ranged from 7 kg P ha<sup>-1</sup> of Ofanto to 13 kg P ha<sup>-1</sup> of Bronte at Grosseito and from 14 of Durfort to 20 kg P ha<sup>-1</sup> of Cirillo at Arezzo.

Phosphorus remobilization was similar in the two localities, but differences among varieties were high. Values ranged from 4.5 kg P ha<sup>-1</sup> of cv. Ares to 9.2 kg P ha<sup>-1</sup> of cv. Rusticano at Arezzo from 5.5 kg P ha<sup>-1</sup> of cv. Ciccio to 10.2 kg P ha<sup>-1</sup> of cv. Neodur at Grosseito.

Table 5. Phosphorus contents of vegetative plant part at anthesis and maturity and of grain in the 25 wheat varieties at the two localities (Locality x Variety interaction).

Variety	Vegetative Plant Part				Grain	
	Anthesis		Maturity		Grosseto	Arezzo
	Grosseto	Arezzo	Grosseto	Arezzo		
	P kg ha <sup>-1</sup>					
Ares	14.6	20.1	7.1	15.6	16.7	23.0
Bronte	12.7	22.9	6.8	16.2	19.0	24.0
Ceedur	15.4	20.7	6.4	13.0	17.9	23.6
Ciccio	13.9	24.1	8.5	17.4	18.1	21.9
Cirillo	15.3	22.2	8.0	16.0	17.4	25.9
Colosseo	12.0	23.0	5.8	14.0	16.0	25.6
Creso	14.0	24.7	6.2	16.6	17.1	23.5
Duilio	15.1	25.0	8.2	19.5	19.7	22.4
Durfort	15.5	23.8	6.2	16.6	18.2	21.3
Exeldur	17.1	21.9	7.9	16.5	18.0	21.5
Gianni	16.9	28.1	10.2	20.4	19.3	23.0
Giemme	15.7	23.7	8.4	17.6	19.3	22.9
Grazia	17.5	23.2	7.4	17.1	19.1	25.4
Iride	14.8	25.9	7.6	18.2	16.2	22.6
Italo	12.0	21.1	6.0	12.7	17.9	22.7
Ixos	16.6	24.7	8.2	16.4	16.2	26.1
Lloyd	15.2	22.8	8.5	15.3	17.3	24.3
Neodur	18.2	25.9	8.0	18.0	18.2	23.3
Ofanto	15.3	22.5	7.2	17.7	14.9	21.2
Parsifal	13.9	22.0	6.0	15.7	15.1	21.7
Rusticano	15.5	27.5	8.1	18.4	18.6	23.8
San Carlo	17.1	25.1	9.1	20.5	18.3	24.4
Simeto	15.3	24.1	8.5	16.1	18.3	23.0
Solex	17.6	25.0	7.7	17.1	19.2	22.4
Svevo	14.2	26.9	6.9	19.1	19.6	26.6
LSD <sub>P ≤ 0.05</sub>	1.7		9.8		2.0	

Phosphorus remobilization efficiency was higher at Grosseto than at Arezzo for all varieties. At Arezzo values ranged from 18.6% of cv. San Carlo to 39.7% of cv. Italo, while at Grosseto from 39.2% of cv. Ciccio to 59.8% of cv. Durfort.

The contribution of remobilized phosphorus to grain was higher at Grosseto than at Arezzo for 18 of the 25 varieties and the remaining did not differ significantly for the two localities. At Arezzo CPRG ranged from 19.6% of cv. San Carlo to 36.9% of cv. Italo and at Grosseto from 30.2% of cv. Ciccio to 56.2% of cv. Neodur.

Differently from dry matter and nitrogen, no correlations were found between remobilized phosphorus and P content at anthesis and between grain P content and P remobilization.

#### 4. Conclusions

In the present research durum wheat varieties exhibited great variation in different characters

in well-watered (Arezzo) and drought conditions (Grosseto). All varieties produced higher grain yield and number of kernels per unit area at Arezzo. Moreover, for most varieties the number of spikes per square meter, the number of kernels per spike and the Harvest Index were higher at Arezzo, while the mean kernel weight was higher at Grosseto. Similarly, N and P content in grain of all varieties was also higher at Arezzo.

The pattern of accumulation and remobilization of dry matter, N and P of the 25 varieties in the two sites was different. In durum wheat dry matter, N and P remobilization depends on: i) the amount of material available for remobilization, i.e. dry matter, N and P accumulated up to anthesis, ii) the sink capacity of spikes and iii) the efficiency of remobilization. Environmental conditions up to anthesis greatly affect the first two parameters, while conditions during grain filling affect the third.

Post-anthesis dry matter accumulation was

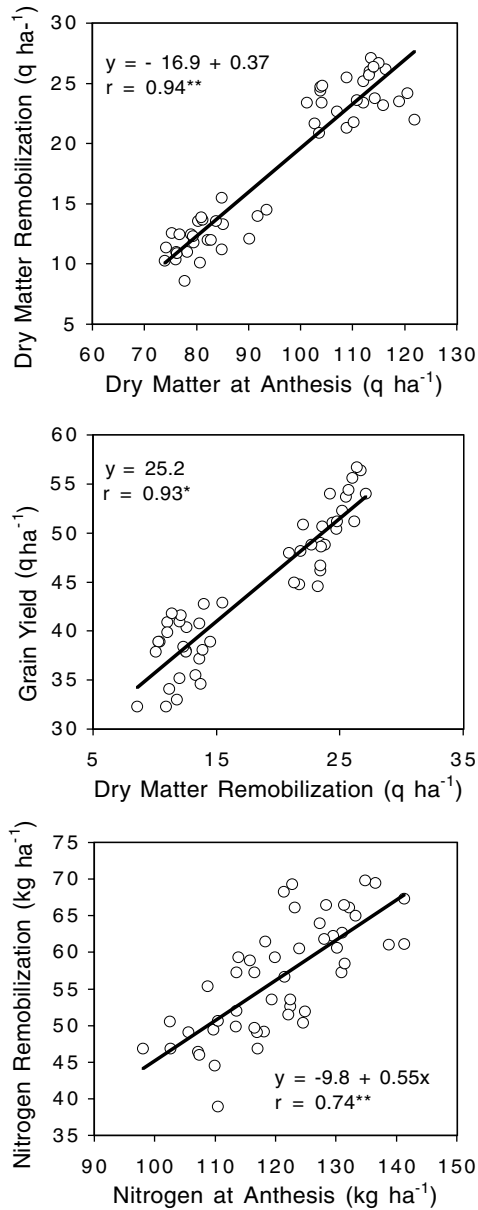


Figure 5. Relationships between post-anthesis dry matter remobilization and dry matter accumulation at anthesis (A) between post-anthesis nitrogen remobilization and nitrogen accumulation at anthesis (B) and between post-anthesis dry matter remobilization and grain yield (C) in durum wheat under the combinations of the 25 varieties and the two locations. The lines represent the fitted functions.

approximately the same in the two localities, while dry matter remobilization during grain filling at Arezzo was approximately double of that at Grosseto, owing to a higher biomass at anthesis and a higher efficiency of remobilization. Dry matter remobilized during grain fill-

ing was closely related to the biomass accumulated at anthesis.

Nitrogen accumulation during grain filling was higher at Arezzo, while N remobilization varied little in the two environments, owing to little variations in N content at anthesis and N remobilization efficiency. Finally, P accumulation during grain filling was higher at Arezzo, while P remobilization varied little in the two environments, owing to lower P content at anthesis at Grosseto that compensated a higher efficiency of P remobilization. Nitrogen remobilized during grain filling was related to N accumulated at anthesis, while P remobilization was not.

Environmental constraints on carbon, N and P availability in the plant are crucial factors in determining grain yield and N and P content in grain, affecting both accumulation and remobilization. In the low rainfall site of Grosseto, most of the grain yield originated from dry matter accumulation, while in the wetter environment of Arezzo accumulation and remobilization contributed equally to grain yield. Conversely, at Grosseto grain N content relied most on remobilization and at Arezzo remobilization and accumulation contributed equally. Finally, at Grosseto and at Arezzo accumulation of P was the main source of grain P content.

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